



This book is provided in digital form with the permission of the rightsholder as part of a Google project to make the world's books discoverable online.

The rightsholder has graciously given you the freedom to download all pages of this book. No additional commercial or other uses have been granted.

Please note that all copyrights remain reserved.

About Google Books

Google's mission is to organize the world's information and to make it universally accessible and useful. Google Books helps readers discover the world's books while helping authors and publishers reach new audiences. You can search through the full text of this book on the web at <http://books.google.com/>

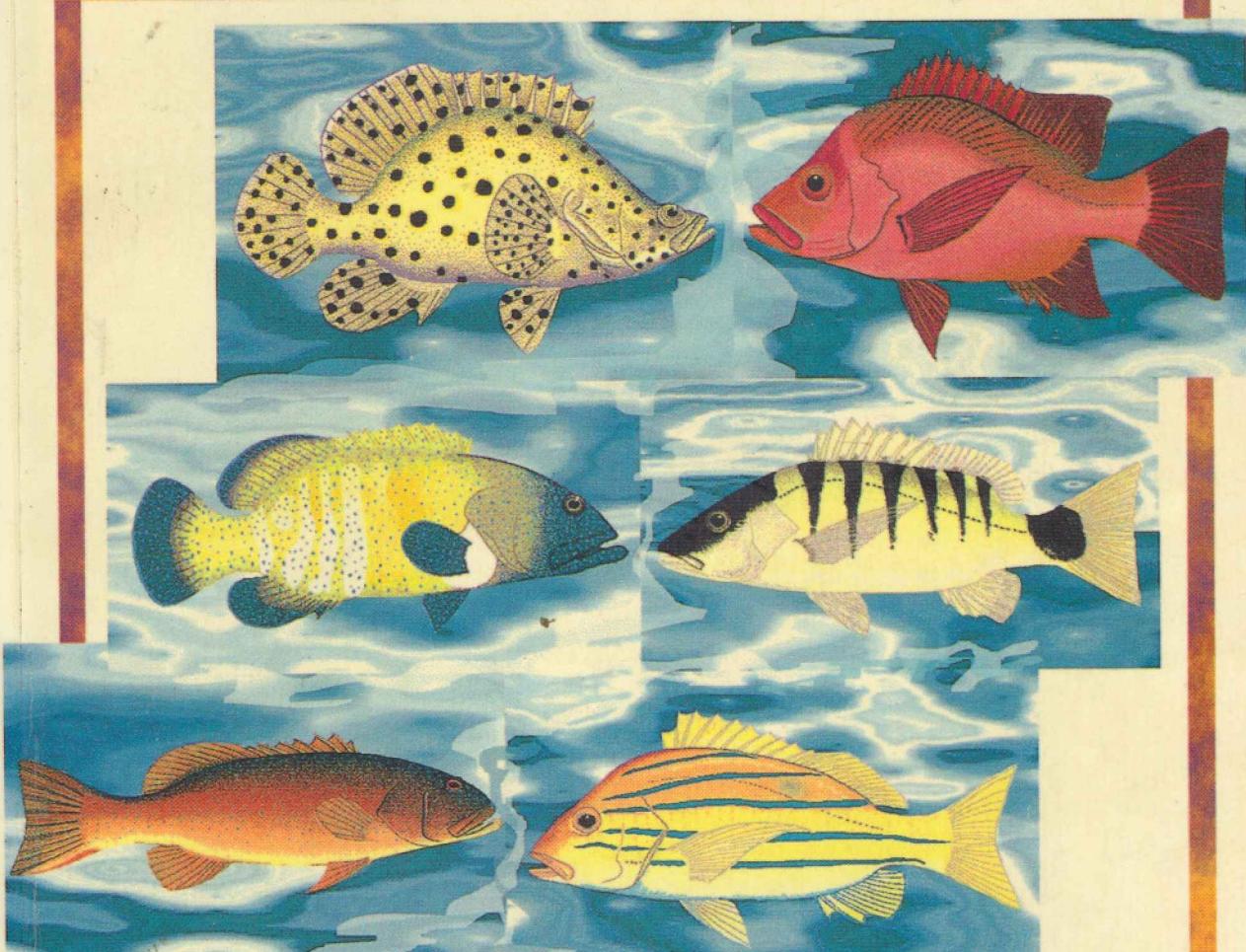
Biology, fisheries and culture of tropical groupers and snappers

TG
ARM

Edited by

Francisco Arreguín-Sánchez, John L. Munro

Miriam C. Balgos and Daniel Pauly



ICLARM

International Center for Living Aquatic
Resources Management

EPOMEX

Universidad Autónoma
de Campeche



Library

APR 14 1998

ENTERED IN RACK
csl

Anal

Biology, fisheries and culture of tropical groupers and snappers

Proceedings of an EPOMEX/ICLARM International Workshop
on Tropical Snappers and Groupers
held at the University of Campeche
Campeche, Mexico
26-29 October 1993

Edited by

Francisco Arreguín-Sánchez
John L. Munro
Miriam C. Balgos
Daniel Pauly



International Center for Living Aquatic Resources Management



EPOMEX/Universidad Autónoma de Campeche

*SH
207
CP6
E48
2.1*

Biology, fisheries and culture of tropical groupers and snappers

AUG 20 1997

Edited by

FRANCISCO ARREGUÍN-SÁNCHEZ
JOHN L. MUNRO
MIRIAM C. BALGOS
DANIEL PAULY

1996

Printed in Manila, Philippines

Published by the International Center for Living Aquatic Resources Management (ICLARM), MCPO Box 2631, 0718 Makati City, Philippines and Programa de Ecología, Pesquerías y Oceanografía del Golfo de México (EPOMEX), Universidad Autónoma de Campeche, Apdo. Postal 520 Campeche 24030, México

Arreguín-Sánchez, F., J.L. Munro, M.C. Balgos and D. Pauly, Editors. 1996. Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

2
ISSN 0115-4435
ISBN 971-8709-62-2

ICLARM Contribution No. 1323

Cover: Groupers and snappers of different species (from FishBase illustrations by Roberto Cada)
Cover design by Alan Sigfried Esquillon

Copyediting: Casilda I. Guevarra and Leticia B. Dizon
Indexing: Miriam C. Balgos and Audrey Banzon
Layout: Audrey Banzon
Graphs and artwork: Albert Contemprate and Roberto Cada

13784

CONTENTS

Foreword • M.J. Williams.....	vi
Preface and Acknowledgements • F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly	vii
Part I: Workshop Conclusions	
Biology, fisheries and culture of snappers and groupers: workshop conclusions and updates to 1996 • D. Pauly, F. Arreguín-Sánchez, J.L. Munro and M.C. Balgos	1
Part II: Biology, Ecology and Distribution	
Ecology and population dynamics of <i>Lutjanus synagris</i> on Campeche Bank • E. Rivera-Arriaga, A.L. Lara-Domínguez, J. Ramos-Miranda, P. Sánchez-Gil and A. Yáñez-Arancibia	11
Trophic role of the red grouper (<i>Epinephelus morio</i>) in the ecosystem of the northern continental shelf of Yucatan, Mexico • F. Arreguín-Sánchez and E. Valero	19
Biological research on the red grouper (<i>Epinephelus morio</i>) from the southern Gulf of Mexico • T. Brulé and C. Déniel.....	28
Seasonal patterns of distribution and abundance of snappers in the Mexican Caribbean • S. Díaz-Ruiz, A. Aguirre-León, C. Macuitl and O. Pérez	43
Biological aspects of the yellow eye snapper (<i>Lutjanus vivanus</i>) (Pisces: Lutjanidae) from Los Hermanos Islands, Eastern Venezuela • G.J. Gómez, R.A. Guzmán and L.A. Marcano	51
Species composition, distribution and trends in abundance of snappers of the southeastern USA, based on fishery-independent sampling • N. Cuellar, G.R. Sedberry, D.J. Machowski and M.R. Collins	59
The ecology of shallow-water groupers (Pisces: Serranidae) in the Upper Florida Keys, USA • K.M. Sullivan and R. Sluka	74
A molecular approach to stock identification and recruitment patterns in red snapper (<i>Lutjanus campechanus</i>) • R.W. Chapman, S.A. Bortone and C.M. Woodley	85
Large catches of red snappers by tuna purse seiners off the West African continental shelf • A. Caverivière	92
Uncommon mortality of groupers at the end of the warm season in the coastal area of Sénégäl (West Africa) • A. Caverivière and D. Touré	96
Groupers and snappers of India: biology and exploitation • P.S.B.R. James, V. Sriramachandra Murty and P. Nammalwar	106
Part III: Age, Growth and Reproduction in the Wild	
Reproduction, age and growth of the Caribbean red snapper (<i>Lutjanus purpureus</i>) in waters off Trinidad and Tobago • S.C. Manickchand-Heileman and D.A.T. Phillip	137
Validation of ageing technique for Nassau grouper (<i>Epinephelus striatus</i>) in the Cayman Islands • P.G. Bush, G.C. Ebanks and E.D. Lane	150
Age validation, movements and growth rates of tagged gag (<i>Mycteroperca</i> <i>microlepis</i>), black sea bass (<i>Centropristes striata</i>) and red porgy (<i>Pagrus pagrus</i>) • M.R. Collins, S.B. Van Sant and G.R. Sedberry.....	158

The validity of length-based methods for estimating growth and mortality of groupers, as illustrated by comparative assessment of the Creole fish <i>Paranthias furcifer</i> (Pisces: Serranidae) • J.M. Posada and R.S. Appeldoorn	163
Spawning and annual fecundity of the red snapper (<i>Lutjanus campechanus</i>) from the northeastern Gulf of Mexico • L.A. Collins, A.G. Johnson and C.P. Keim	174
Reproductive biology of the gray snapper (<i>Lutjanus griseus</i>), with notes on spawning for other western Atlantic snappers (Lutjanidae) • M.L. Domeier, C. Koenig and F. Coleman	189
Population dynamics and stock assessment of red grouper (<i>Epinephelus morio</i>) fishery on Campeche Bank, México • F. Arreguin-Sánchez, M. Contreras, V. Moreno, R. Burgos and R. Valdés	202
FishBase and AUXIM as tools for comparing life-history patterns, growth and natural mortality of fish: applications to snappers and groupers • D. Pauly and C. Binohlan	218
Part IV: Fisheries Assessments	
Effect of gas bladder deflation on mortality of hook-and-line caught and released red snappers: implications for management • J.H. Render and C.A. Wilson	244
Demersal fish stock assessment in Seychelles: an analysis of a mothership/catcher boat fishery • C.C. Mees	254
Abundance and distribution of snappers and groupers targeted by the artisanal medium range fishery off northeastern Venezuela (1981-1992) • J.J. Mendoza and A. Lárez	266
Trends in commercial fishery landings of groupers and snappers in Bermuda from 1975 to 1992 and associated fishery management issues • B.E. Luckhurst	277
Catch, effort and sustainable yield for Australia's northern trawl fishery • D.C. Ramm and Y. Xiao	289
Reproduction in gag (<i>Mycteroperca microlepis</i>) (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations • C.C. Koenig, F.C. Coleman, L.A. Collins, Y. Sadovy and P.L. Colin	307
Assessment of a snapper complex (<i>Lutjanus</i> spp.) of the eastern tropical Pacific • M. Cruz-Romero, E.A. Chávez, E. Espino and A. García	324
Exploratory fishing with traps in oceanic islands off eastern Venezuela during 1992 • L.A. Marcano, R. Guzmán and G.J. Gómez	331
Impact of variability in numbers and size at first recruitment on the $F_{0,1}$ reference point in the US red snapper fisheries of the Gulf of Mexico • N.M. Ehrhardt and C.M. Legault	337
Analyses of catch-per-effort data for red snapper on Campeche Bank in 1992 • M. Del Carmen Monroy-García, R. Burgos Rosas, M.E. González y De la Rosa and M. Carduño-Andrade	350
Time series analysis and multivariate methods applied to the red grouper fishery on Campeche Bank, Mexico • J. Pol and S. Moreno	355
Shrimp trawl bycatch research in the US Gulf of Mexico and southeastern Atlantic • E. Scott-Denton and J. Nance	360

Part V:	Aquaculture and Controlled Reproduction	
Nassau grouper aquaculture • <i>J.W. Tucker, Jr. and P.N. Woodward</i>	363	
Maturation and induced spawning of the mangrove red snapper (<i>Lutjanus argentimaculatus</i>) reared in a floating net cage in the Philippines • <i>A.C. Emata</i>	378	
Ultrastructural study of lymphocystis in kelp bass (<i>Epinephelus moara</i> ; Serranidae) • <i>Z. Yongjia, W. Zeyang and C. Kangrong</i>	385	
Development from egg to juvenile of the red grouper (<i>Epinephelus morio</i>) (Pisces: Serranidae) in the laboratory • <i>P.L. Colin, C.C. Koenig and W.A. Laroche</i>	399	
Appendices		
1. List of Participants.....	415	
2. Author Index.....	420	
3. Geographic Index	434	
4. Species Index	441	

FOREWORD

This volume of papers from the 1993 workshop on snappers and groupers presents important scientific findings and views on two important groups of fish.

Groupers, in the family Serranidae, and snappers, in the family Lutjanidae, are amongst the most valuable components of catches in tropical and subtropical seas. The families are diverse but all species are highly valued as food fish and are actively sought by fishers wherever they are found. They are vulnerable to a wide range of fishing gears. Not only can they be caught in various nets but, being predators, they will also take baited hooks and enter baited traps. Many species are large, curious and unwary and easy prey for spearfishers. Many, particularly groupers, form spawning aggregations at clearly established times and places, where the aggregations can be relentlessly exploited. The unfortunate consequence of all this is that many stocks are overfished and, in some cases, threatened with extinction on a local scale.

Groupers are also protogynous hermaphrodites. This means that they first mature as females and later, at a large size, change into males. Such a life history raises the very real possibility that heavily exploited stocks, in which the average size has been drastically reduced, will suffer an acute shortage of males at spawning times, resulting in unfertilized eggs and, carried to an extreme, the collapse and extinction of the stock. In the past few years, since this conference was held, an additional threat has emerged in the form of great demand for live groupers in Southeast Asia, and at premium prices. This has prompted even greater onslaughts on the stocks in the Indo-Pacific Region.

All these features of the snappers and groupers alone justify the investment of considerable time and expense in research on the assessment and management of snappers and groupers and, in more recent years, on their artificial propagation for cultivation in cages or ponds, or for stock enhancement. The papers presented in this volume are evidence of the importance attached to these species by governments and research institutions and, ultimately, by the fishing communities who depend on the well-being of the stocks. They also attest to the advances in knowledge which have emerged in recent years through the support of well-planned research. However, they also show that the quest for knowledge is not over and that further effort is needed if these most vulnerable species are to be rationally managed and sustainably exploited.

Meryl J. Williams
Director General
ICLARM

PREFACE AND ACKNOWLEDGEMENTS

Groupers and snappers are important fishery resources of the tropics and subtropics, where their high values have caused most of their stocks to be heavily exploited, some even to the point of collapse. Trends towards heavy demand and decreasing natural supply, which are accelerating in several parts of the world, prompted various mariculture ventures — but these have not yet generated sufficient supply to satisfy the soaring demand, especially for live fish.

Focused research on the biology and the population dynamics of groupers and snappers, and on their reproduction and growth under controlled condition — while no panacea — will remain essential for dealing with the questions on how to better manage their fisheries, and to farm them, and workshops where such research can be presented and evaluated are crucial if progress is to be made.

To date, three international workshops have been devoted to groupers and snappers:

- 1) one held in October 1975, in Pensacola Beach, Florida and documented in Bullis, H.R. and A.C. Jones (1976) *Proceedings: colloquium on snapper-grouper fishery resources of the Western Central Atlantic Ocean*. Florida Sea Grant College Program, University of Florida, Gainesville, 337 p.;
- 2) another held in May 1985, in Honolulu and documented in Polovina, J.J. and S. Ralston. 1987. *Tropical snappers and groupers: biology and fisheries management*. Westview Press, Boulder, Colorado, 659 p.; and
- 3) a third, which led to this document, held in October 1993 in Campeche, Mexico, jointly organized by EPOMEX (Programa de Ecología, Pesquerías y Oceanografía del Golfo de México) and ICLARM (International Center for Living Aquatic Resources Management).

This latest workshop resulted from a meeting in May 1992 of two of us (Francisco Arreguín-Sánchez and Daniel Pauly) at the First World Fisheries Congress.

The workshop proper was prepared by an organizing committee headed by Francisco Arreguín-Sánchez who, jointly with John Munro, also chaired the workshop sessions.

The objectives of the workshop were to:

- 1) assess the status of knowledge about groupers and snappers as tropical fishing resources;
- 2) identify the gaps in knowledge; and
- 3) promote worldwide scientific collaboration.

The workshop's strategy and linkages were:

Experts were invited to attend the workshop. They were all chosen as recognized scientists in their fields and balanced representation was sought from most of the tropical regions of the world: i.e., the South Pacific, Gulf of Thailand, Southeast Asia, Western Coast of Africa, Northeastern Coast of Australia, Caribbean Sea, and the Gulf of Mexico. Participants came with prepared manuscripts. Theme sessions were integrated through working groups. This initiative was under the framework of the Program of Ocean Science and Living Resources (OSLR), specifically the Tropical Demersal Recruitment Project (TRODERP) and the Subproject Coral Reef Demersal Recruitment Project (CORDERP) in the Caribbean and Adjacent Regions (IOCARIBE, IOC/FAO).

Altogether 60 scientists met on 26-29 October 1993 in Campeche, Mexico and presented papers, most of which are included here, along with a few contributions sent in later by authors who were not able to attend.

We thank these colleagues for their patience in waiting for the proceedings. And we are aware that the "update to 1996" tagged onto the workshop conclusions will not fully compensate for the anguish of some authors who feared that their paper would *never* come out.

It is our pleasure to conclude this by acknowledging those who made this workshop possible:

First our thanks go to the staff of EPOMEX who, under the dynamic leadership of Dr. A. Yañez-Arancibia, organized and hosted this workshop and its cultural program, including much appreciated visits to a Mayan temple, some fishing villages and several restaurants that proved Mexican food to be not "hot", but *savory*.

We also acknowledge the crucial support provided by the Government of Campeche State, and several of its agencies: Secretaría Particular del Gobierno del Estado de Campeche; Secretaría de Educación, Cultura y Deporte; Secretaría de Desarrollo Pesquero; Secretaría de Desarrollo Económico; Secretaría de Turismo. We also thank the (Federal) Secretaría de Educación Pública, through the Subsecretaría de Educación Superior e Investigación Científica/Sep-Fomes; and the Instituto Nacional de la Pesca, Mexico for their input and collaboration.

The Editors

PART I: WORKSHOP CONCLUSIONS

Biology, Fisheries and Culture of Snappers and Groupers: Workshop Conclusions and Updates to 1996^a

D. PAULY^b

*Fisheries Centre, 2204 Main Mall
University of British Columbia, Vancouver, B.C.
Canada V6T 1Z4*

F. ARREGUÍN-SÁNCHEZ^c

*Programa de Ecología, Pesquerías
y Oceanografía del Golfo de México
U.A.C. Ap. Postal 520, Campeche 24030
Campeche, México*

J.L. MUNRO^d

M.C. BALGOS

*International Center for Living
Aquatic Resources Management
MCPO Box 2631
0718 Makati City, Philippines*

PAULY, D., F. ARREGUÍN-SÁNCHEZ, J.L. MUNRO and M.C. BALGOS. 1996. Biology, fisheries and culture of snappers and groupers: workshop conclusions and updates to 1996 [*Biología, pesquerías y cultivo de pargos y meros: conclusiones del taller de trabajo y actualización a 1996*]. p. 1-10. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

A summary of the findings of the three working groups (on population dynamics and ecology; fisheries management; and biology and aquaculture) of the International Workshop on Tropical Snappers and Groupers organized by EPOMEX (Programa de Ecología, Pesquerías y Oceanografía del Golfo de México) and ICLARM, and held 26-29 October 1993 in Campeche, Mexico, is presented. Recent references are included to update coverage to 1996, particularly concerning issues of growth and integration of groupers and snappers in ecosystems and models thereof.

^a ICLARM Contribution No. 1312.

^b Also International Center for Living Aquatic Resources Management, MCPO Box 2631, 0718 Makati City, Philippines; e-mail: pauly@fisheries.com

^c Present address: Centro Interdisciplinario de Ciencias Marinas, Instituto Politécnico Nacional, A.P. 592, 23000 La Paz, Baja California Sur, Mexico; fax 52(112) 25322; tel. 52(112) 25344/25366; e-mail: farregui@vmredipn.ipn.mx

^d Present address: c/o Laboratoire de Biologie Marine et Malacologie, EPHE, Université de Perpignan, Perpignan 66860 Cedex, France; fax (33) 68 50 36 86; tel. (33) 68 66 20 55; e-mail: j.munro-t@cernet.com

Resumen

Se presenta una síntesis de los principales hallazgos de los tres grupos de trabajo (sobre dinámica de poblaciones y ecología, manejo de pesquerías, y biología y acuacultura) del Taller Internacional sobre Pargos y Meros Tropicales organizado por EPOMEX e ICLARM, efectuado del 26 al 29 de Octubre de 1993 en Campeche, México. Referencias recientes son incluidas para obtener una cobertura actualizada a 1996, particularmente sobre aspectos como crecimiento y la integración de pargos y meros en el contexto del ecosistema y modelos asociados.

Introduction

The following is a summary of the findings of the three working groups which met on 28-29 October 1993 during the "International Workshop on Tropical Snappers and Groupers" organized by EPOMEX and ICLARM, and documented in this volume. This is complemented, in areas where the authors are knowledgeable, by references to documents updating some earlier citations, or recent research trends.

Population Dynamics and Ecology

The working group concentrated on the identification of the status of knowledge, needs for further research and identification of priorities, where deemed appropriate. A summary of conclusions by topic are as follows:

Age and growth studies

Age determination techniques based on the examination of skeletal structures (otoliths, scales, other bones) are reliable in areas where seasonal temperature fluctuations exceed 3-4°C (Williams 1986; Longhurst and Pauly 1987), though validation continues to be important (Beamish and McFarlane 1983).

On the other hand, further research is needed in areas where seasonal temperature differences are slight, i.e., where spawning checks on skeletal parts may be mistaken for seasonal checks. Here validation is crucial, whether based on the seasonal pattern of ring formation (Manickchand-Dass 1987) (see also Manickchand-Heileman and Phillip, this vol.), or on tetracycline or other otolith marks (Ferreira and Russ 1992, 1994) (see also Bush et al.; Collins et al., this vol.).

For estimation of von Bertalanffy growth parameters from size-at-age data, the use of nonlinear fitting techniques (see, e.g., Saini et al. 1988) is recommended over the use of linearizing transformation (e.g., Ford-Walford plots).

Estimation of growth parameters from length-frequency (L/F) data is problematic in long-lived organisms such as groupers and snappers, in which individual growth trajectories are highly variable, and which, moreover, may display "square" growth curves, wherein a steeply ascending juvenile growth phase is followed by a long, flat adult phase (Newman et al. 1996). Indeed, such estimation should be undertaken only when L/F data are available which include small, fast-growing specimens (Isaac 1990). Both ELEFAN I (Pauly 1987) and SLCA (Shepherd 1987) may be used in such cases^a (see also Arreguín-Sánchez et al., this vol.).

^a Since the workshop was held, the Shepherd's Length Composition Analysis (SLCA) method was considerably improved (see Pauly and Arreguín-Sánchez 1995), especially for application to long-lived organisms. Both ELEFAN and SLCA are available as routines of the FiSAT software (Gayanilo et al. 1995), and the improvement of SLCA is available as an update to FiSAT (contact ICLARM@cgnet.com for details).

Another rapid technique is the use of otolith weights as an indicator of age (Worthington et al. 1995).

Growth parameter estimates, particularly when based on unvalidated ages, or on length-frequency data, should be compared with previous estimates in the same, or closely related species. This can be done using the growth performance index ϕ' defined as

$$\phi' = \log_{10} K + 2 \log_{10} L_{\infty} \quad \dots 1)$$

where K is put on an annual basis, L_{∞} is standardized, e.g., to total length in cm (Pauly and Munro 1984).

The coefficient of variation of ϕ' within species tends to be less than 5% (Moreau et al. 1986), which provides a criterion for identifying outliers and thus, indirectly, to validate growth parameter estimates and their underlying age readings (see Pauly and Binohlan; Arreguín-Sánchez et al., this vol.).

Also, growth comparisons can be done using auximetric grids, as illustrated by Pauly and Binohlan (this vol.). Published growth parameters can be obtained from the FishBase 1996 CD-ROM (Froese and Pauly 1996) which contains 150 pairs of L_{∞} , K values for snappers (for 42 of the 106 species of the family Lutjanidae in the world; Allen 1985), and 86 for groupers (for 47 of the 159 species of the subfamily Epinephelinae in the world; Heemstra and Randall 1993), with more to be included in the mid-1997 release of FishBase.

Total and natural mortalities

The standard techniques for estimation of total (Z) and natural mortalities (M) (Ricker 1975) can be usually applied to groupers and snappers, though some methods may fail because of some particular behaviors (sex changes, spawning aggregations, etc.). Also, emphasis should be given to methods for improving the estimation of M (see Pauly and Binohlan, this vol.).

Particularly, emphasis should be given to:

1. estimation of M in marine protected areas (MPA);
2. estimation of Z using length-converted catch curves which explicitly account for seasonal growth oscillations (Pauly et al. 1995) and individual growth variation, as discussed by Sainsbury (1980) for growth estimation from tagging data;
3. environmental effects on M (but see Pauly and Binohlan, this vol.), and hence on cohort strength (Arreguín-Sánchez et al., this vol.), including stock dislocations that may result from global climate changes; and
4. using variable (age-specific or length-specific) estimates of M and/or estimates changing with environmental forcing in models requiring inputs of natural mortality.

Finally, particular attention should be given to the interrelationships between estimates of mortality and of catchability, which are strongly affected by gregarious behavior (Arreguín-Sánchez 1996).

Reproduction and recruitment

It was considered that the reproductive strategies of groupers and snappers (batch spawning, sex reversal, spawning aggregations) are reasonably well known. However, further research is needed on the interrelationships among sex reversal, formation of spawning aggregations and population dynamics, as well as their impacts on the location of spawning aggregations and nursery grounds. As a priority, two aspects were mentioned: early life history in relation to habitat protection, and the effects of fishing on spawning aggregations.

On the other hand, spawning stock/recruitment relationships were given lower priority, because they usually fail to resolve uncertainties about effects of environmental factors on recruitment and thus, even

when established, still leave unexplained most of the variability of recruitment levels.

Ecological, especially food web considerations

The working group felt that the food and feeding habits of groupers and snappers are known in general terms (see also data in FishBase CD-ROM), and that further research on trophic interaction should be focused on:

- food consumption estimates (for individual fish and for age-structured populations);
- quantitative food webs, constructed using ECOPATH (Polovina 1984; Christensen and Pauly 1992; Pauly and Christensen 1996)^f (see also Arreguín-Sánchez and Valero, this vol.) or other approaches suitable for describing the trophic role of groupers and snappers; and
- models of diet selection (including opportunistic feeding) and prey switching.

Here, particular attention should be given to model validation, and to evaluation of the sensitivity of prediction to uncertainty in input parameters^f.

Natural and artificial habitats

The differential use of habitat space by early life stage, juvenile and adult groupers and snappers are generally well documented (see, e.g., Doherty and Williams 1988; Beets

and Hixon 1994) (see also Cuellar et al.; Diaz-Ruiz et al.; Domeier et al.; and Rivera-Arriaga et al., this vol.), as is the use of artificial reefs.

Still, further research is required on:

- distinguishing the aggregative role from the habitat-enhancing role of artificial reefs (see also Polovina 1989 and contributions in Munro and Balgos 1995);
- economic aspects of artificial reefs, especially their cost/benefit ratios;
- potential effects of habitat degradation and/or loss on stock size and structure; and
- the fractal nature of habitats, i.e., the availability of suitable crevices/holes for the successive life stages of cohorts, especially in groupers (Hixon and Beets 1993).

The general characterization of stocks is a priority subject for some regions. Techniques are well known, including molecular genetic techniques (Chapman et al., this vol.). Further research on stock identification must be addressed using these and allozyme techniques to provide the information necessary to manage mixed or locally discrete stocks, and to avoid stock collapse and losses of genetic diversity.

Fisheries Management

The working group dealing with fisheries management issues concentrated on issues specific to groupers and snappers, i.e., the recommendations below do not cover general issues of fisheries management, applicable to any type of fisheries resource

^f Extensions of the ECOPATH software for construction of mass-balance models have recently become available which allow explicit consideration of uncertainty, using a semi-Bayesian approach (Christensen and Pauly 1995). This re-expresses these models in the form of simulations, enabling predictions in time of the effects of changing the fishing regime impacting the different elements of an exploited ecosystem. The latter approach will generally require, in the case of groupers and snappers, that the underlying mass-balance model includes separate boxes (each with its own parameter set and diet composition) for the juveniles and the adults (Walters et al. 1997).

(e.g., the need for effort controls). The resulting list of recommendations is as follows:

- Whenever possible, fisheries management plans concerned with demersal fish should deal with groupers and snappers as separate groups, i.e., acknowledge their particular growth/mortality schedules and mode of reproduction.
- Continental and insular populations of groupers and snappers may require different management advice due, e.g., to differences in their seasonal patterns of reproduction.
- There is a need to identify and quantify sources of fishing mortality including cryptic mortality due to the passage of undersized fish through the cod-end of trawls, and to bycatch in nondirected fisheries, e.g., in the Gulf of Mexico shrimp fisheries, which have an immense impact on red snappers and other demersal fish species (see also Ehrhardt and Legault; Scott-Denton and Nance, this vol.)^g.
- There is a need to statistically validate population parameters which have been estimated with inappropriate models and/or with restricted data sets; this applies particularly to models which do not account for the peculiar mode of reproduction of groupers (Bannerot et al. 1987).
- There is an urgent need to define management strategies specifically adapted to groupers and snappers. Several options may be considered, depending on management effectiveness: (a) marine protected areas (i.e., reserves), which can ensure conservation of genetic diversity; (b) seasonally closed areas to reduce fishing pressure during critical stages;
- (c) quotas to control fishing mortality (but which, however, may lead to overcapitalization); (d) minimum size regulations to prevent growth overfishing (which however, may increase cryptic mortality); and (e) maximum size limits^g (to protect large fish).
- Risk analysis and bioeconomic considerations should be incorporated in management advice whenever possible, with the latter considering the changes of price that generally accompany changes in size.
- Most grouper and snapper fisheries are multispecies fisheries. This aspect must be explicitly considered in any management policy.

One item only briefly discussed at the workshop, but which has become very important since, are marine protected areas (MPA) as fisheries management tools. We cite a recent document to this effect:

'There is an emerging consensus among fisheries scientists and managers throughout the world that marine fisheries reserves (sanctuaries, *no-take* refuges) if well placed and of the appropriate size can achieve many of the goals that fishery management has failed to achieve using conventional methods. Particularly, there is overwhelming evidence from both temperate and tropical areas that exploited populations in protected areas will recover following cessation of fishing and that spawning biomass will be rebuilt. Also there is widespread recognition throughout the world that loss of biodiversity is largely driven by ecosystem modifications and the habitat loss that ensues. Hence preserving biodiversity implies the maintenance or re-establishment of the natural ecosystems as in marine reserves in

^g These points are perhaps more relevant to snappers, often caught as juveniles by trawling, than to groupers, often caught with hook-and-lines that target the adults.

which no extractive anthropogenic effects are allowed or minimized" (Roberts et al. 1995).

The possible effects of *no-take* MPAs are particularly marked for groupers and snappers (Ferreira and Russ 1995; Newman et al. 1996; Russ et al., in press), though populations may be slow to recover (Russ and Alcala 1996), due to their low turnover rates.

One reason for the positive effect of MPAs seems to be the high-site fidelity of snappers and especially groupers. Thus, in a recent study on the Great Barrier Reef, only 1 of over 100 tag returns of *Plectropomus leopardus* performed between-reef movements, all other returns indicating within-reef movements, on a scale of 0.1 to 3 km, and especially during the spawning season (Davies 1995).

Biology and Aquaculture

Discussions within this working group attempted to identify the most important aspects to be addressed through further research, with particular emphasis on the need to develop biotechnology for production.

Mariculture

Rearing

- improvement of water quality for larval culture (mainly an engineering problem);
- larval nutrition: studies of nutritional requirements of larval stages, finding smaller prey for small-mouthed individuals, and development of formulated feeds; and

- improvement of broodstock management and technology for growout to market size.

Early Life History

- description of larval development (Masuma et al. 1993; Colin et al., this vol.); and
- description and experimental evaluation of processes controlling sexual differentiation.

Other Items

- developing techniques to control or minimize environmental pollution resulting from aquaculture enterprises;
- increasing exchange of information among East Asian, American and European aquaculture groups, notably via translation of key documents^b; and
- discouraging aquaculture of non-native species, and hence the required introductions of exotics.

Biology

Reproduction

- identifying proximate causes of adult sex change at multiple levels of causation; behavioral, genetic, neuroendocrine and hormonal, with emphasis on collaboration with aquaculture environments; relating adult sex change to processes controlling initial sexual differentiation in juveniles (see also Sadovy and Figuerola 1992; Sadovy et al. 1992; Ferreira 1993, 1995; Sadovy et al.

^b The FishBase CD-ROM (see Pauly and Binohlan, this vol.) contains two tables (on culture systems and culture experiments) which offer a standard format for reporting/standardizing aquaculture data, including reports on groupers and snappers (Agustín et al. 1996a, 1996b). However, these tables, containing hundreds of entries for freshwater fishes, presently contain only one entry for groupers or snappers, describing experiments with *Plectropomus leopardus* in Indonesia (Lanjumin 1982). The FishBase project seeks collaborators in this area; contact r.froese@cgnet.com.

1994; Shapiro et al. 1994; and Sadovy and Colin 1995);

- evaluating hypotheses concerning the function of spawning aggregations, including measurement, at several scales, of physical oceanographic characteristics, rates of predation on adults and eggs, downcurrent trajectories of eggs, and fertilization rates at aggregation sites (see Doherty et al. 1994);
- describing internal structure of aggregations, including mating structure and sex ratio (Samoilys and Squire 1994);
- identifying aggregation sex ratios at which sperm may become limiting; measuring fertilization rates of eggs; changing numbers of sperm released by males, and oocyte atresia and rejuvenelization under different sex ratios (Samoilys and Squire 1994);
- identifying which species spawn in aggregations, with greater attention to snappers, for which this phenomenon is not as well documented (nor probably as common) as for groupers;
- choosing species carefully for detailed studies to produce quick returns on research effort; using most accessible species, which life history offers the greatest promise of providing answers to critical questions, including presently non-commercial species.

Policy Implications of Current Knowledge

- some participants felt that, based on current knowledge, it would be best for the fish populations if all forms of fishing were banned from spawning aggregation sites at least at spawning times. The dissenters felt that sustainable yields from aggregations

are possible, i.e., yields that would not markedly reduce population size. This remains one of the scientific questions to be addressed in further research efforts.

- set-aside reserves, both for conservation and as reference (i.e., control) communities for comparison with impacted populations.

Larval Dispersal and Recruitment

- addressing the large issue concerning what controls population size in unexploited populations: rates of settlement, predation, food availability and substrate limitation, if any;
- addressing the second large question of whether, and to what extent, populations are self-recruiting: this includes many related issues, such as the ability of larvae to swim against residual currents¹, and by migrating vertically, to control position over substrates. Other issues are larval survivorship; transport mechanisms from the pelagic phase to reef settlement areas; and factors influencing the timing and location of settlement (Doherty et al. 1994).

Life History Strategies

- evaluating consequences of possible fishing selection for genetically large individuals on size structure and genetic diversity of population. Compare heavily fished with underfished stocks;
- basic descriptions of age and growth rates, onset of maturity, and degree of plasticity of time of maturity and sex change. These descriptions should be made for species for which such

¹ We note that recent work in Australia has shown that beyond 20 days, and especially during pre-settlement (i.e., at about 1 cm), most reef fishes have phenomenal swimming abilities, with sustained speeds of around 30-40 cm per second (Stobutzki and Bellwood 1994).

- data do not currently exist in formal literature. Complete FishBase coverage of species for which information is available, if only in the "grey literature" (see Pauly and Binohlan, this vol.);
- evaluating predation mortality of all life stages, including identification of predators and predation rate; and evaluating feeding habits of different life history stages.

The latest threat

One issue that has become important since the workshop was held is the live trade to Hongkong (and China) of live groupers and snappers and similar high value fish (Johannes 1995; Johannes and Riepen 1995). The press has emphasized the use of sodium cyanide in this trade. The major threat, though, is overexploitation, with large areas of Southeast Asia and the South Pacific being successively depleted (Erdmann and Pet-Soede 1996); a threat to which an adequate response has yet to be found.

Acknowledgements

We thank the participants, who exhibited great interest and dynamism during the plenary workshop sessions. We are especially grateful to those who accepted to chair working group discussions, i.e., Tony J. Pitcher and Sherry Manickchand-Heileman, who led the discussions on Population Dynamics and Ecology; Douglas Shapiro and John Tucker, on Aquaculture and Biology; and Brian E. Luckhurst and Jaime González-Cano, on Fisheries Management. Finally, we thank Garry Russ for reviewing the draft of this contribution, and suggesting we incorporate recent references from Australia; this added a flavor that had been missing at the workshop.

References

- ✓ Agustin, L., R.S.V. Pullin and C. Casal. 1996a. The CULTSYS table, p. 129-132. In R. Froese and D. Pauly (eds.) FishBase 96: concepts, design and data sources. ICLARM, Manila, Philippines.
- ✓ Agustin, L., R.S.V. Pullin and C. Casal. 1996b. The CULTSPEC table, p. 132-134. In R. Froese and D. Pauly (eds.) FishBase 96: concepts, design and data sources. ICLARM, Manila, Philippines.
- Allen, G.R. 1985. Snappers of the world: an annotated and illustrated catalogue of lutjanid species known to date. FAO species catalogue. Vol. 6, 208 p. + 28 plates.
- Arreguin-Sánchez, F. 1996. Catchability, a key parameter for fish stock assessment. Rev. Fish Biol. Fish. 6(2):221-242.
- Bannerot, S., W.W. Fox, Jr. and J.E. Powers. 1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and Caribbean, p. 561-603. In J.J. Polovina and S. Ralston (eds.) Tropical groupers and snappers: biology and fisheries management. Westview Press, Boulder, Colorado.
- Beamish, R.J. and G.A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Trans. Am. Fish. Biol. 112:735-743.
- Beets, J. and M.A. Hixon. 1994. Distribution, persistence, and growth of groupers (Pisces: Serranidae) on artificial and natural patch reefs in the Virgin Islands. Bull. Mar. Sci. 55(2/3):470-483.
- Christensen, V. and D. Pauly. 1992. The ECOPATH II - a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Modelling 61:169-185.
- Christensen, V. and D. Pauly. 1995. Fish production, catches and the carrying capacity of the world oceans. Naga, ICLARM Q. 18(3):34-40.
- Davies, C.R. 1995. Movement studies of three species of coral reef fish at Lizard Island, Great Barrier Reef, Australia. James Cook University of North Queensland, Australia. 212 p. Ph. D. thesis.

- Doherty, P.J., A.J. Fowler, M.A. Samoilys and D.A. Harris. 1994. Monitoring the replenishment of coral trout (Pisces: Serranidae) populations. Bull. Mar. Sci. 54:343-355.
- Doherty, P.J. and D.M. Williams. 1988. The replenishment of coral reef fish populations. Oceanogr. Mar. Biol. Annu. Rev. 26:487-551.
- Erdmann, M.V. and L. Pet-Soede. 1996. How fresh is too fresh? The live reef food fish trade in Eastern Indonesia. Naga, ICLARM Q. 19(1):4-8.
- Ferreira, B.P. 1993. Reproduction of the inshore coral trout, *Plectropomus maculatus* (Perciformes: Serranidae) from the central Great Barrier Reef, Australia. J. Fish Biol. 42:831-844.
- Ferreira, B.P. 1995. Reproduction of the common coral trout, *Plectropomus leopardus* (Serranidae: Epinephelinae) from the central and northern Great Barrier Reef, Australia. Bull. Mar. Sci. 56:653-669.
- Ferreira, B.P. and G.R. Russ. 1992. Age, growth and mortality of the inshore coral trout, *Plectropomus maculatus* (Pisces: Serranidae) from the central Great Barrier Reef, Australia. Fish. Bull. 92:46-57.
- Ferreira, B.P. and G.R. Russ. 1994. Age and growth of coral trout, *Plectropomus leopardus* (Pisces: Serranidae) from the northern Great Barrier Reef, Australia. Fish. Bull. 92:46-57.
- Ferreira, B.P. and G.R. Russ. 1995. Population structure of the leopard coral grouper, *Plectropomus leopardus*, on fished and unfished reefs off Townsville, central Great Barrier Reef, Australia. Fish. Bull. 93:629-642.
- Froese, R. and D. Pauly, Editors. 1996. FishBase 96: concepts, design and data sources. ICLARM, Manila, Philippines. 179 p.
- Gaynilo, F.C., Jr., P. Sparre and D. Pauly. 1995. The FAO-ICLARM stock assessment tools (FISAT) user's guide. FAO Comp. Inf. Ser. (Fish.) No. 7, 126 p. Rome, Italy.
- Heemstra, P.C. and J.E. Randall. 1993. Groupers of the world (Family Serranidae, subfamily Epinephelinae). An annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper, and lyretail species known to date. FAO species catalogue. Vol. 16, 382 p. +31 plates.
- Hixon, M.A. and J.P. Beets. 1993. Predation, prey refuges, and the structure of coral reef fish assemblages. Ecol. Monogr. 63(1):77-101.
- Isaac, V.J. 1990. The accuracy of some length-based methods for fish population studies. ICLARM Tech. Rep. 27, 81 p.
- Johannes, R.E. 1995. Fishery for live reef food fish is spreading human death and environmental degradation. Coast. Manage. Trop. Asia. (September) (5):8-9.
- Johannes, R.E. and M. Riepen. 1995. Environmental, economic, and social implications of the live reef fish trade in Asia and the Western Pacific. Nature Conservancy, Jakarta Selatan, Indonesia. 81 p.
- Lanjumin, L. 1982. Development of cage culture for finfish in Riau Archipelago - Riau Province, Indonesia, p. 165-166. In R.D. Guerrero and V. Soesanto (eds.) Report of the Training Course on Small-scale Pen and Cage Culture for Finfish. SCS/GEN/82/34. South China Sea Fisheries Development and Coordinating Programme, Manila, Philippines.
- Longhurst, A.R. and D. Pauly. 1987. Ecology of tropical oceans. Academic Press, San Diego. 407 p.
- Manickchand-Dass, S. 1987. Reproduction, age and growth of lane snapper *Lutjanus synagris* (Linnaeus) in Trinidad, West Indies. Bull. Mar. Sci. 40(1):22-28.
- Masuma, S., N. Tezuka and K. Teruya. 1993. Embryonic and morphological development of larval and juvenile coral trout, *Plectropomus leopardus*. Jap. J. Ichthyol. 40(3):333-342.
- Moreau, J., C. Bambino, and D. Pauly. 1986. A comparison of four indices of overall fish growth performance, based on 100 tilapia populations (Fam. Cichlidae), p. 201-206. In J.L. Maclean, L.B. Dizon and L.V. Hosillos (eds.) The First Asian Fisheries Forum. Asian Fisheries Society, Manila, Philippines.
- Munro, J.L. and M. Balgos, Editors. 1995. Artificial reefs in the Philippines. ICLARM Conf. Proc. 49, 56 p.
- Newman, S.J., D. McB. Williams and G.R. Russ. 1996. Variability in the population structure of *Lutjanus adetil* (Castelnau, 1873) and *L. quinquefasciatus* (Bloch, 1790) among reefs in the central Great Barrier Reef, Australia. Fish. Bull. 94:313-329.
- Pauly, D. 1987. A review of the ELEFAN system for analysis of length-frequency data

- in fish and aquatic invertebrates, p. 7-34. In D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.
- Pauly, D. and F. Arreguin-Sánchez. 1995. Improving Shepherd's length composition analysis (SLCA) method for growth parameter estimations. Naga, ICLARM Q. 18(4):31-33.
- Pauly, D. and J.L. Munro. 1994. Once more on the comparison of growth in fish and invertebrates. Fishbyte 2(1):21.
- Pauly, D., J. Moreau and N. Abad. 1995. Comparison of age-structured and length-converted catch curves of brown trout *Salmo trutta* in two French rivers. Fish. Res. 22: 197-204.
- Pauly, D. and V. Christensen. 1996. ECOPATH models of coral reef ecosystems, p. 137-144. In J.W. McManus and M.C. Ablan (eds.) ReefBase: a global database on coral reefs and their resources. ICLARM, Manila.
- Polovina, J.J. 1984. Model of a coral reef ecosystem. I. The ECOPATH model and its application to French Frigate Shoals. Coral Reefs 3(1):1-11.
- Polovina, J.J. 1989. Artificial reefs: nothing more than benthic fish aggregators. Calif. Coop. Ocean. Fish. Invest. Rep. 30:37-39.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish population. Bull. Fish. Res. Board Can. 191, 382 p.
- Roberts, C., W.J. Ballantine, C.D. Buxton, P. Dayton, L.B. Crowder, W. Milon, M.K. Orbach, D. Pauly, J. Trexler and C.J. Walters. 1995. Review of the use of marine fishery reserves in the U.S. Southeastern Atlantic. NOAA Tech. Mem. NMFS-SEFC-376, 31 p.
- Russ, G.R. and A.C. Alcala. 1996. Marine reserves—rates and patterns of recovery and decline of large predatory reef fish. Ecol. Appl. 6(3):947-961.
- Russ, G.R., D.C. Lou and B.P. Ferreira. Tracking a strong cohort in the age structure of a coral reef fish, the coral trout, *Plectropomus leopardus*, on reefs of the central Great Barrier Reef, Australia. Can. J. Fish. Aquat. Sci. (In press).
- Sadovy, Y. and P.L. Colin. 1995. Sexual development and sexuality in the Nassau grouper. J. Fish Biol. 46:961-976.
- Sadovy, Y. and M. Figuerola. 1992. The status of the red hind fishery in Puerto Rico and St. Thomas as determined by yield-per-recruit analysis. Proc. Gulf Caribb. Fish. Inst. 42:23-38.
- Sadovy, Y., M. Figuerola and A. Roman. 1992. Age and growth of red hind *Epinephelus guttatus* in Puerto Rico and St. Thomas. US Fish. Bull. 90:516-528.
- Sadovy, Y., A. Rosario and A. Roman. 1994. Reproduction in an aggregating grouper, the red hind, *Epinephelus guttatus*. Env. Biol. Fish. 41:269-286.
- Saila, S.B., C.W. Recksiek and M.H. Prager. 1988. Basic fishery science programming. Dev. Aquacult. Fish. Sci. 18: 230 p.
- Sainsbury, L. 1980. Effect of individual variability of the von Bertalanffy growth equation. Can. J. Fish. Aquat. Sci. 37:241-247.
- Samoilys, M.A. and L.C. Squire. 1994. Preliminary observations on the spawning behaviour of coral trout, *Plectropomus leopardus* (Pisces: Serranidae), on the Great Barrier Reef. Bull. Mar. Sci. 54:332-342.
- Shapiro, D.Y., G. Garcia-Moliner and Y. Sadovy. 1994. Social system of an inshore stock of the red hind grouper, *Epinephelus guttatus* (Pisces: Serranidae). Env. Biol. Fish. 41:415-422.
- Shepherd, J.G. 1987. A weakly parametric method for estimating growth parameters from length-composition data, p. 113-119. In D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.
- Stobutzki, I.C. and D.R. Bellwood. 1994. An analysis of the sustained swimming abilities of pre-settlement and post-settlement coral reef fishes. J. Exp. Mar. Biol. Ecol. 175:275-286.
- Walters, C., V. Christensen and D. Pauly. 1997. Structuring dynamic models of exploited ecosystems from trophic mass-balance assessments. Rev. Fish Biol. Fish. 7:139-172.
- Williams, T.P. 1986. Ageing manual for Kuwaiti fish. Kuwait Institute for Scientific Research, Safat, Kuwait. 57 p.
- Worthington, D.G., P.J. Doherty and A.J. Fowler. 1995. Variation in the relationship between otolith weight and age: implications for the estimation of age of two tropical damselfish (*Pomacentrus moluccensis* and *P. wardi*). Can. J. Fish. Aquat. Sci. 52:233-242.

APR 14 1998

ENTERED IN NAGA

PART II: BIOLOGY, ECOLOGY AND DISTRIBUTION

Ecology and Population Dynamics of *Lutjanus synagris* on Campeche Bank

E. RIVERA-ARRIAGA

A.L. LARA-DOMÍNGUEZ

J. RAMOS-MIRANDA

P. SÁNCHEZ-GIL

A. YÁÑEZ-ARANCIBIA

*Programa de Ecología, Pesquerías
y Oceanografía del Golfo de México
U.A.C. Ap. Postal 520, Campeche 24030
Campeche, México*

RIVERA-ARRIAGA, E., A.L. LARA-DOMÍNGUEZ, J. RAMOS-MIRANDA, P. SÁNCHEZ-GIL and A. YÁÑEZ-ARANCIBIA. 1996. Ecology and population dynamics of *Lutjanus synagris* on Campeche Bank [*Ecología y dinámica poblacional de Lutjanus synagris en la Sonda de Campeche, México*], p. 11-18. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Lutjanus synagris is a commercially important member of the demersal fish community on Campeche Sound, adjacent to Terminos Lagoon, southern Gulf of Mexico. Its life history and seasonality are described, with emphasis on its reproductive and trophic strategies.

L. synagris is a stenohaline species with preference for deep and clear water in the Campeche Sound. Reproduction takes place from May to October on the inner shelf.

The population near the Puerto Real of Terminos Lagoon was mainly composed of juveniles feeding over seagrass beds, and occurs in waters of less than 20 m depth.

The trophic spectrum is wide with at least nine important items, with penaeid shrimps (46%), carideans (40%), fishes (49%), and other crustaceans (33%) being dominant at different periods of the year.

The von Bertalanffy growth parameters were estimated, based on length-frequency data and using ELEFAN I and SLCA, both parts of the FISAT software. This led to $TL_{\infty} = 35.2$ cm and $K = 0.26-0.29 \text{ year}^{-1}$, i.e., values compatible with estimates from earlier studies.

Resumen

Lutjanus synagris es una especie de importancia comercial de la comunidad de peces demersales de la Sonda de Campeche, adyacente a la Laguna de Términos. Se describe su ciclo de vida y estacionalidad, con énfasis en sus estrategias reproductiva y trófica.

L. synagris es una especie estenohalina con preferencia por aguas profundas y claras de la Sonda de Campeche. La reproducción tiene lugar de Mayo a Octubre sobre la parte interna de la plataforma continental. La población, cerca de Puerto Real, Laguna de Términos, estuvo compuesta principalmente por juveniles que se alimentan en las áreas de pastos marinos, en profundidades menores a 20 m.

El espectro trófico es amplio, con al menos nueve componentes de importancia: camarones penéidos (46%), carídeos (40%), peces (49%) y otros crustáceos (33%), siendo dominantes en diferentes períodos del año.

Los parámetros de crecimiento de la ecuación de von Bertalanffy fueron estimados con base en datos de frecuencia de longitudes utilizando los métodos ELEFAN I y SLCA, ambos contenidos en el paquete de programas FiSAT. Las estimaciones fueron: $LT_{\infty} = 35.2$ cm y $K = 0.26 - 0.29$ año⁻¹, los cuales son compatibles con estudios anteriores.

Introduction

On the continental shelf of Campeche Sound, adjacent to Terminos Lagoon there are at least 350 fish species, of which 21 species are dominant. These include the commercially important snapper *Lutjanus synagris*.

The biology and ecology of *L. synagris* have been described by Reshetnikov and Claro (1975) and Claro (1983) (see Diaz-Ruiz et al.; and Cuellar et al., this vol.). Growth parameter analyses in the Yucatan shelf are given by Torres Lara and Chávez (1987), Torres Lara and Salas Márquez (1988, 1990), Torres Lara et al. (1991); and for Puerto Rico by Acosta and Appeldoorn (1992). The purpose of this paper is to add to this body of knowledge, with emphasis on the ecology and growth of *L. synagris*.

Study Area

In the southern Gulf of Mexico, the Campeche Sound and Terminos Lagoon constitute a complex ecosystem involving transport and mixing processes, complex trophic webs and migratory processes, particularly near or through the two estuarine inlets of Terminos Lagoon (Yáñez-Arancibia et al. 1991). The prevailing winds, littoral currents and river discharges cause a net inflow at the eastern inlet (Puerto Real), and a net outflow through the western inlet (El Carmen). There are three climatic seasons in the region, according to temperature, precipitation and wind patterns: the "Nortes" (Northern winds) season from October to February, the dry season from February to May, and the rainy season from June to October. Detailed weather

descriptions for the area are provided by Yáñez-Arancibia and Day (1988) and Yáñez-Arancibia and Sánchez-Gil (1986).

Campeche Sound has an area of 129 500 km² within the 200 m isobath (Fig. 1). Terminos Lagoon has an area of 1 662 km², and mean depth of 3.5 m. There are 933 km² of wetlands and a number of associated lagoons (Yáñez-Arancibia and Day 1988).

Methods

Trawl catches of lane snapper *L. synagris* were made from June 1976 to September 1985, at 18 sampling stations inside the lagoon, 81 in the Campeche Sound, and two in front of the Terminos Lagoon inlets (Fig. 1). These latter stations were sampled every four hours over 24-hour periods during the "Nortes", rainy and dry seasons, and were used for trophic dynamics and gonadal maturity studies. The other samples were used to determine distribution, abundance and growth parameters.

The gear used were shrimp trawls of 2.5-m opening and 1.90-cm mesh in the lagoon; and 9-m opening and 3.38-cm mesh in the Campeche Sound (Sánchez-Gil et al. 1981; Yáñez-Arancibia and Sánchez-Gil 1986).

The trophic spectrum of *L. synagris* was analyzed following Hyslop (1980), De Sylva (1985) and Yáñez-Arancibia et al. (1986). The gonadal maturity was determined using the scale proposed by Hilge (1977).

Length-frequency data were analyzed using SLCA (Shepherd 1987), ELEFAN I (Pauly 1987) and Extreme Value (Formacion et al. 1991) routines of the FiSAT software (Gayanilo et al. 1995). The growth parameter estimates were compared with

other estimates using the growth performance index (ϕ') of Pauly and Munro (1984):

$$\phi' = 2\log_{10}L_\infty + \log_{10}K.$$

Results and Discussion

The sample of 656 *L. synagris* that was obtained consisted of 88 specimens from the Campeche Sound, 31 from Terminos Lagoon, 444 from Puerto Real and 93 from El Carmen. *L. synagris* is a dominant species on the Campeche Sound, and an occasional visitor to Terminos Lagoon. Abundances are highest over carbonate bottoms

and seagrass bed (Yáñez-Arancibia and Sánchez-Gil 1986).

In the inlet areas, *L. synagris* is present throughout the year but abundances were higher during dry and rainy seasons (Fig. 1).

The range of lengths caught was 5 to 31 cm, with the smaller sizes at depths of about 10 m near the inlets, and the adults in 20-40 m (Fig. 2).

Most juveniles were found in El Carmen during the rainy season (Fig. 2), possibly because of the river discharge resulting in a high input of nutrients.

L. synagris is a second- or third-order consumer, and feeds mainly on organisms

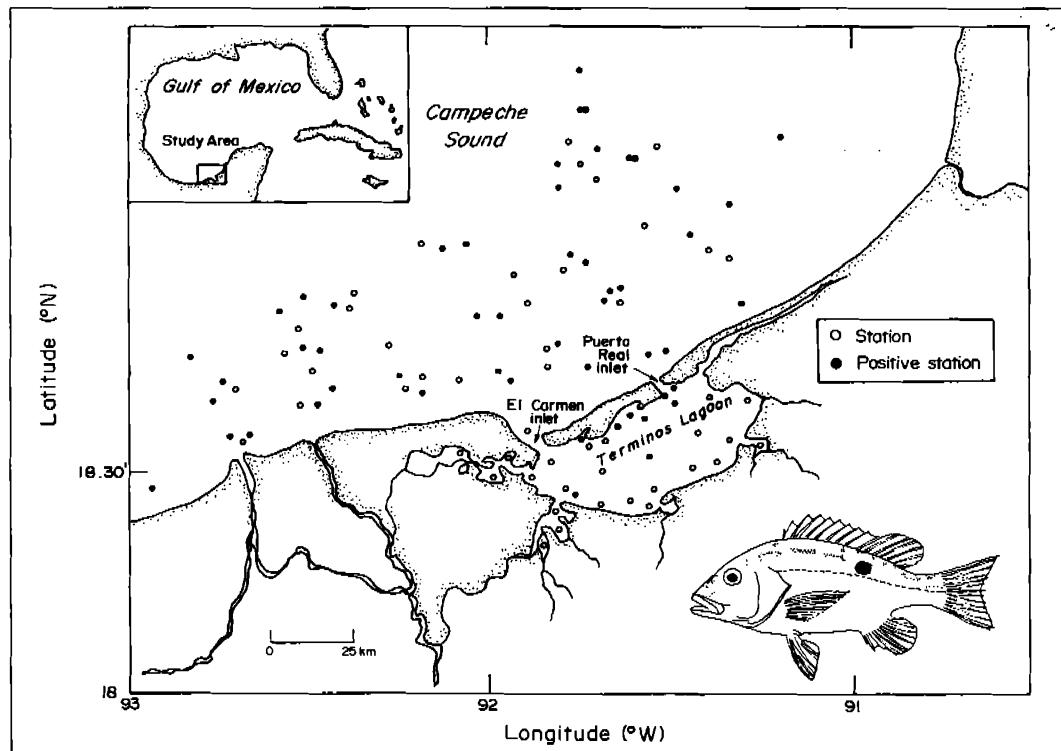


Fig. 1. Map of study area, i.e., the Campeche Sound and Terminos Lagoon. The dots represent the sampling stations of 13 trawl surveys from 1976 to 1985. The full dots are the sampling stations where *Lutjanus synagris* occurred; the open dots represent the other stations. [Área de estudio incluyendo la Sonda de Campeche y la región de la Laguna de Términos. Los puntos corresponden a las estaciones de muestreo de 13 cruceros efectuados de 1976 a 1985. Los puntos negros muestran las estaciones donde la colecta de *Lutjanus synagris* fué positiva.]

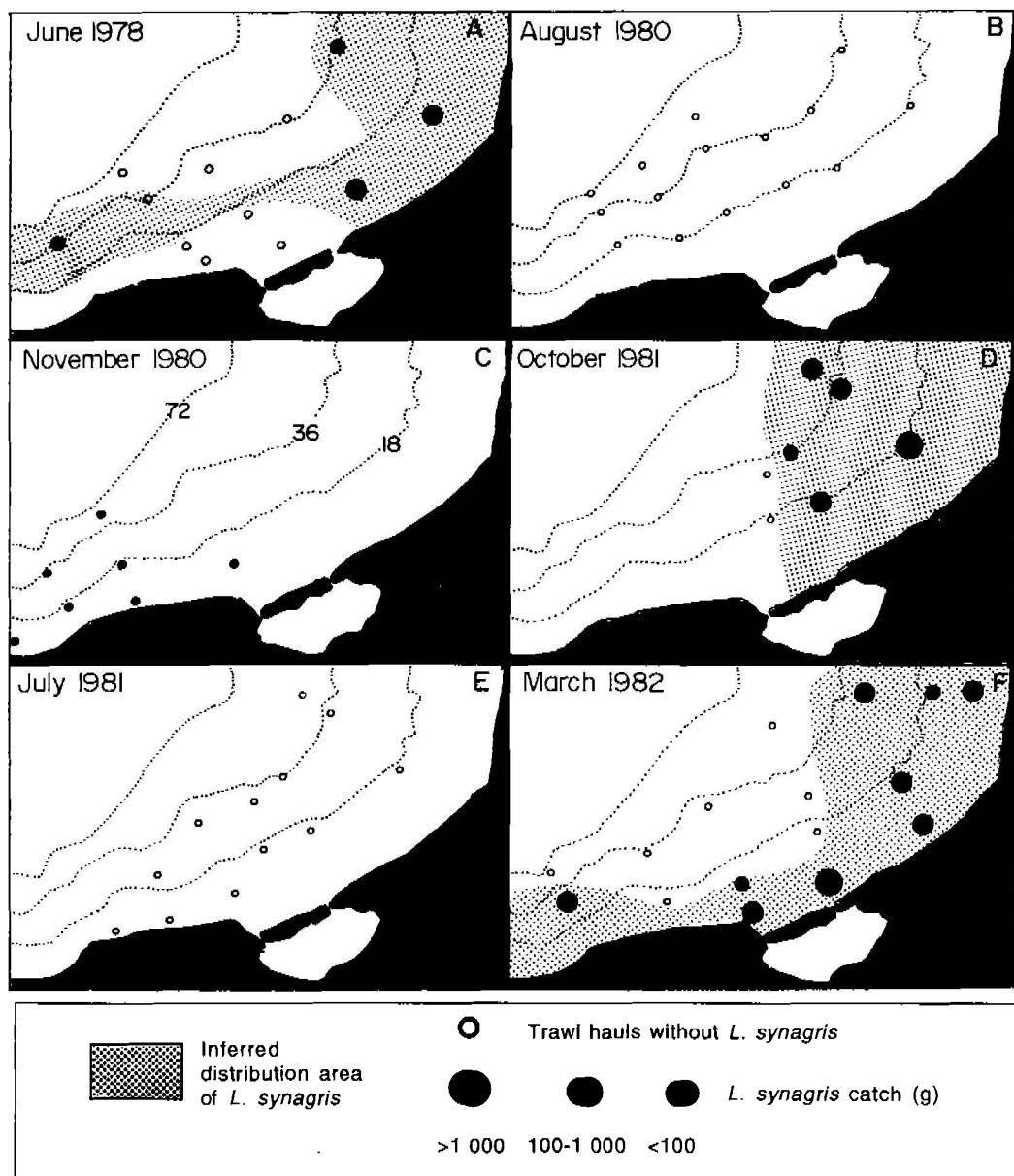


Fig. 2. Distribution of *Lutjanus synagris* in Campeche Sound (June 1978-March 1982); the depth (in m) in panel C also apply to panels A-B and D-F (modified from Sánchez-Gill et al. 1981). [Distribución de *Lutjanus synagris* en la Sonda de Campeche (Junio 1978 - Marzo 1982). La profundidad (m) en el diagrama C se aplica también a los diagramas A-B y D-F (adaptado de Sánchez-Gill et al. 1981).]

Table 1. Comparison of growth parameters of *Lutjanus synagris* from different areas. [Comparación de parámetros de crecimiento de *Lutjanus synagris* de diferentes áreas.]

Area	L_{∞} (cm)	K (year ⁻¹)	ϕ' ^a	Methods	Authors
Florida	46.0	0.13	4.45	otoliths	Manooch and Mason (1984)
Trinidad & Tobago	70.8 m	0.22	5.04	otoliths	Manickchand-Dass (1987)
	60.3 f	0.22	4.97	otoliths	
Cuba	38.0	0.35	4.63	otoliths, scales and urohyal	Rodriguez-Pino (1962)
Cuba	51.6	0.20	4.65	otoliths, scales and urohyal	Claro and Reshetnikov (1981)
Yucatan	41.0	0.25	4.61	ELEFAN I, Ford-Walford	Torres-Lara (1984)
Yucatan	42.8	0.28	4.71	-do-	Mexicano-Cintora and Arréguin-Sánchez (1987)
Yucatan	33.0	0.27	4.48	-do-	Torres-Lara and Salas-Marquéz (1990)
Yucatan	41.0	0.25	4.61	-do-	Torres-Lara (1987)
Yucatan	49.0	0.23	4.67	-do-	Torres-Lara and Chávez (1987)
Puerto Rico	49.0	0.23	4.67	-do-	Acosta and Appeldoorn (1992)
Campeche Sound	35.2	0.26	4.51	ELEFAN I, SLCA	This study

^a $\phi' = \log_{10} K + 2 \log_{10} L_{\infty}$ (Pauly and Munro 1984)

which live in seagrass beds in Puerto Real. Its prey consists of at least nine items varying according to the availability of the prey, the season and size. Penaeid shrimps, fishes and other crustaceans predominate in terms of weight, with strong seasonal variations (Rivera-Arriaga 1990).

The sex ratio was close to 1 in both inlets during the year. Juveniles were found in both inlets, while a few maturing adults were found in Puerto Real during the rainy season. According to Torres-Lara and Salas-Márquez (1988), *L. synagris* matures in two or three years, at a size of 18 cm.

The growth parameters obtained were $L_{\infty} = 35.2$ cm, $K = 0.29$ year $^{-1}$ using SLCA

and $L_{\infty} = 35.2$ cm, $K = 0.26$ year $^{-1}$ using ELEFAN I, which is similar to reports from other areas of the Gulf of Mexico (Table 1).

Proposed model of the life history of Lutjanus synagris

The migratory strategy of *L. synagris* includes depth and distance from the coast. The population studied here includes juveniles which feed near the coast, while the adults migrate to depths exceeding 40 m and distances of more than 70 km from the coast. Fig. 3 summarizes the life cycle of *L. synagris* on Campeche Sound.

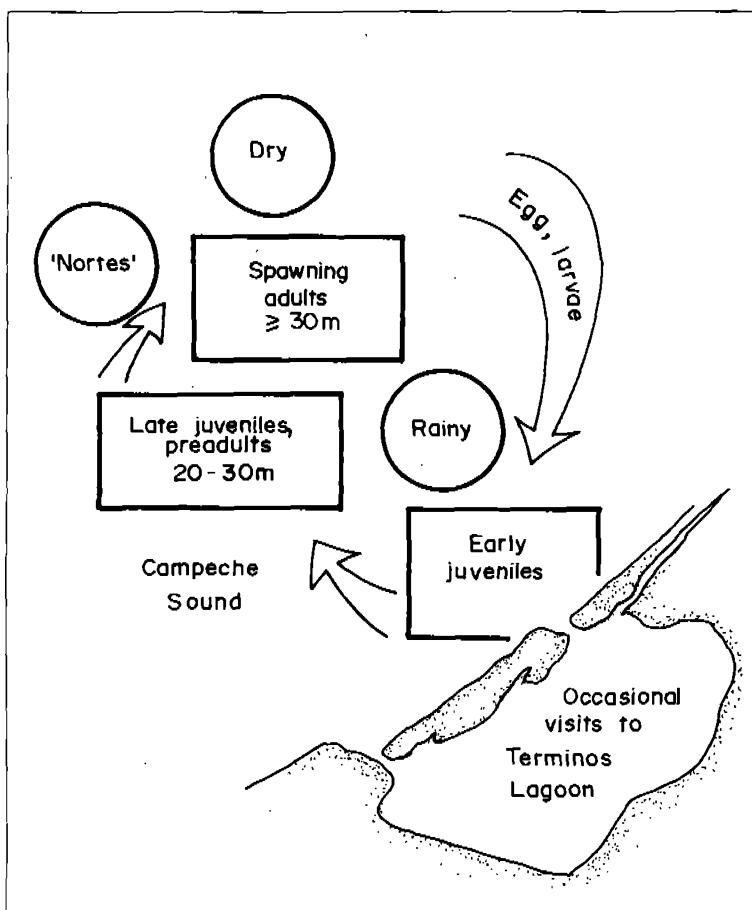


Fig. 3. Schematic representation of the life cycle of *Lutjanus synagris* on Campeche Sound. Arrows indicate stage and spatial transitions; circles indicate seasons of the year when most transitions occur, though some stages occur throughout the year. [Representación esquemática del ciclo de vida de *Lutjanus synagris* en la Sonda de Campeche. Las flechas indican los estados y las transiciones espaciales; los círculos indican las estaciones del año cuando la mayoría de las transiciones ocurren, aunque algunos estados se presentan a lo largo del año.]

References

- Acosta, A. and R.S. Appeldoorn. 1992. Estimation of growth, mortality and yield per recruit for *Lutjanus synagris* (Linnaeus) in Puerto Rico. Bull. Mar. Sci. 50(2):282-291.
- Claro, R. 1983. Ecología y ciclo de vida de la biajaiba, *Lutjanus synagris*, en la Plataforma Cubana. V. Dinámica estacional de algunos indicadores morfofisiológicos. Reporte de Investigación, Inst. de Oceanología. Academia de Ciencias de Cuba 16, 38 p.
- De Silva, D.P. 1985. Nektonic food webs in estuaries, p. 35-56. In A. Yáñez-Arancibia (ed.) Fish community ecology in estuaries and coastal lagoons: towards an ecosystem integration. UNAM Press, México. 645 p.
- Formación, S.P., J.M. Rongo and V.C. Sambilay. 1991. Extreme value theory applied to the statistical distribution of the largest lengths of fish. Asian Fish. Sci. 4:123-135.
- Gayanilo, F.C., Jr., P. Sparre and D. Pauly. 1995. The FAO-ICLARM stock assessment tools (FISAT) user's guide. FAO Comp. Inf. Ser. (Fish.) 7, 126 p.
- Hilge, V. 1977. On the determination of the stages of gonad ripeness in female bony fishes. Meeresforsch. Rep. Mar. Res. 25(3-4):149-155.
- Hyslop, E.J. 1980. Stomach contents analysis; a review of methods and their application. J. Fish Biol. 17: 411-429.
- Manickchand-Dass, S. 1987. Reproduction, age and growth of the lane snapper, *Lutjanus synagris* (Linnaeus), in Trinidad, West Indies. Bull. Mar. Sci. 40(1): 22-28.
- Manooch, C.S., III and D.L. Mason. 1984. Age, growth and mortality of lane snapper from Southern Florida. Northeast Gulf Sci. 7: 109-115.
- Mexicano-Cintora, G. and F. Arreguín-Sánchez. 1987. Dinámica de las poblaciones de rubia (*Lutjanus synagris*) y canane (*Ocyurus chrysurus*) de las costas de Yucatán. Congreso de Ciencias del Mar. La Habana Cuba.
- Pauly, D. 1987. A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic invertebrates, p. 7-34. In D. Pauly and G. R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.
- ✓ Pauly, D. and J.L. Munro. 1984. Once more on the comparison of growth in fish and invertebrates. Fishbyte 2(1):21.
- Reshetnikov, Y.S. and R. Claro. 1975. Cycles of biological processes in tropical fishes with reference to *Lutjanus synagris*. S.N. Severtsov. Institute of Evolutionary Morphology and Animal Ecology (IMEZH). Moscow and Institute of Oceanology, Habana, Cuba.
- Rivera-Arriaga, E. 1990. Ecología trófica en dos poblaciones de peces tropicales costeros (*Polydactylus octonemus* y *Lutjanus synagris*) del sur del Golfo de México. Universidad Nacional Autónoma de México, México, D.F. 60 p. M. thesis.
- Rodríguez-Pino, Z. 1962. Estudios estadísticos y biológicos sobre la biajaiba *Lutjanus synagris*. Centro de Investigaciones Pesqueras. Nota sobre Investigaciones (4), 99 p.
- Sánchez-Gil, P., A. Yáñez-Arancibia and F. Amezcua Linares. 1981. Diversidad, distribución y abundancia de las especies y poblaciones de peces demersales de la Sonda de Campeche (verano 1978). An. Inst. Cienc. del Mar y Limnol. Univ. Natl. Autón. México 8(1):209-240.
- Secretaría de Pesca. 1992. Estadísticas de resumenes anuales por oficina, 1992. Delegación Federal de Pesca, Campeche, México.
- ✓ Shepherd, J.G. 1987. A weakly parametric method for estimating growth parameters from length composition data, p. 113-119. In D. Pauly and G.R. Morgan (eds.), Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.
- Torres-Lara, R. 1984. Diagnosis de la pesquería de la rubia (*Lutjanus synagris*, Linnaeus, 1758) en las costas de Yucatán. Escuela Nacional de Estudios Profesionales IZTACALA, Universidad Nacional Autónoma de México, México. 89 p. Tesis profesional.
- Torres-Lara, R. 1987. Análisis biológico-pesquero de dos temporadas de pesca de la rubia (*Lutjanus synagris*, L., 1758) en las costas de Yucatán. CINVESTAV-IPN-Unidad Mérida, Yucatán, México. 154 p. Tesis de maestría.
- Torres-Lara, R. and E. Chávez. 1987. Evaluación y diagnóstico de la pesquería de rubia

- (*Lutjanus synagris* (L)) en el Estado de Yucatán. Cienc. Mar. 13(1):7-29.
- Torres-Lara, R. and S. Salas Márquez. 1988. Fecundidad de la rubia (*Lutjanus synagris*) en las costas de Yucatán. Contribuciones de Investigación Pesquera. Inst. Nac. Pesca (5):21-31.
- Torres-Lara, R. and S. Salas Márquez. 1990. Crecimiento y mortalidad de la rubia *Lutjanus synagris* de las costas de Yucatán durante las temporadas de pesca 1983-1985. An. Inst. Cienc. del Mar y Limnol., Univ. Nal. Autón. México 17(2): 205-214.
- Torres-Lara, R., S. Salas Márquez, G. Mexicano-Cintora and M.A. Cabrera-Vasquez. 1991. Sinópsis de la dinámica poblacional de cinco especies de la familia Lutjanidae en la costa de Yucatán. An. Inst. Cienc. del Mar y Limnol., Univ. Nal. Autón. México 18(2):189-198.
- Yañez-Arancibia, A., A.L. Lara-Dominguez and A. Aguirre-Leon. 1986. Feeding ecology of tropical estuarine fishes in relation to recruitment processes, p. 73-94. In A. Yañez-Arancibia and D. Pauly (eds.) Recruitment processes in tropical coastal demersal communities. Ocean Science in Relation to Living Resources (OSRL), International Recruitment Project (IREP). COI-FAO-UNESCO Workshop Press Series (44). Unesco, Paris.
- Yañez-Arancibia, A. and J.W. Day, Jr. 1988. Caracterización ecológica de la Laguna de Términos, p. 1-26. In A. Yañez-Arancibia and J.W. Day (eds.) Ecology of coastal ecosystems in the southern Gulf of Mexico: The Terminos Lagoon region. Instituto de Ciencias del Mar y Limnología, Universidad Nacional Autónoma de México and Coastal Ecology Institute Louisiana State University, Ed. Universitaria, México, D.F.
- Yañez-Arancibia, A. and P. Sánchez-Gil. 1986. Los peces demersales de la plataforma continental del sur del Golfo de México: caracterización ambiental, ecología y evaluación de las especies, poblaciones y comunidades. Inst. Cienc. del Mar y Limnol. Univ. Nal. Autón. (México) Publ. Esp. 9:230 p.
- Yañez-Arancibia, A., P. Sánchez-Gil and A.L. Lara-Dominguez. 1991. Interacciones ecológicas estuario-mar: estructura funcional de bocas estuarinas y su efecto en la productividad del ecosistema. Publ. ACIESP 71(4):49-83.

ENTERED IN NAGA

APR 14 1998

Trophic Role of the Red Grouper (*Epinephelus morio*) in the Ecosystem of the Northern Continental Shelf of Yucatan, Mexico^a

F. ARREGUÍN-SÁNCHEZ^b

Programa de Ecología, Pesquerías
y Oceanografía del Golfo de México
U.A.C. Ap. Postal 520, Campeche 24030
Campeche, México

E. VALERO

Centro de Investigación y de Estudios Avanzados del IPN
Unidad Mérida, Ap. Postal 73-Cordemex. 97310
Mérida, Yucatán, México

ARREGUÍN-SÁNCHEZ, F. and E. VALERO. 1996. Trophic role of the red grouper (*Epinephelus morio*) in the ecosystem of the northern continental shelf of Yucatan, Mexico [Papel trófico del mero americano (*Epinephelus morio*) en el ecosistema del norte de la plataforma continental de Yucatán, México], p. 19-27. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

The trophic role of red grouper (*Epinephelus morio*) on the northern continental shelf of Yucatan, Mexico, is analyzed through simulated changes in its biomass, based on a previous study using the ECOPATH model and which emphasized the commercially important fish resources. Red groupers occupy a high trophic level in the ecosystem, together with mojarras, king mackerels, snappers, sharks and octopuses. Except for the octopus, all others can be grouped as a single box in the model without loss of structural information. When decreases in biomass of red groupers were simulated, the contributions to detritus from primary producers and the sum of all exportations increased, along with other commercially important groups of fishes such as snappers, mojarras, king mackerels and sharks. Net primary production, sum of flows to respiration, the sum of all consumptions and ascendancies decreased, along with the biomasses of sea trouts and sardines. In general terms, observed changes result in the ecosystem maintaining its thermodynamic equilibrium.

Resumen

El papel trófico del mero americano (*Epinephelus morio*) de la plataforma continental al norte de la Península de Yucatán, México es analizado a través de cambios simulados en su biomasa, con base en un estudio previo que utilizó el modelo ECOPATH, y hace énfasis en los recursos pesqueros de mayor importancia comercial. El mero americano ocupa un alto nivel trófico en el ecosistema, junto con las

^a EPOMEX Contribution 240.

^b Present address: Centro Interdisciplinario de Ciencias Marinas del IPN, Playa Conchalito s/n; Apartado Postal 592. La Paz 23000, Baja California Sur. México.

mojarras, el carito, los pargos, el tiburón y el pulpo. Con excepción del pulpo, las otras especies pueden ser reunidas en un solo grupo sin pérdida de información estructural. Cuando los cambios en la biomasa de los meros fueron simulados, las contribuciones a detritus desde productores primarios y la suma de todas las exportaciones incrementaron, junto con otros grupos importantes como los pargos, mojarras, carito y tiburón; mientras que la producción primaria neta, la suma de flujos a respiración, la suma de todos los consumos y las ascendencias decrecieron, junto con las biomassas de la trucha de mar y sardinas. En términos generales, los cambios observados son resultado del mantenimiento del equilibrio termodinámico del ecosistema.

Introduction

The northern continental shelf of Yucatan is an important fishing ground in the Gulf of Mexico, with a high diversity of resource species and fisheries. Most fishing is carried out by small- or middle-sized fleets which tend to operate close to the coast. Red grouper is the most important fish resource in this region after shrimp; annual yields reached more than 19 000 t in the early 1970s, but in the last years, they declined to about 11 000 t (see Arreguín-Sánchez et al.; Brûlé and Déniel; Sullivan and Sluka, this vol.). The fishers use long-lines, or hand-lines, depending on the type of boats, and fishing areas. Fishing occurs throughout the year, and the fishery is a multispecies fishery (Fuentes 1991), although red grouper constitutes more than 80% of the total catch.

This fishery has been studied by several authors who determined its status at the time corresponding to their analysis. Klima (1976), Muhlia (1976), Moreno (1980), Doi et al. (1981) and Stevenson (1982), concluded that the fishery was still developing and that higher yields could be obtained. Some years later, Seijo (1986), Arreguín-Sánchez (1987a, 1987b), Arreguín-Sánchez et al. (1987), noted a decline in relative abundance, i.e., catch/effort, while Contreras et al. (1994) suggested that there had been a decrease in the average population size of around 30%.

Arreguín-Sánchez (1992) undertook a study based on a detailed analysis of catchability patterns involving time, age-length, fleet and density dependent effects

on the vulnerability of fish and concluded that the population had remained reasonably stable during the last 15 years, with two peaks in abundance separated by a period of around eight years (Fig. 1). He also suggested that variations in population abundance were related to the amount of fishing, to annual reproductive success in relation to some environmental variables, such as temperature, and the primary production induced by the seasonal upwelling. Also, an oil spill occurred in the Southern Gulf of Mexico in 1980, for a nine-month period (Anon. 1980), but failed to have a significant long-term impact on population size (Fig. 1).

On the other hand, González et al. (1994) studied the population dynamics of the red snapper (*Lutjanus campechanus*) and indicated that the stock was underexploited in the early 1980s, and that annual yields were progressively increasing, reaching over 4 000 t at the end of the period, in contrast with the decreasing trend of the red grouper population. Moreover, Arreguín-Sánchez (1992) showed the life cycles of most fish populations on Campeche Bank to be in synchrony with the seasonal upwelling occurring on the central-eastern end of the continental shelf of Yucatan. Such is the case for example with the porgies (*Calamus* spp.), grunts (*Haemulon* spp.) and some snappers (*Lutjanus* spp. and *Ocyurus chrysurus*). Arreguín-Sánchez and Chávez (in press) mentioned the specific case of the king mackerel (*Scomberomorus cavalla*), explaining its dynamics in the Campeche Bank by its relation to the pulses of primary production due to the seasonal upwelling mentioned above, and that induced by outwelling from the Terminos Lagoon system.

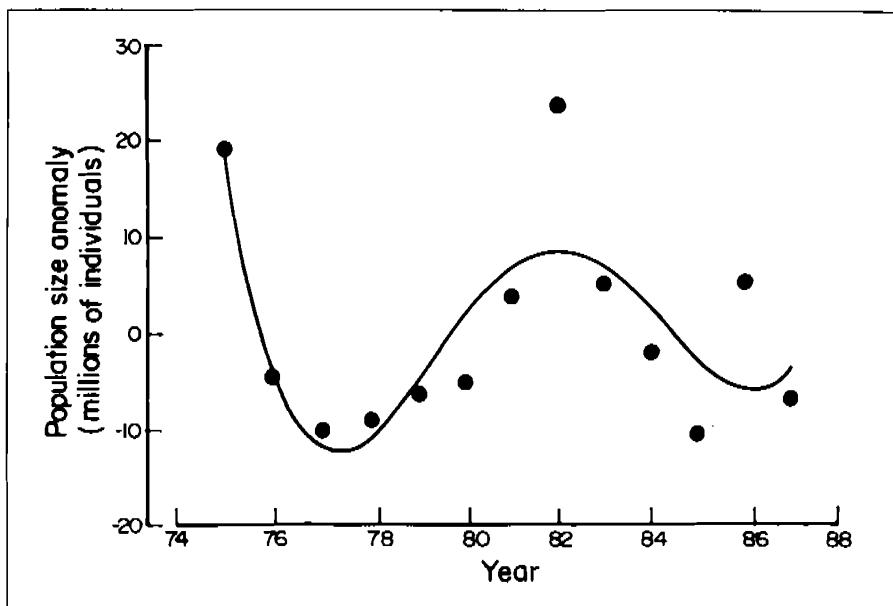


Fig. 1. Differences between observed and mean population size of red grouper on the Northern Shelf of Yucatan, 1975-1987. The solid line is a fourth order polynom fitted to the data so as to show trends (modified from Arreguín-Sánchez 1992). [Tendencia oscilatoria del tamaño de la población del mero americano (*Epinephelus morio*) del Banco de Campeche, expresado como la diferencia respecto al tamaño promedio de la población para el período 1975 a 1987 (adaptado de Arreguín-Sánchez 1992).]

These characteristics suggest the hypothesis that fluctuations of the red grouper population could be explained by the trophic dynamic structure of an ecosystem dominated by pulses of primary production. Therefore, this contribution is focused on the understanding of the trophic dynamics of the ecosystem, with emphasis on the red grouper population.

Materials and Methods

Arreguín-Sánchez et al. (1993) analyzed the trophic structure of a fish community on the North continental shelf of Yucatan, through the application of the ECOPATH model (Christensen and Pauly 1992a, 1992b). Input data consisted of prey/predator matrix, biomasses, consumption rates, exports (including catches), and production/biomass

ratios, and produced a thermodynamically balanced model representing the flows of biomass/energy within the ecosystem, and also provided a number of parameters expressing ecosystem properties defined in Ulanowicz (1986).

The basic assumption of the ECOPATH approach is that mass-balance occurs within the ecosystem and that the trophic relationships between functional groups can be described by linear equations as follows:

$$P_i \cdot B_i \cdot M2_i - P_i \cdot (1 - EE_i) - EX_i = 0 \quad ...1$$

which can be re-expressed as

$$B_i \cdot PB_i \cdot EE_i - \sum_j B_j \cdot QB_j \cdot DC_{ji} - EX_i = 0 \quad ...2$$

where P_i , B_i , $M2_i$, EE_i , and EX_i are the production, biomass, predation mortality, ecotrophic efficiency, and exportation of functional group (or species), while PB_i is

the production/biomass ratio; QB_j is the consumption/biomass ratio; and DC_{ij} the fraction of prey i in the diet of predator j .

The system is then represented for n simultaneous linear equations corresponding to n functional groups or species. For a full description see Christensen and Pauly (1992a).

To evaluate the trophic role of the red grouper, simulations were conducted by progressively reducing the biomass of the stock on successive ECOPATH models given the following considerations:

- a) The catch rate, defined here as the catch/biomass ratio, was maintained constant. This implies that observed changes cannot be attributed to changes of fishing mortality;
- b) Because biomass was the major variable affected by changes, the production/biomass (PB) and consumption/biomass (QB) ratios were assumed to change as well and re-estimated by the model (see equation 2);
- c) Ecotrophic efficiency, gross efficiency, and net efficiency were assumed constant, and thus kept fixed for each run.

In general terms, the idea with this strategy was to evaluate the impact of changes of the red grouper biomass on the rest of the ecosystem. Each change required the model to be re-equilibrated. Differences between the new estimates relative to the original ones were then computed; from these we then identified various aspects of the trophic role of the red grouper in the ecosystem.

Results

Following the criteria mentioned above, gradual reductions of 20% of red grouper biomass were performed. Ecosystem responses were analyzed both at the ecosystem level, using indices by Ulanowicz

(1986), and at the level of the various groups, by considering direct and indirect impacts.

Changes at the ecosystem level

The reduction in biomass has a proportional effect on total catch, total net primary production, full ascendancy, as well as on the sum of all respiratory flows and the sum of all consumptions. On the other hand, it has an inverse relationship with the contribution of primary production to detritus, sum of all flows to the detritus and the sum of all exports. As the decreases of total biomass (TB) and total respiration (TR) were lower than the decreases in total primary production (TPP), the quotients TB/TPP and TR/TPP increased with red grouper biomass (Table 1).

The reduction of the respiratory flows represents a loss of biomass/energy which cannot be used by other components: a compensatory mechanism tending to maintain the thermodynamic equilibrium. These losses occurred through several ways:

- a) Because the removed biomass is that of an important top predator, the sum of all consumption is strongly affected, and the respiratory flows decrease because ecosystem metabolism also decreases;
- b) The increase of exports (biomass moving out of the ecosystem) represents the excess of biomass which cannot be used by the ecosystem after it was thermodynamically re-equilibrated.
- c) The increase of the contribution of primary producers to the detritus represents another loss of biomass at the ecosystem level;
- d) The losses of biomass/energy from the ecosystem are reflected in a decrease of full ascendancy *sensu* Ulanowicz (1986).

Table 1. Effect of reducing the biomass of red grouper on various groups and system indices of Northern Yucatan shelf ecosystem model of Arreguín-Sánchez et al. (1993). [Efecto de la reducción de biomasa de mero americano en varios grupos e Indicadores del ecosistema según el modelo de la plataforma continental norte de Yucatán de Arreguín-Sánchez et al. (1993).]

Effect (%) on	Reduction of red grouper biomass (%)				
	20	40	60	80	100
Snappers	3	7	12	19	-
Sharks	-	-	8	9	-
Grunts	-	-	-	-	-
King mackerel	-	8	9	17	-
Herrings	-12	-13	-21	-21	-
Porgies	-	-	-	-	-
Mojarra	-	4	11	21	-
Sea trout	-3	-13	-28	-42	-
Jacks	-	-	-	-	-
Total catch	-	-	-	-	-38
Total biomass	-18	-19	-28	-22	-33
Total biomass/Full ascendancy	-22	-8	-18	-13	-18
Total primary production/ Total biomass	26	14	37	30	42
Total primary production/ Total respiration	23	12	36	19	42
Contribution to detritus from primary production	20	14	28	22	36
Total net primary production	-17	-12	-24	-21	-31
Full ascendancy	-8	-4	-12	-10	-12
Sum of all flows to detritus	1	1	3	3	4
Sum of all respiratory flows	-19	-12	-27	-22	-31
Sum of all exports	39	23	56	46	62
Sum of all consumptions	-18	-11	-28	-22	-31

Changes at the level of functional groups

To facilitate the understanding of the individual (group) interdependencies, and their responses to changes in the biomass of the red grouper, it is convenient to analyze the trophic levels of the main groups in the ecosystem. Fig. 2 represents a dendrogram of the groups in the ecosystem with respect to their trophic level. It can be observed that some groups can be pooled without loss of ascendancy: such is the case for the main predators; sharks, snappers, red groupers, king mackerels and jacks. This occurs because they occupy similar trophic levels and thus play a similar role

in the ecosystem (see also Exhibit 16.1 in Christensen and Pauly 1992a).

When the biomass of red grouper is reduced, the impact on other predators is that their biomass is increased (Table 1); this is because the trophic resources that the red grouper is no longer using become available to their competitors. Although the direction of the changes on other components of the same trophic level is similar, its impact on the ecosystem is different depending on individual abundances. This could partially explain why the yield of red snapper, which is abundant, increased in the 1980s while red grouper abundance decreased (Fig. 1). Note that this is not observed in the case of mojarras, because red snapper

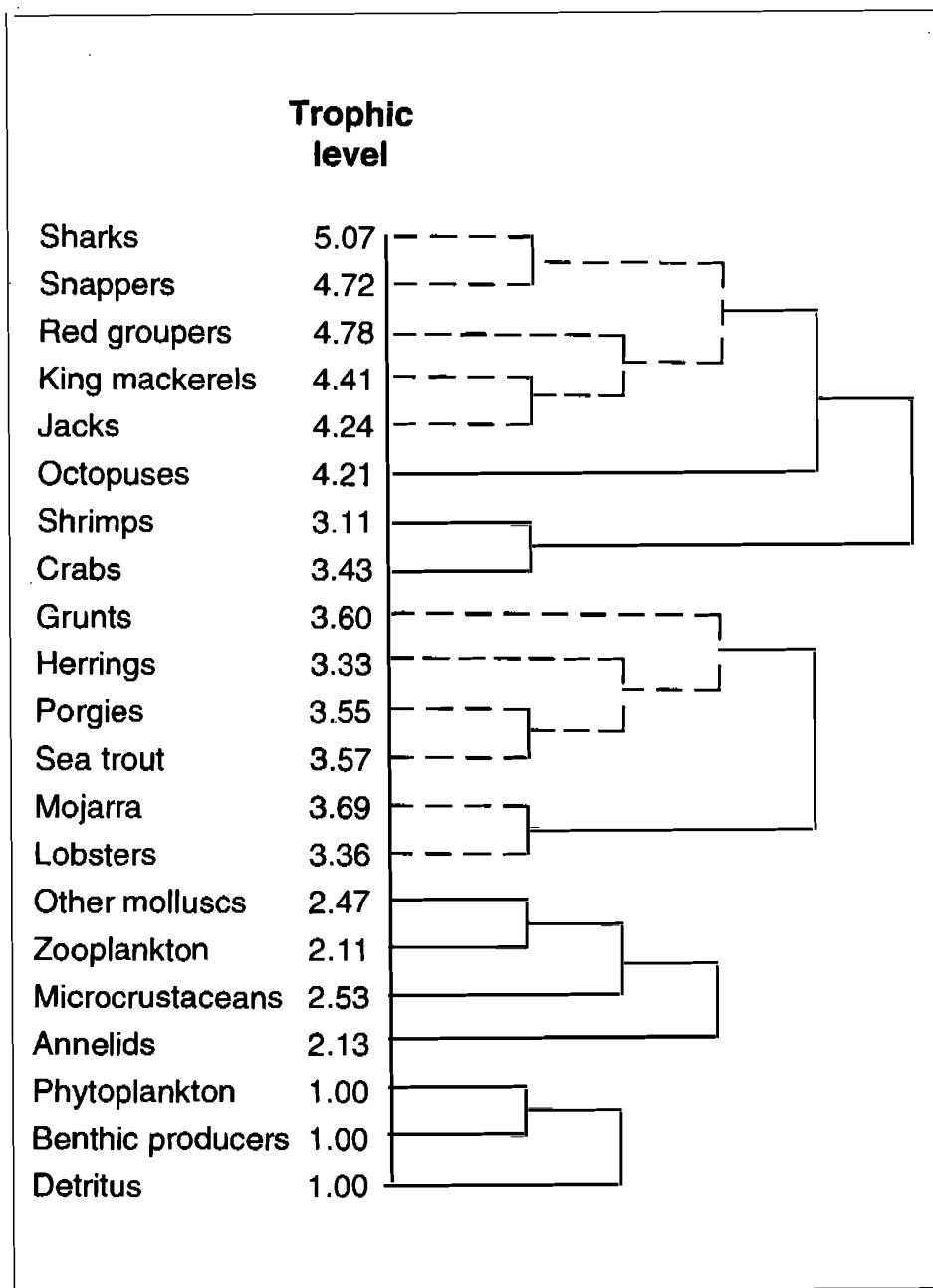


Fig. 2. Dendrogram representing the aggregation of groups with respect to their trophic level. Dashed lines indicate groups which can be aggregated with less than 1% of loss of ascendancy. [Dendrograma representando la agregación en grupos del ecosistema con respecto a su nivel trófico. Las líneas punteadas indican los grupos que pueden ser agregados con pérdida menor a 1% de ascendencia.]

is a target species, while mojarras are considered to be second or third class fishes, and are thus not targeted.

Some other groups or species exhibit a tendency to decrease, such as the sea trout and herrings (Table 1). This is easy to explain by the increased abundance of their main predator, king mackerel, as well as by the decrease of total primary production. The case of sea trout is not so obvious, though it appears to compete with various groups for food resources, notably with mojarras (whose biomass increased) and invertebrates such as lobsters, crabs and molluscs (Table 2). The mojarra group is an interesting case; it

occupies an intermediate trophic level when the red grouper biomass decreased, this reduced its predation, and although red snapper biomass increased, and the fraction of mojarras in their diet is twice that for red grouper, the abundance of the latter species dominates, so that the total biomass of predators remains almost constant. Further, the mojarras benefit from the reduction of biomass of sea trout and herrings, because they are its main competitors. Thus, biomass increase of the mojarra group occurs because the loss of biomass due to predation is over-compensated for by a reduction of competition.

Table 2. Section of the predator-prey matrix from the northern continental shelf of Yucatan (from Arreguín-Sánchez et al. 1993), emphasizing consumption by fishes. [Sección de la matriz predador-presa de la plataforma continental norte de Yucatán, México (dada por Arreguín-Sánchez et al. 1993), enfatizando el consumo por los peces.]

Discussion

Results derived from simulations suggest that the fluctuations in the abundance of red grouper could be a response to changes in the trophic dynamics of the ecosystem; probably associated with medium-term fluctuations in primary production. This also means that the role of the fishery is limited to intra-annual changes in biomass, and that the losses caused by fishing are recovered after each reproductive cycle. This apparently was what occurred with the fall in the 1980 year class, in the sense that it was not a serious impact in the longer term. The recognition of this kind of event is of importance in terms of management of the fishery. Decreases in the population abundance observed through the studies of the catch per unit of effort in the early 1980s suggested a trend toward overfishing. The results of this analysis, and the additional available elements, suggest that the diagnosis was correct in terms of a decreasing abundance, but failed to correctly identify the cause of the trend.

Recent studies (Arreguín-Sánchez et al., this vol.) show that fishing mortality must be limited using some kind of control. In Mexico, most controls involve limitation of fishing effort. It is also shown that the fish resource is fully exploited, and that juveniles (one-year old recruits) and adults are submitted to intensive exploitation. The juveniles are caught by small-scale fleet, while the commercial fleets concentrate on the areas where reproductive aggregations occur. If fishing effort controls are imposed under these conditions at a time when abundance is high, after some few years (since abundance cycles are around eight years) the amount of fishing effort will become excessive, and a real overfishing situation could emerge. This concept is very important, especially as indications of

interference among fleets were detected in the first years of the present decade (González-Cano et al. 1993). The conclusion in this case is that fishing effort must be limited but based on a dynamic strategy in accordance with the current abundance of the stock.

References

- Anon. 1980. Informe de los trabajos realizados para el control del pozo "Ixtoc", el combate del derrame de petróleo y determinación de sus efectos sobre el ambiente marino. Programa de Coordinación de Estudios Ecológicos en la Sonda de Campeche. Sec. Marina, Departamento de Pesca y PEMEX, México. 242 p.
- Arreguín-Sánchez, F. 1987a. Present status of the red grouper fishery in the Campeche Bank. Proc. Gulf Caribb. Fish. Inst. (38):498-509.
- Arreguín-Sánchez, F. 1987b. Estado actual de la explotación del mero (*Epinephelus morio*) del Banco de Campeche. 25 Aniv. Inst. Nat. Pesca. Centro Regional de Investigaciones Pesqueras. Yucalpetén, Instituto Nacional de Pesca, México. 23 p.
- Arreguín-Sánchez, F. 1992. An approach to the study of the catchability coefficient with application to the red grouper (*Epinephelus morio*) fishery from the continental shelf of Yucatan, Mexico. Centro de Invest. Estudios Avanzados del IPN, México. 222 p. Ph.D. dissertation.
- Arreguín-Sánchez, F. and E.A. Chávez. How marine shelf fisheries are depending of mangrove ecosystems: the Campeche Bank, Mexico as an example. In A. Yáñez-Arancibia and A.L. Lara-Domínguez (eds.). Valoración económica de los manglares. EPOMEX Ser. Cient. (In press).
- Arreguín-Sánchez, F., J.C. Seijo, D. Fuentes and M.J. Solís-Ramírez. 1987. Estado del conocimiento de los recursos pesqueros de la península de Yucatán y región adyacente. Centro Regional de Investigaciones Pesqueras-Yucalpetén, Instituto Nacional de Pesca, México. Contr. Inv. Pesq. Dcto. Técnico 4. 41 p.

- Arreguín-Sánchez, F., J.C. Seijo and E. Valero. 1993. An application of ECOPATH II to the north continental shelf of Yucatan, Mexico, p. 269-278. In V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.
- ✓ Christensen, V. and D. Pauly. 1992a. A guide to the ECOPATH II software system (version 2.1). ICLARM Software 6, 72 p.
- ✓ Christensen, V. and D. Pauly. 1992b. ECOPATH II, a software for balancing steady-state ecosystem models and calculating network characteristics. Ecol. Modelling 61:169-185.
- Contreras, M., F. Arreguín-Sánchez, J.A. Sánchez, V. Moreno and M.A. Cabrera. 1994. Mortality and population size of the red grouper (*Epinephelus morio*) fishery from the Campeche Bank. Proc. Gulf Caribb. Fish. Inst. (43):309-410.
- Doi, T., D. Mendizabal and M. Contreras. 1981. Análisis preliminar de la población de mero *Epinephelus morio* (Valenciennes) en el Banco de Campeche. Cienc. Pesq. (México) 1(1):1-16.
- Fuentes, D. 1991. La pesquería de mero en el Banco de Campeche. Mem. VII Congr. Nal. Oceanol. Ensenada, B.C., México (1): 361-374.
- González-Cano, J., F. Arreguín-Sánchez, M. Contreras, V. Moreno, R. Burgos, C. Zetina and V. Ríos. 1993. Diagnóstico del estado de la pesquería de mero (*Epinephelus morio*) en el Banco de Campeche. Grupo de Trabajo sobre el recurso mero. Instituto Nacional de Pesca, México. 26 p.
- González, M.E., J.A. Sánchez and F. Arreguín-Sánchez. 1994. Population dynamics of the red snapper (*Lutjanus campechanus*) fishery from the Campeche Bank, Mexico. Proc. Gulf Caribb. Fish. Inst. (43):29-40.
- Klima, E.F. 1976. Snapper and grouper resources of the Western Central Atlantic Ocean, p. 5-40. In H.R. Bullis, Jr. and A.C. Jones (eds.) Proceedings of a Colloquium on Snapper-Grouper Resources of the Western Atlantic Ocean. Florida Sea Grant Rep. 17, 333 p.
- Moreno, V. 1980. La pesquería de mero (*Epinephelus morio*) en el Estado de Yucatan. Univ. Autón. Edo. Morelos, México. Tesis profesional.
- Muhlia, A. 1976. Aspectos biológico-pesqueros de *Epinephelus morio* (Val.): mero. Instituto Nacional de Pesca, México. Mem. Primer Simp. al. Rec. Pesq. Mas. (México) 2:223-265.
- Seijo, J.C. 1986. Comprehensive simulation model of the tropical demersal fishery: red grouper (*Epinephelus morio*) of the Yucatan continental shelf. Michigan State University. 210 p. Ph.D. dissertation.
- Stevenson, D.K. 1982. Una revisión de los recursos marinos de la región de la Comisión de Pesca para el Atlántico Centro Occidental (COPACO). FAO Doc. Tec. Pesca. 211, 143 p.
- Ulanowicz, R.E. 1986. Growth and development: ecosystem phenomenology. Springer-Verlag, New York. 203 p.

ENTERED IN NAGA

APR 14 1998

Biological Research on the Red Grouper (*Epinephelus morio*) from the Southern Gulf of Mexico

T. BRULÉ

*Centro de Investigación y de Estudios Avanzados del IPN
Unidad Mérida, Ap. Postal 73-Cordemex. 97310
Mérida, Yucatán, México*

C. DÉNIEL

*Laboratoire de Biologie Animale-Poissons Marins
Université de Bretagne Occidentale, B.P. 809
29275 Brest, Cedex, France*

BRULÉ, T. and C. DÉNIEL. 1996. Biological research on the red grouper (*Epinephelus morio*) from the Southern Gulf of Mexico [*Investigaciones biológicas del mero americano (Epinephelus morio), del Sureste del Golfo de México*], p. 28-42. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Epinephelus morio is one of the most common large serranids in the Gulf of Mexico. The Mexican red grouper fishery on Campeche Bank is a very important source of food and revenue for the state of Yucatan, but the fishery seems to be operating at a level of effort beyond that generating maximum sustainable yield. Hence, management interventions are needed to protect this important fishery, but these can be developed only with a thorough knowledge of the biology of the species. Given the paucity of data available on the life history of *E. morio* from Campeche Bank, a joint research project involving Mexico and France was initiated in 1989 aimed at improved understanding and management of this fishery resource. The first results obtained on sexual maturation, spawning period, sex change and food and feeding habits are presented and discussed.

Resumen

Epinephelus morio es uno de los serránidos más grandes del Golfo de México. La pesquería mexicana del mero americano en el Banco de Campeche es una fuente muy importante de alimento e ingreso económico para el Estado de Yucatán. Sin embargo se ha observado que esta pesquería está operando en un nivel de esfuerzo por encima del que genera el rendimiento máximo sostenible. En consecuencia, se requieren medidas de manejo para proteger este importante recurso, y ésto solo puede ser hecho a través del conocimiento de la biología de las especies. Dada la carencia de datos sobre el ciclo de vida de *E. morio* del Banco de Campeche, un proyecto de investigación conjunto entre México y Francia fue iniciado en 1989 con el objeto de mejorar el conocimiento de este recurso pesquero. Los primeros resultados obtenidos sobre maduración sexual, período de desove, cambio de sexo y alimentación son presentados y discutidos.

Introduction

The family Serranidae, which includes some 300 species, is an important part of the marine shore fauna in tropical and subtropical areas (Smith 1971). All serranid fishes are carnivorous, feeding mainly on fishes and invertebrates. Most are hermaphroditic, synchronous or protogynous (Tortonese 1986). Some such as species of *Serranus* and *Hypoplectrus* are both male and female at the same time; others such as the genera *Epinephelus*, *Cephalopholis* and *Mycteroperca* start out mature life as females and change over to males when they are larger (Randall 1983). According to Manooch (1987), worldwide studies on the age and growth of serranids indicate that these fishes are long lived, slow growing, and have relatively low rates of natural mortality.

The red grouper (*Epinephelus morio*) is the most common and commercially important grouper in the Gulf of Mexico, with two centers of abundance: off the west coast of Florida and off the north coast of the Yucatan Peninsula on Campeche Bank (Moe 1969; Sevilla 1987) (see Arreguín-Sánchez and Valero; Arreguín-Sánchez et al., this vol.). In 1969, Moe published the results of the first major investigation of the biology of this species from the eastern Gulf of Mexico, and established the format and standards for future research on this important group of fishes (see Colin et al., this vol.). In Yucatan, despite the commercial value of *E. morio*, studies on its life history, particularly those pertaining to fishery biology, have been few (González et al. 1974a, 1974b; Zupanovic and González 1975; Valdés and Padrón 1980). Since 1988, a basic research program on the biology of red grouper from Campeche Bank has been conducted from the Centro de Investigación y de Estudios Avanzados del IPN (CINVESTAV-IPN) Unidad Mérida, Yucatán. The purposes of this paper are to describe the background and objectives of this program and to present the results obtained to date.

Background and Objectives

The aim of this project was established bearing in mind the socioeconomic and geographical position of Yucatan. This is one of the poorest regions in Mexico, lacking in mineral and oil resources. The flat northern Yucatan Peninsula (350 000 km²) is composed of extensive outcrops of limestone. However, the lack of upper clays and marls overlying the limestone causes the rainfall to infiltrate rapidly and prevents development of surface drainage. Areas of soil cover are interspersed with bare limestone outcrops and seldom exceeds 30 cm in thickness (Back and Hanshaw 1978). Consequently, intensive agriculture cannot be developed in this region. The only alternative source of development was the industrialization of marine fisheries. This has been clearly perceived by Mexico and, between 1975 and 1980, fish production in the Yucatan Peninsula increased from 40 000 to 85 000 t. However, increasing pressure on the marine environment has given rise to biological imbalances and it seems that the principal species landed in the Peninsula (shrimps in Campeche and groupers in Yucatan) have been heavily fished in recent years (Le Bail 1984).

The Campeche Bank red grouper fishery is very important for the economy of the state of Yucatan (Solís Ramírez 1970; Klima 1976). *E. morio* accounts for more than 87% of the Mexican grouper catch (Contreras, in Klima 1976). From 1969 to 1988, fluctuating landings of red grouper were observed with a maximum in 1972 (14 000 t) and a minimum in 1983 (6 700 t). In 1988, the catch of red grouper (11 887 t) was 49% of the total marine production for the state, equivalent to 34% of the annual revenue for Yucatan (Rihani Vales et al. 1989). Cuba's Gulf Fleet also fishes on the Campeche Shelf. When Mexico extended her Exclusive Economic Zone (EEZ) to 200 nautical miles offshore in 1976, a bilateral fisheries agreement between Cuba and

Mexico was ratified. This permitted Cuba to continue fishing in waters that were under the jurisdiction of Mexico, but within the constraint of a catch quota. From 1976 to 1987, the Cuban catch quotas for groupers caught within the EEZ were reduced by Mexican authorities from 10 000 to 3 500 t (Tashiro and Coleman 1977; Arreguín-Sánchez et al. 1987b). Although effort is higher than that required to generate maximum sustainable yield (MSY), the stock does not show typical signs of overfishing (Arreguín-Sánchez 1987; Arreguín-Sánchez et al. 1987a, 1987b). However in 1993, leaders of the National Chamber of Fisheries of Yucatan petitioned the Fisheries Secretary for the establishment of a closed season for red grouper, during May and June (*Diario de Yucatan*, 27-28-29/05/1993; *Por Esto*, 28/05/1993).

According to Sadovy (1994) considerable data are required to better understand and manage grouper stocks. This author states that a number of biological questions, particularly those regarding recruitment and reproduction, need to be addressed. Only scanty published information was available concerning the basic biology of the red grouper from Campeche Bank. In 1989 a joint research project, supported by the European Commission, was developed between the Laboratory of Marine Biology from CINVESTAV-IPN-Unidad Mérida, México and the Laboratory of Animal Biology of the Université de Bretagne Occidentale, Brest, France. The principal objective of this project was to provide essential knowledge on the biology of *E. morio* on Campeche Bank, for management of this poorly known stock of tropical reef fish. Biological research, as related to fishery management requirements, focused on reproduction (sexual maturation, spawning period, sex change, fecundity), food and feeding, and age and growth (rate of growth, longevity, age at sexual maturity).

Materials and Methods

Area Investigated

Campeche Bank is part of the region covered by the Western Central Atlantic Fishery Commission (WECAFC), the international body concerned with fisheries management for the Caribbean Sea, the Gulf of Mexico and their Atlantic approaches from Cape Hatteras (35°N latitude) to Recife, Brazil (10°S latitude). In the WECAFC area, the continental margins of the eastern US, the Gulf of Mexico, the Caribbean and the Guianas and Brazil contribute 80% of the total shelf area (0-200 m). Three locations with a wide continental shelf within the Gulf of Mexico are western Florida, the Texas and Louisiana coasts and Campeche Bank (Stevenson 1981). Campeche Bank (about 175 000 km²) includes the continental shelf from Terminos Lagoon to Cancun Island and extends to about 24°N latitude. Its maximum dimension from North to South is 260 km (Carranza 1957; Weidie et al. 1978).

Biological sampling

On Campeche Bank, small red groupers are found in shallow waters and their size increases with depth (González et al. 1974b; Valdés and Padrón 1980). Thus, red groupers were sampled through the commercial offshore and inshore fisheries. Red groupers were obtained from the commercial long-line offshore fishery based in Progreso, from May 1989 to April 1991. Offshore operations were also conducted monthly between November 1991 and April 1992, near the time of full moon, from an offshore grouper vessel based at the harbor of Progreso. All fish were captured in the northern region of Campeche Bank between 20° and 23°N latitudes at depths ranging from 30 to 90 m. Red groupers were also obtained from the commercial hook-and-line inshore fishery

based in Celestún, Progreso, Telchac Puerto and Rio Lagartos, from August 1988 to November 1989. All specimens were caught in inshore areas of Campeche Bank near to these four ports, at depths ranging from 7 to 27 m (Fig. 1).

The fish were examined either fresh a few hours after fishing, on arrival at the port (inshore collections), or after having been kept on ice aboard the fishing vessel for one or two days before landing (off-shore collections). For each specimen the fork length (FL), standard length (SL), total weight (TW), eviscerated weight (EW), gonads weight (GW) and liver weight (LW) were recorded and stomachs and otoliths (sagittae) were removed.

Reproduction

Samples of gonads were fixed in Bouin's fluid for the histological study of oogenesis and spermatogenesis. The preserved gonads

were embedded in paraffin, thin-sectioned at 6 µm, and stained as suggested in Gabe (1968). Sections were examined to determine sex and gonad development. In sections, the shape of red groupers' oocytes was ellipsoidal. According to Coleman's formula (Coleman 1991), an 'effective diameter' (d_e) = $[ab^2]^{1/2}$, with a: major axis and b: minor axis) was calculated for 100 oocytes of each oocyte stage. The reproductive state of red grouper was further examined by calculating a gonadosomatic index for each fish (GSI = GW·100/EW). Data from the same months for the three years were combined and the results were presented as monthly means.

Food and feeding

Stomachs, including the contents, were preserved in 10% formalin. Each stomach was opened and analyzed individually, the contents were sorted by taxa, counted, drained, and weighed to the nearest 0.1 g.

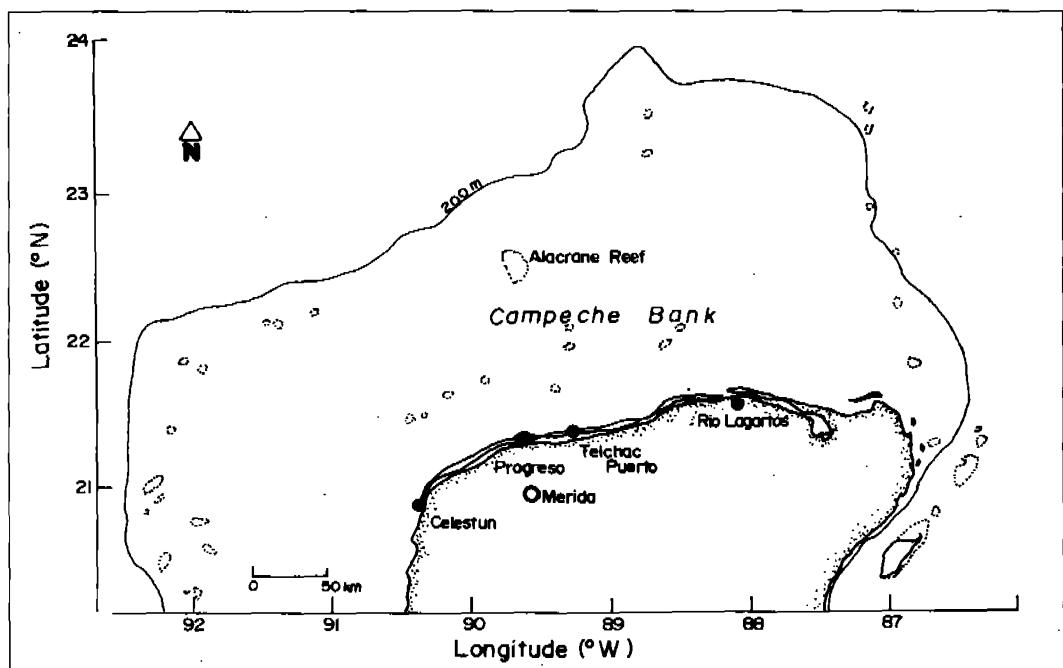


Fig. 1. Map of the north coast of Yucatan Peninsula and of Campeche Bank. [Mapa de la costa Norte de la Península de Yucatán y del Banco de Campeche.]

Fragments of pilchards (*Harengula humeralis*), used as bait in this fishery, were easily recognized and discarded. In each stomach, all fragments attributed to the same taxon were scored as a single individual prey, unless two (or more) pieces obviously came from two (or more) different individuals. Stomach contents were analyzed by three parameters: frequency of occurrence (%F), percentage number (%N) and percentage weight (%W), which partly overcame the disadvantage of using only one of these methods (Hyslop 1980).

Diet overlaps between red groupers of different size classes and between individuals from the four different collection sites were estimated by calculating Schoener's index (Schoener 1970) which ranges from 0 (no overlap) to 1 (complete overlap). Following Zaret and Rand (1971) and Wallace (1981), index values above 0.6 were considered to represent a significant overlap. This index was calculated from percentage number of the main prey categories.

Results

A total of 1 323 red groupers, ranging from 13.5 to 88.0 cm FL and 45 to 12 000 g TW were examined during this study. Inshore collections ($N = 446$) included specimens ranging from 13.5 to 55.5 cm FL and 45 to 2 475 g TW whereas offshore collections ($N = 877$) included individuals ranging from 38.9 to 88.0 cm FL and 1 000 to 12 000 g TW.

Reproduction

One hundred and thirteen red groupers (15.0 - 55.5 cm FL) caught in inshore waters and all specimens caught in offshore waters were sexed through histological preparations. No males were found among the 113 specimens caught in inshore waters. All were juvenile females (immature).

Offshore collections included juvenile and adult females, transitinals and adult males.

The principal cytologic changes observable during gametogenesis permitted the identification of six stages to describe oogenesis (post-ovulatory follicles and atretic oocytes were not identified as stages) (Table 1), and five stages to describe spermatogenesis: spermatogonia, 1^o and 2^o spermatocytes, spermatid and spermatozoan.

The seasonal and ontogenetic changes in gonad development were divided into nine classes (Table 2). Vitellogenesis started in September for the most precocious females and high percentages of ripening and ripe females were observed in January, February and March. By April only primary, immature and atretic vitellogenic oocytes remained in the ovaries, indicating that females entered the spent-resting period. Ripening males were observed from September to March. Red grouper with ripe testes were more prevalent from January to April. By April-May, males entered the spent-resting period. Thus, peak spawning seemed to occur from January to March. Transitional individuals were observed throughout the year (Fig. 2).

Changes on monthly mean gonadosomatic indices confirmed the histological observations on spawning and resting periods. For both females and males, GSI values followed a similar pattern (Fig. 3). From October to December, the relative weight of gonads increased slowly. The GSIs reached maximum values in January (female: 0.90% and male: 0.28%) and in March (female: 1.15% and male: 0.24%), indicating ripening. Relative weight decreased in April to reach minimum values (female: 0.13-0.24% and male: 0.13-0.14%) in spring and summer months, indicating that gametes had been shed.

Fig. 4 shows distribution of sex in 5 cm FL size groups. Female red groupers ranged from 14.5 to 84.5 cm FL and no male smaller than 39.5 cm FL was found. The percentage of males in each size group where they

were present progressively increased with size of individuals. An equal distribution of the sexes did not occur until the individuals approached a fork length of about 74.5 cm. The size range for fish undergoing sex transformation was from 49.5 to 74.5 cm FL and fell within the overlap zone between sizes of females and males (from 39.5 to 84.5 cm FL).

Food and feeding

Two hundred and eighty-three juveniles (13.5 to 51.5 cm FL) collected in inshore waters and 37 specimens (43 to 73 cm FL) collected in offshore waters were caught

with stomach contents. The small number of fish with food collected in offshore waters suggests that a large number of specimens had regurgitated their stomach contents. Consequently, only stomach contents data of juveniles fished in inshore waters were considered for the quantitative analysis.

Prey species identified in stomach contents are presented in Table 3. Reptant decapods, including a large variety of true crabs (brachyurans), were the most diverse group.

To measure the relationship between size and diet, the fish were grouped into seven arbitrary size classes (Table 4). Schoener's index showed a significant dietary overlap among all size classes (Table 5).

Table 1. Microscopic characteristics for the determination of the oogenesis stages in *Epinephelus morio* ovaries. [Características microscópicas para la determinación de los estadios de la oogénesis en ovarios de *Epinephelus morio*.]

Oogenesis stage		Histological feature	Mean oocyte diameter (μm)
I	Primary oocyte	Nucleus with a large central nucleolus; nucleolus moves to the periphery of the nucleus during this stage	22
II	Immature oocyte	Nucleus with several nucleoli, one larger than the other, present around the nuclear periphery	67
III	Primary vitellogenesis	Scattered vacuoles in cytoplasm, around the nuclear margin and near the cellular periphery; thin zona radiata present	133
IV	Early secondary vitellogenesis	Yolk droplets appear around the vacuoles; cytoplasm divided in two concentric zones by a ring of yolk droplets; follicular layer well formed (granulosa, theca)	207
V	Late secondary vitellogenesis	Yolk as numerous globules filling the cellular volume; vacuoles usually surround the nucleus; zona radiata remains as a broad striated band	389
VI	Hyaline oocyte	Oocyte hydrated; yolk as an homogeneous mass, lightly stained; thin and nonstriated zona radiata; nucleus not visible	896*

* Value obtained by measuring, under a binocular dissecting microscope, fresh hyaline oocytes ($N = 60$) sampled from ripe ovaries.

Table 2. Gonad development and corresponding histological condition stages of gonads of female, transitional and male red grouper. [Estadios de desarrollo gonádico y características histológicas correspondientes a hembras, individuos en transición y machos de mero americano.]

Gonad development	Histological condition
Immature/resting female	Stage I and stage II oocytes
Ripening female	Stage I to stage V oocytes; stages III, IV and V dominate
Ripe female	Stage I to stage VI; stage VI dominates
Spent female	Stage I and II oocytes; degenerating stage V; post-ovulatory follicles
Transitional	Stage I and II oocytes; stage III oocytes sometimes present; proliferation of small crypts of spermatogonia and spermatocytes; crypts of spermatozoa sometimes present
Resting male*	Spermatogonia; 1° and 2° spermatocytes; spermatozoa occur rarely
Ripening male*	Spermatogonia; 1° and 2° spermatocytes and spermatids dominate crypts; spermatozoa present
Ripe male*	Spermatids and spermatozoa dominate and fill crypts; intralobular sinuses and vas deferens-like dorsal sinuses present
Spent male*	New crypts of spermatogonia and 1° spermatocytes; old crypts empty with few residual spermatozoa

* Stages I, II and rarely stage III oocytes have been observed in various testes.

Variations in food categories of juveniles were analyzed on a regional basis (Table 6). The results showed a significant overlap of prey taken by red grouper among all the studied areas (Table 7).

Discussion

Although some grouper species are known to spawn over 6-8 months, most spawn over 1-5 months and many spawn primarily during 1-2 months (Shapiro 1987). Consistent with these observations, the study

of histological changes in gonad development and seasonal variation in mean GSI indicated a gonadal activity from September to March with a peak spawning activity from January to March and a resting period from April to August. Zupanovic and González (1975) and Valdés and Padrón (1980) reported that the spawning period of red grouper population on Campeche Bank should occur during spring with a possible peak of spawning activity in March or April. The present study showed that *E. morio* on Campeche Bank spawn earlier than the red grouper population from the eastern Gulf of Mexico.

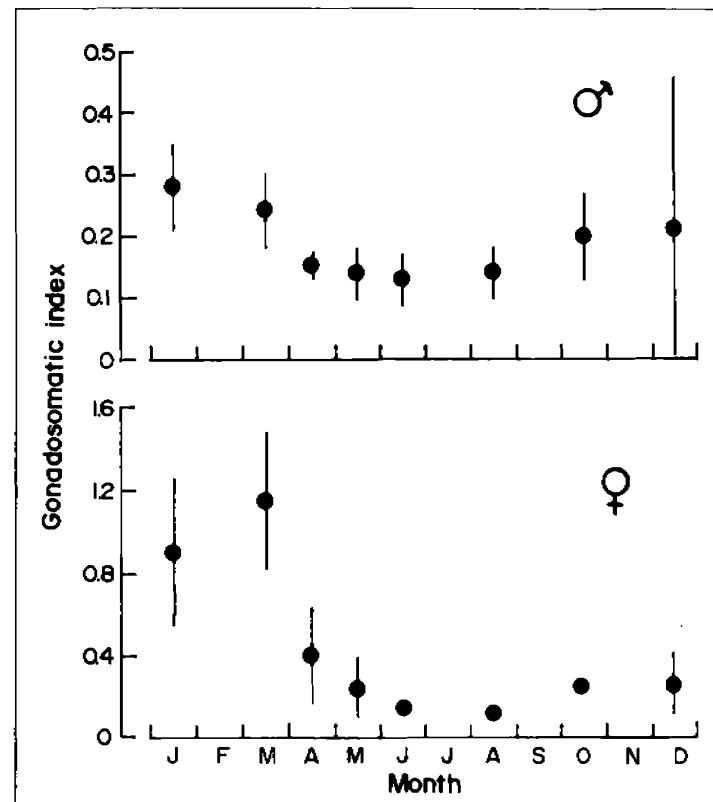
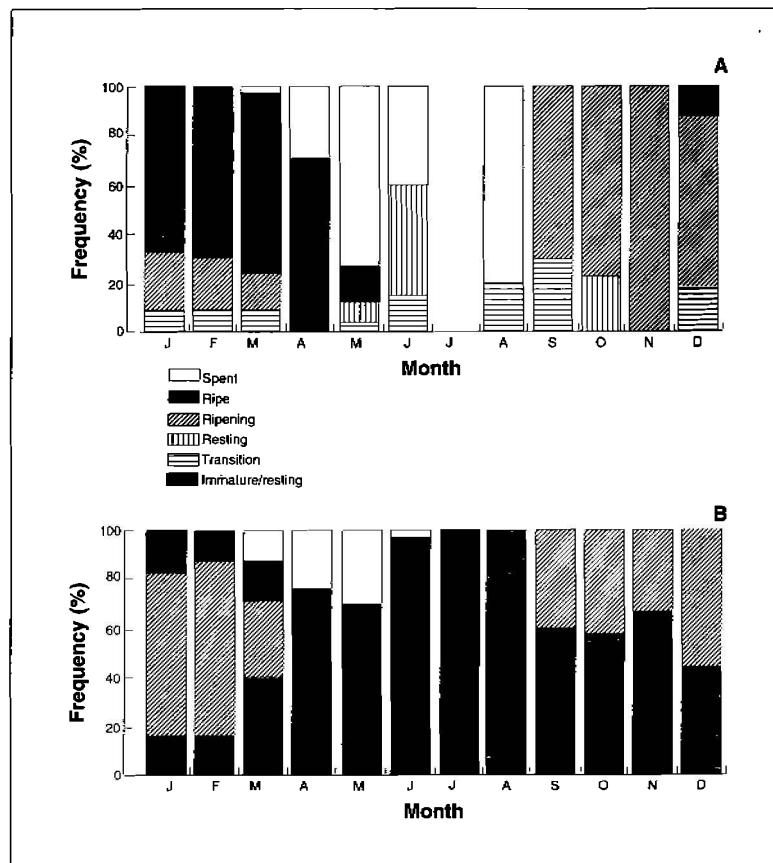


Fig. 3. Seasonal variations in mean gonadosomatic index of female and male red grouper. Vertical bars represent confidence Interval of mean (95% confidence limits) (from Brulé et al., In press). [Variaciones estacionales del índice gonadosomático promedio de las hembras y de los machos de mero americano. Las baras verticales representan el Intervalo de confianza del promedio (95% límites de confianza) (tomado de Brulé et al., en prensa).]

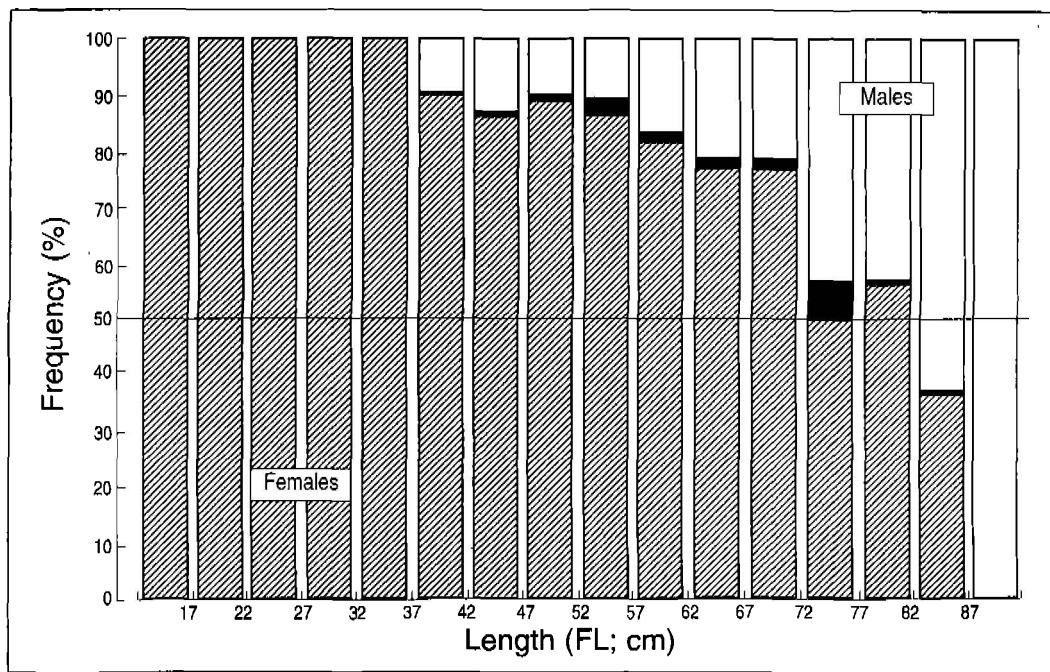


Fig. 4. Percent frequency distribution of female, transitional (black section of histograms) and male red grouper by length. [Distribución de frecuencia en porcentaje de hembras, individuos en estado de transición (sección negra del histograma) y machos de mero americano, por grupos de tallas de 5 cm de longitud furcal.]

For *E. morio* from the west coast of Florida, Moe (1969) stated that gonadal activity occurs in January and February, while spawning takes place from March to July with peak activity in April and May. The colder temperatures in the northern Gulf contrast with the warmer temperatures in the southern portion during late fall through spring. The southern and northern Gulf surface temperatures extend to depths of at least 46 m in the winter (Rivas 1968). So, the marked fluctuation in sea surface temperature between summer and winter in the northern Gulf could be the cause of the asynchronism observed between spawning periods of red grouper from the eastern and southern Gulf

of Mexico. But, according to Shapiro (1987), no factor or combination of factors (water temperature, changes in water temperature, day length, plankton abundance or latitude) clearly explains the variability in time of year at which groupers spawn.

Zupanovic and González (1975) and Valdés and Padrón (1980) did not provide information on multiple spawning by *E. morio* during each reproductive period. Moe (1969) did not find histological or analytical evidence to suggest that individual red grouper spawned more than once a season. However, during this work we observed females with ovaries containing both post-ovulatory follicles and numerous vitellogenic oocytes

Table 3. Prey species grouped into nine main categories recorded in stomach contents of red grouper from Campeche Bank (X: present, O: absent). [Presas encontradas en los contenidos estomacales del mero americano del Banco de Campeche, clasificadas en nueve categorías (x= presente; o= ausente).]

Main prey groups	Specific prey	Inshore	Offshore
Plant material	Alga	X	X
Natant crustaceans	<i>Penaeus duorarum notialis</i>	X	O
	<i>Penaeus</i> sp.	X	X
	<i>Palaemonidae</i>	X	O
	<i>Alpheus armatus</i>	X	O
	<i>Alpheus</i> sp.	X	X
	<i>Synalpheus brevicarpus</i>	X	O
	<i>Synalpheus</i> sp.	X	X
Reptant crustaceans	<i>Scyllaridae</i>	X	O
	<i>Callidactylus</i> sp.	O	X
	<i>Stenorhynchus seticornis</i>	X	X
	<i>Eplaltus bituberculatus</i>	X	O
	<i>Macrocoeloma camptocerum</i>	X	O
	<i>Macrocoeloma eutheca</i>	X	X
	<i>Macrocoeloma</i> sp.	O	X
	<i>Mithrax forceps</i>	X	O
	<i>Mithrax acuticornis</i>	O	X
	<i>Mithrax hispidus</i>	O	X
	<i>Mithrax pleuracanthus</i>	X	X
	<i>Stenocionops furcata</i>	O	X
	<i>Parthenope agonus</i>	O	X
	<i>Solenolambrus tenellus</i>	O	X
	<i>Callinectes</i> sp.	X	X
	<i>Portunus floridanus</i>	O	X
	<i>Portunus sayi</i>	X	O
	<i>Portunus spinimanus</i>	X	X
	<i>Portunus</i> sp.	X	X
	<i>Actaea acantha</i>	X	O
	<i>Carpilius corallinus</i>	X	O
	<i>Heteractea ceratopus</i>	X	X
	<i>Lobopilumnus agassizii</i>	X	O
	<i>Menippe mercenaria</i>	X	O
	<i>Panopeus americanus</i>	X	O
	<i>Pilumnus dasypodus</i>	X	X
	<i>Pilumnus sayi</i>	X	X
	<i>Pilumnus</i> sp.	X	O
Stomatopods	<i>Gonodactylus bredini</i>	X	O
Unidentified crustaceans	-	X	X
Molluscs	<i>Nassarius hlnia</i>	X	O
	<i>Turridae</i>	X	O
	<i>Anadara notabilis</i>	X	O
	<i>Isognomon alatus</i>	X	O
	<i>Argopecten gibbus</i>	O	X
	<i>Laevicardium mortoni</i>	X	O
	<i>Octopus</i> sp.	X	X
Unidentified echinoids	-	X	O
Unidentified fishes	-	X	X
Unidentified remains	-	X	X

Table 4. Percentage number (%N) of main prey categories of juvenile red grouper, according to size of predator (N: number of fish with stomach contents) (from Brûlé and Rodríguez 1993). [Porcentaje en número (%N) de las principales categorías de presas de Juveniles de mero americano de acuerdo al tamaño del predador (N: número de peces con contenido estomacal) (tomado de Brûlé y Rodríguez 1993).]

Predator FL (cm)	Crustaceans					Molluscs	Fishes	Uniden- tified food	N
	Natantia	Reptantia	Stomato- pods	Uniden- tified					
12.1-16.0	20.0	60.0	0.0	20.0	0.0	0.0	0.0	0.0	4
16.1-20.0	7.6	65.8	1.3	17.7	5.1	2.5	0.0	0.0	46
20.1-24.0	1.9	61.0	0.6	27.0	2.5	5.7	1.3	0.0	78
24.1-28.0	0.0	50.0	4.6	22.6	9.1	9.1	4.6	0.0	9
28.1-32.0	3.9	53.8	23.1	11.5	0.0	7.7	0.0	0.0	12
32.1-36.0	5.9	47.1	23.5	23.5	0.0	0.0	0.0	0.0	5
36.1-40.0	0.0	60.0	20.0	20.0	0.0	0.0	0.0	0.0	5

Table 5. Dietary overlap between the size classes of juvenile red grouper (from Brûlé and Rodríguez 1993). [Traslape de dietas entre clases de talla de Juveniles de mero americano (tomado de Brûlé y Rodríguez 1993).]

Size classes FL (cm)	12.1-16.0	16.1-20.0	20.1-24.0	24.1-28.0	28.1-32.0	32.1-36.0	36.1-40.0
12.1-16.0	-	0.86	0.82	0.70	0.69	0.73	0.80
16.1-20.0	-	-	-	0.77	0.73	0.72	0.79
20.1-24.0	-	-	-	0.83	0.74	0.73	0.81
24.1-28.0	-	-	-	-	-	0.75	0.75
28.1-32.0	-	-	-	-	-	0.86	0.86
32.1-36.0	-	-	-	-	-	-	0.87
36.1-40.0	-	-	-	-	-	-	-

Table 6. Percentage (%N) of main prey categories of juvenile red grouper, according to collection site (N: number of fish with stomach contents) (from Brûlé and Rodríguez 1993). [Porcentaje en número (%N) de las principales categorías de presas de Juveniles de mero americano, de acuerdo al sitio de colecta (N: número de peces con contenido estomacal) (tomado de Brûlé y Rodríguez 1993).]

Collection site	Crustaceans					Molluscs	Fishes	Uniden- tified food	N
	Natantia	Reptantia	Stomato- pods	Uniden- tified					
Celestún	3.2	53.2	21.0	14.5	1.6	6.5	0.0	0.0	29
Progreso	5.9	66.5	1.3	15.8	3.9	5.3	1.3	0.0	89
Telchac Puerto	0.0	65.1	0.0	18.6	4.7	9.3	2.3	0.0	21
Río lagartos	1.5	49.3	0.0	46.3	0.0	2.9	0.0	0.0	24

Table 7. Dietary overlap between juvenile red grouper from four collection sites (from Brulé and Rodríguez 1993). [Traslape de dietas entre juveniles de mero americano provenientes de cuatro sitios de colecta (tomado de Brulé y Rodríguez 1993).]

Site	Celestún	Progreso	Telchac Puerto	Río Lagartos
Celestún	-	0.79	0.76	0.68
Progreso	-	-	0.92	0.70
Telchac Puerto	-	-	-	0.71
Río Lagartos	-	-	-	-

in stages II, III or IV (January-March) and a high percentage of males with ripe testes during a long period (January-April), suggesting that individual females and males may spawn repeatedly during each reproductive period.

It is not generally known whether groupers spawn continually during the spawning period or at regular intervals, each lasting only a few days. Individuals of various grouper species aggregate at what seem to be traditional sites and spawn intensively for 1-2 weeks (Shapiro 1987). Spawning aggregations have been reported for *E. striatus* in the Bahamas, in the Virgin Islands, in Puerto Rico, in Honduras and Cayman Islands; for *E. guttatus* in the Virgin Islands and in Puerto Rico; for *E. merra* in Tahiti (Randall and Brock 1960; Smith 1972; Olsen and Laplace 1979; Colin et al. 1987; Fine 1990; Tucker et al. 1991). Aggregations of *E. striatus* were observed around the full moon during two of the months between November and February in the Virgin Islands, in January in Puerto Rico, and from late December to March in the Cayman Islands (Olsen and Laplace 1979; Colin et al. 1987; Tucker et al. 1991). In Tahiti, *E. merra* was found to spawn over a period of 3-4 days once each a month from January to April. The peak of

spawning occurred 2-3 days before full moon (Randall and Brock 1960). To date, periodicity of spawning, spawning aggregations and relationship of migration and spawning to the full moon remain undescribed for *E. morio*. In our study, the final egg stage (hyaline oocyte) was only observed in ovaries of individuals caught after and near the time of full moon (8 days after full moon in January 1990 and 2-3 days after full moon in March 1992). During winter, González et al. (1974a), Zupanovic and González (1975) and Valdés and Padrón (1980) reported movement of red groupers from west to east on Campeche Bank and stated that the eastern part of this area could be a site of reproduction for *E. morio*. But one of our collections from the western part of Campeche Bank (20°N ; 91°W) in March 1992, showed that 11 of the 19 females caught in this area had ripe ovaries (stage VI oocyte). These observations suggest that red groupers spawn on various grounds distributed all over the Bank.

According to Shapiro (1987), one of the several difficulties with defining the time of sex change from the occurrence of transitionals in monthly samples is the relatively small number of transitional gonads that are generally found. One reason for finding small numbers of transitionals is that

sex change may be completed rapidly. Moe (1969) examined 790 sets of gonads and found 11 transitional gonads (1.4%). This author reported that sexual transition took place during the months of active sexual development and also during the resting period of the species. In our study, of the 877 gonads histologically examined, only 16 were transitional gonads (1.8%). Transitional red groupers were found during eight months of the year, including the three months of peak spawning. Transforming individuals generally fall within the overlap zone between sizes of females and males (Shapiro 1989). The overlapping of the sexes observed for *E. morio* on Campeche Bank indicated that sex change can take place over a broad range of sizes (from 39.5 to 84.5 cm FL).

Parrish (1987) pointed that various studies have shown that the dominant food for groupers are fish and decapod crustaceans. Results obtained in this work on food habits of juvenile red grouper agreed with those reported by Randall (1967), Moe (1969) and Valdés and Padrón (1980). The majority of the prey organisms taken were reef-associated, indicating that most of the feeding was done over reefs. Algae found in red grouper stomach contents were probably taken incidentally and not utilized as food. Fishes that feed on benthic invertebrates from rocky bottom frequently ingest algae along with their prey (Hobson 1968).

The diet of juvenile red grouper did not substantially change with increasing predator size. Over the size range examined, crustaceans were always the chief items in the diet of *E. morio*. Parrish (1987) reported that, independent of the size of the groupers, the spectrum of major food items remains essentially the same. This study showed also that primary prey items in red groupers were comparable over most of Campeche Bank. Crustaceans were the most important food and of these, true crabs (*Brachyura*:

Reptantia) were found at all four sampling sites (Brûlé and Rodríguez Canché 1993). Randall (1967) reported that stomachs of two Caribbean red groupers contained 33.3% crabs, 50% unidentified crustaceans and 16.7% fishes. *E. morio*, like other commercially and recreationally important grouper species, occupies a role of top predator in marine food webs and can be characterized as a generalized opportunistic carnivore.

Acknowledgements

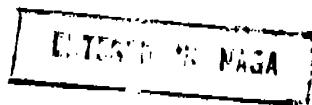
This study was supported by Grant No. CII* 0432.ME(JR) from the European Commission, and by Grant No. P 65000 ME from the Science and Technology Council of the French Embassy (CST) and the Foreign Office of France (DCST). We are grateful to Mrs. A.M. Pech de Quezada (Congeladora Pascual, Progreso) for providing the red groupers for this study.

References

- Arreguín-Sánchez, F. 1987. Present status of the red grouper fishery of the Campeche Bank. Proc. Gulf Carib. Fish. Inst. 37:498-509.
- Arreguín-Sánchez, F., M.A. Cabrera and G. Mexicano. 1987a. Dinámica de la pesquería de mero (*Epinephelus morio*) del Banco de Campeche, p. 81-87. In M. Ramírez Rodríguez (ed.) Memorias del simposium sobre investigación en biología y oceanografía pesquera en México. Consejo Nacional de Ciencia y Tecnología-Instituto Politécnico Nacional, México.
- Arreguín-Sánchez, F., J.C. Seijo Gutiérrez, D. Fuentes Castellanos and M.J. Solís Ramírez. 1987b. Estado del conocimiento de los recursos pesqueros de la plataforma continental de Yucatán y región adyacente. Contr. Inv. Pesq. CRIP-Yucalpetén-IPN, SEPESCA Doc.Tec. 4, 41 p.
- Back, W. and B.B. Hanshaw. 1978. Hydrogeochemistry of the northern Yucatan Peninsula, Mexico with a section on Mayan

- water practices, p. 229-261. In W.C. Ward and A.E. Weidie (eds.) Geology and hydrogeology of northeastern Yucatan. New Orleans Geological Society, New Orleans.
- Brulé, T. and L.G. Rodríguez Cánchez. 1993. Food habits of juvenile red groupers, *Epinephelus morio* (Valenciennes, 1828), from Campeche Bank, Yucatan, Mexico. Bull. Mar. Sci. 52:772-779.
- Brulé, T., T. Maldonado Montiel, L.G. Rodríguez Cánchez and G. Mexicano Cíntora. Aspectos sobre la biología reproductiva y trófica del mero *Epinephelus morio* del banco de Campeche, Yucatán, México. Proc. Gulf Caribb. Fish. Inst. 44. (In press).
- Carranza, J. 1957. Marine fisheries of the Yucatan Peninsula, Mexico. Proc. Gulf Caribb. Fish. Inst. 9:145-150.
- Coleman, R.M. 1991. Measuring parental investment in nonspherical eggs. Copeia 4:1092-1098.
- Colin, P.L., D.Y. Shapiro and D. Weiler. 1987. Aspects of the reproduction of two groupers, *Epinephelus guttatus* and *E. striatus* in the West Indies. Bull. Mar. Sci. 40(2):220-230.
- Fine, J.C. 1990. Groupers in love: spawning aggregations of Nassau groupers in Honduras. Explorer J. (Fall 1990):130-134.
- Gabe, M. 1968. Techniques histologiques. Masson, Paris. 1113 p.
- González, P.D., S. Zupanovic and H.E. Ramis. 1974a. Biología pesquera de la cherna americana del banco de Campeche. INP/CIP (Cuba) Res. Invest. 1:107-111.
- González, P.D., S. Zupanovic and H.E. Ramis. 1974b. Evaluación de los niveles de explotación de la cherna americana en el banco de Campeche. INP/CIP (Cuba); Res. Invest. 1:172-175.
- Hobson, E.S. 1968. Predatory behavior of some shore fishes in the Gulf of California. Res. Rep. U.S. Bur. Sport Fish Wildl. 73:92 p.
- Hyslop, E.J. 1980. Stomach contents analysis - a review of methods and their application. J. Fish Biol. 17:411-429.
- Klima, E.F. 1976. An assessment of the fish stocks and fisheries of the Campeche Bank. WECAF Stud. 5:24 p.
- Le Bail, J. 1984. Pêche et développement de la péninsule de Yucatan. Bull. Assoc. Géogr. Franç. (Paris) 503:183-192.
- Manooch, C.S. 1987. Age and growth of snappers and groupers, p. 329-373. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Moe, M.A. 1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Prof. Pap. Ser. Fla. Dep. Nat. Resour. Mar. Res. Lab. 10, 95 p.
- Olsen, D.A. and J.A. LaPlace. 1979. A study of a Virgin Islands grouper fishery based on a breeding aggregation. Proc. Gulf Caribb. Fish. Inst. 31:130-144.
- Parrish, J.D. 1987. The trophic biology of snappers and groupers, p. 405-463. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Randall, J.E. 1967. Food habits of reef fishes of the West Indies. Stud. Trop. Oceanogr. 5:665-847.
- Randall, J.E. 1983. Caribbean reef fishes. Second Edition, Revised. T.F.H. Publications, Neptune City. 350 p.
- Randall, J.E. and V.E. Brock. 1960. Observations on the ecology of Epinepheline and lutjanid fishes of the Society Islands, with emphasis on food habits. Am. Fish. Soc. Publ. 89:9-16.
- Rihani Vales, C., R. Torres Lara, J. Peraza Menendez, I. Mendoza Rodríguez and F. Dominguez Rivas. 1989. Información basica de la actividad pesquera en Yucatán, 1988. Departamento de Desarrollo Pesquero del Gobierno del Estado de Yucatán, Delegación Federal de Pesca. 59 p.
- Rivas, L.R. 1968. Fisherman's atlas of monthly sea surface temperatures for the Gulf of Mexico. U.S. Fish Wildl. Serv. Circ. 300, 33 p.
- Sadovy, Y. 1994. Grouper stocks of the Western Central Atlantic: the need for management and management needs. Proc. Gulf Caribb. Fish. Inst. 43:43-64.
- Schoenerer, T.W. 1970. Nonsynchronous spatial overlap of lizards in patchy habitats. Ecology 51:408-418.
- Sevilla, M.L. 1987. Biología pesquera. CECSA, México. 100 p.
- Shapiro, D.Y. 1987. Reproduction in groupers, p. 295-327. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers:

- biology and fisheries management. Westview Press, Boulder.
- Shapiro, D.Y. 1989. Sex reversal and sociodemographic processes in coral reef fishes, p. 103-118. In G.W. Potts and R.J. Wootton (eds.) Fish reproduction: strategies and tactics. Academic Press, London.
- Smith, C.L. 1971. A revision of the American groupers; *Epinephelus* and allied genera. Bull. Am. Mus. Nat. Hist. 146:67-242.
- Smith, C.L. 1972. A spawning aggregation of Nassau grouper, *Epinephelus striatus* (Bloch). Trans. Am. Fish. Soc. 2:257-261.
- Solis Ramírez, M. 1970. The red grouper fishery of Yucatan peninsula, Mexico. Proc. Gulf Carib. Fish. Inst. 22:122-129.
- Stevenson, D.K. 1981. A review of the marine resources of the Western Central Atlantic Fisheries Commission (WECAFC) region. FAO Fish. Tech. Pap. 211, 132 p.
- Tashiro J.E. and S.E. Coleman. 1977. The Cuban grouper and snapper fishery in the Gulf of Mexico. Mar. Fish. Rev. 39(10):1-6.
- Tortonese, E. 1986. Serranidae, p. 780-792. In P.J.P. Whitehead, M.L. Bauchot, J.C. Hureau, J. Nielsen and E. Tortonese (eds.) Fishes of the North-eastern Atlantic and the Mediterranean. Volume II. UNESCO, Paris.
- Tucker, J.W., J.E. Parsons, G.C. Ebanks and P.G. Bush. 1991. Induced spawning of Nassau grouper *Epinephelus striatus*. J. World Aquacult. Soc. 22(3):187-191.
- Valdés, E. and G. Padrón. 1980. Pesquerías de palangre. Rev. Cub. Inv. Pesq. 5:38-52.
- Wallace, R.K. 1981. An assessment of diet overlap indexes. Trans. Am. Fish. Soc. 110:72-76.
- Weidie A.E., W.C. Ward and R.H. Marshall. 1978. Geology of Yucatan platform, p. 3-29. In W.C. Ward and A.E. Weidie (eds.) Geology and hydrogeology of northeastern Yucatan. New Orleans Geological Society, New Orleans.
- Zaret, T.M. and A.S. Rand. 1971. Competition in tropical stream fishes: support for the competitive exclusion principle. Ecology 52:336-342.
- Zupanovic, S. and P. González. 1975. Investigación y pesquería de la cherna en el banco de Campeche. Mar. Pesca Cuba. 112:22-27.



APR 14 1998

Seasonal Patterns of Distribution and Abundance of Snappers in the Mexican Caribbean

S. DÍAZ-RUÍZ^a
A. AGUIRRE-LEÓN^b
C. MACUITL^a
O. PÉREZ^a

^aDepto. de Hidrobiología
UAM-I Ap. Postal 55-535, México 09340, D.F.

^bDepto. El Hombre y su Ambiente
UAM-X Ap. Postal 23-181, México 04960, D.F.

DÍAZ-RUÍZ, S., A. AGUIRRE-LEÓN, C. MACUITL and O. PÉREZ. 1996. Seasonal patterns of distribution and abundance of snappers in the Mexican Caribbean [Patrones estacionales de distribución y abundancia de los pargos del Caribe Mexicano], p. 43-50. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

A total of 1 022 snappers of eight species were collected in the Cozumel reefs, Quintana Roo (Mexico), between 1988 and 1991. The species are *Lutjanus analis*, *L. apodus*, *L. cyanopterus*, *L. griseus*, *L. jocu*, *L. mahogani*, *L. synagris* and *Ocyurus chrysurus*. The biology and population ecology of the snappers are controlled by the seasons and reef habitat. Seasonal variations in density (0.02-0.13 individuals·m⁻²), biomass (1.26-15.1 g·m⁻²) and average weight (58.7-128.4 g) are related to the population structure through the life histories and the environmental seasonal changes of the system.

L. apodus, *L. griseus*, *L. jocu* and *O. chrysurus* have wide distributions and high abundances. These species are typical inhabitants of the reef community, contributing 71% of weight and 85% of individual numbers. Biomass peaked during the rainy season. The juveniles and preadults undertook regular migrations from the barrier reef to the protected seagrass (*Thalassia testudinum*) areas for feeding, while the adults migrated to the barrier reefs for reproduction. More ecological studies of these potentially important fishery resources are necessary in the Mexican Caribbean region.

Resumen

Un total de 1 022 peces de ocho especies de pargos fueron colectados en los arrecifes de Cozumel, Quintana Roo (Mexico), entre 1988 y 1991. Estos pargos fueron: *Lutjanus analis*, *L. apodus*, *L. cyanopterus*, *L. griseus*, *L. jocu*, *L. mahogani*, *L. synagris* y *Ocyurus chrysurus*. La ecología y biología de los pargos están controladas por las estaciones climáticas y el hábitat arrecifal. Las variaciones estacionales en densidad (0.02-0.13 ind·m⁻²), biomasa (1.26-15.1 g·m⁻²) y peso promedio (58.7-128.4 g) están asociadas a la estructura de la población a través de los ciclos de vida y el comportamiento ambiental del sistema a lo largo del año.

L. apodus, *L. griseus*, *L. jocu* y *O. chrysurus* mostraron amplia distribución y alta abundancia. Estas especies son habitantes típicos de la comunidad de arrecife con 71% del peso y 85% del número de individuos. La mayor biomasa (49%) de las poblaciones de pargos fueron encontradas durante la estación de lluvias. Los juveniles y pre-adultos realizan migraciones regulares de los arrecifes de barrera a las áreas protegidas de *Thalassia testudinum* para alimentación, mientras que los adultos migran a la barrera arrecifal para reproducción. Por la importancia de estos recursos pesqueros potenciales se requieren más estudios ecológicos en la región del Caribe Mexicano.

Introduction

The coastal region of Quintana Roo in the Mexican Caribbean is of high value for its fishery potential and is located in a zone of intense recreational activity.

Coral reef ecosystems are areas that support a great biotic diversity, with a high potential for fishery resources such as gastropods, lobsters and fishes. Several fisheries depend on these systems and their habitats and resources are therefore important. The fishes play a significant role in the energy balance of these ecosystems (Ogden and Gladfelter 1983; Shulman et al. 1983; Meyer and Shultz 1985; Lewis 1986; Munro 1987; Sano 1991; Díaz-Ruiz and Aguirre-León 1991, 1993).

Species of snappers, Lutjanidae, play an ecologically important role in the coral reef ecosystem. Studies in the Caribbean have shown that the lutjanids belong to the ten most important families in the fisheries of the region (Munro 1983; Bannerot et al. 1987; Brusher and Palko 1987; Polovina and Ralston 1987; Basurto-Origel 1988; Smith 1988; Dennis 1991). Owing to their economic value, systematic studies are needed on their taxonomy, biology and ecology to evaluate and manage these resources (see Chapman et al.; Gomez et al.; Rivera-Arriaga et al., this vol.). The principal objective of this work was to establish the patterns of distribution and abundance of the snapper species and their relationship to temporal and spatial changes of environmental parameters in the Cozumel coral reef system (see Cuellar et al., this vol.).

Study Area

The Cozumel reef system is located in the Mexican Caribbean ($20^{\circ}28'N$; $87^{\circ}01'W$) (Fig. 1), covering approximately $3\ 200\ km^2$, including barrier reef and seagrass beds, with an average depth ranging from 2 to

15 m. The reef area consists of three habitats: a) Seagrass beds along the coastline; b) the barrier reef characterized by coralline formations; and c) a lagoon between these two habitats.

The seagrass (typically *Thalassia testudinum*) area is a shallow habitat with a mean depth of 1.2 m with strong tidal current. Salinity ranges from 32 ppt (June) to 34.9 ppt (May) and temperature from $26.8^{\circ}C$ (November) to $31.2^{\circ}C$ (May). The barrier reef has an average depth of 15 m on the inner side, with strong south-north currents and persistent winds from the southeast. The salinity varies from 32 ppt (July) to 34.9 ppt (May) and the temperature from $28^{\circ}C$ (February) to $29.3^{\circ}C$ (June). The coral reef communities include *Agaricia agaricites*, *Acropora palmata*, *A. cervicornis*, *Madracis decactis*, *Leptoseris cucullata*, *Diploria strigosa*, *Porites porites*, *Dendrogira cylindrus* and *Millepora alcicornis*.

The lagoon is characterized by isolated coral patches composed of the species previously cited. Salinity ranges from 32.5 ppt (March) to 33.3 ppt (November) and temperature from $25.2^{\circ}C$ (January) to $28.9^{\circ}C$ (May).

The Cozumel reef system experiences three climatic seasons related to the rainfall, frequency of winds and environmental temperature. These are the dry season (February to May), the rainy season (June to September) and the winter storm season ("Nortes") (October to February). Detailed descriptions of the ecosystem are given in García (1987), Jordán (1988), Fenner (1988) and Díaz-Ruiz et al. (1993).

Methods

The fish catches were made in depths of 2-15 m using different fishing methods. In seagrass beds, samples were taken with a beach seine [*chinchorro*], 50 m in length, with mesh of 19 mm (3/4") in the bag and 38 mm (1.5") in the wings. In the lagoon

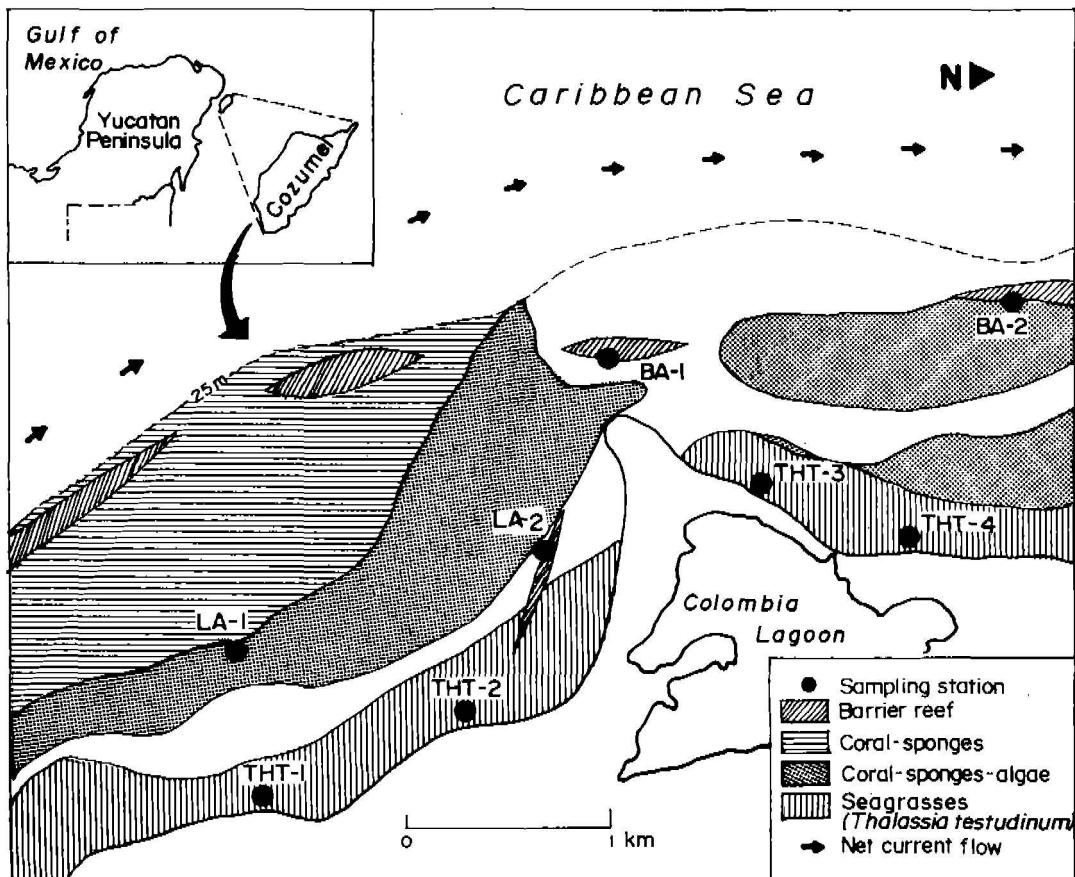


Fig. 1. Cozumel coral reef system, showing the distribution of the sampling stations, the main habitats of the reef system and the main physiographic and bathymetric characteristics in the area. (BA, barrier reef; LA, lagoon; and THT, seagrass beds). [Sistema arrecifal de Cozumel mostrando la distribución de las estaciones de muestreo, así como los principales hábitats del sistema arrecifal. También se muestran las principales características fisiográficas y batimétricas. BA, barrera arrecifal; LA, laguna; y THT, praderas de pastos marinos.]

and in the back reef area samples were taken by free diving using harpoons, and by traps. Additionally, visual census transects were made in the lagoon and back reef at four sampling stations, each 100 m in length, and 4 m wide. The technique is a modification of the visual method of Sale and Sharp (1983). Two observers annotated plastic tables with the numbers of the identified fishes on the transects. Each diver counted the fishes in the 2-m wide strip on each side of the transect. The two counts were added to obtain a total. The 100 m transect was completed in an average time of 30 minutes.

During each collection, salinity, temperature, dissolved oxygen, depth and transparency of the water column were measured. Observations of submerged vegetation, benthic macrofauna and meteorological conditions were also noted.

In the laboratory, fish were identified, counted, weighed and measured. The abundance of fishes was expressed as biomass ($\text{g wet weight} \cdot \text{m}^{-2}$) and density ($\text{number of individuals} \cdot \text{m}^{-2}$). Dominant fish populations were identified on the basis of frequency (percentage of occurrence), weight, numerical abundance and broad distribution in the system.

Results and Discussion

Forty-three fish families were identified in the samples taken between 1988 and 1991 in the Cozumel reef system, and the lutjanids were the fourth most important family by number, density and biomass.

This family group includes eight species: *Lutjanus analis*, *L. apodus*, *L. cyanopterus*, *L. griseus*, *L. jocu*, *L. mahogani*, *L. synagris* and *Ocyurus chrysurus*, jointly representing more than 71% by number and by weight, of the total catch.

Distribution and habitat

Lutjanus apodus, *L. jocu*, *L. griseus*, *L. mahogani*, *L. synagris* and *O. chrysurus* have wide distributions in the system. Some of these species (*L. apodus*, *L. jocu*, *L. griseus* and *O. chrysurus*) reproduce on the barrier reef among mixed colonies of corals in depths of 15 m. Juveniles of these species are found in shallow waters on seagrass beds between 1.0 and 1.7 m. Other species, such as *L. mahogani* and *L. synagris*, utilize the habitats as feeding areas. Species with restricted distributions (*L. analis* and *L. cyanopterus*) are found mainly in the lagoon and seagrass beds.

Abundance

In general, the greatest abundance of lutjanids is on the barrier reef. Biomass, density and average weight are high on the reef during the rainy season whereas biomass and density are high in the seagrass habitat during the dry season. The greatest biomass ($26.3 \text{ g} \cdot \text{m}^{-2}$) was found on the reef during the rainy season and the lowest ($1.59 \text{ g} \cdot \text{m}^{-2}$) in the seagrass beds during the dry season. The highest densities ($0.19 \text{ individuals} \cdot \text{m}^{-2}$) were found on the reef during the dry season and the least

($0.005 \text{ individuals} \cdot \text{m}^{-2}$) on the seagrass beds during the "Nortes" season. These values suggest that the snappers are represented by larger individuals on the reef during the rainy season and by a few juveniles on the seagrass beds during the dry season. Fig. 2 summarizes our observations of density, biomass and mean weight in four key species.

All species have pronounced seasonal variations in biomass and density through the year. This is a consequence of seasonal patterns of utilization in which the snappers optimize their use of food availability, environmental conditions and the structural characteristics of the habitats. This behavior has been observed in other species of snappers in tropical ecosystems by Acero and Garzon 1985; Berrios et al. 1985; Alvarez-Guillén et al. 1986; Leis 1987; Díaz-Ruiz and Aguirre-León 1993.

Fig. 3 shows selected examples of utilization patterns in the coral reef system by lutjanids. In *O. chrysurus*, immature individuals of small sizes are found in the lagoon and in the seagrass beds in March to April. The preadults migrate through the lagoon towards the barrier during the rainy season.

Similar behavior is observed in *L. griseus*, in which the seagrasses represent an important habitat for feeding of juveniles and for the adults during the "Nortes" season. At the end of the "Nortes" and beginning of the dry season, preadults are recruited to the lagoon to feed, mature and later migrate toward the reef.

In contrast, juvenile *L. analis* migrate to the lagoon as preadult to grow, mature and spawn in this area during the rainy season. Adults have been collected in great abundance during July (Díaz-Ruiz et al. 1993).

Similar patterns observed by different authors show that, as in many species of fishes, juvenile lutjanids carry out wide migrations from the areas of reproduction toward the areas of seagrasses, with diurnal and/or seasonal movements related to

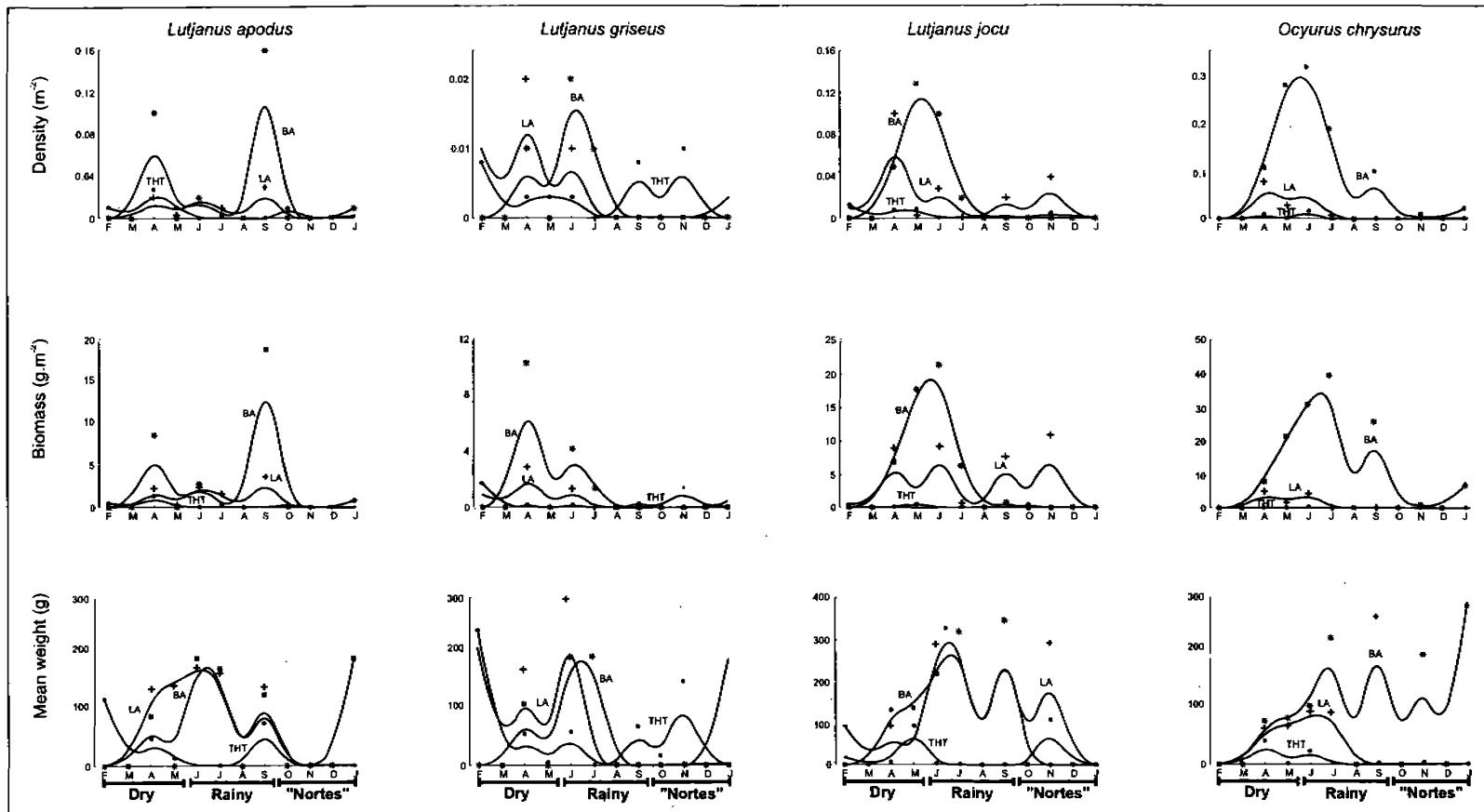


Fig. 2. Seasonal abundance patterns of *Lutjanus apodus*, *L. griseus*, *L. jocu* and *Ocyurus chrysurus* in the Cozumel coral reef system: density ($\text{Ind.} \cdot \text{m}^{-2}$), biomass ($\text{g} \cdot \text{m}^{-2}$) and mean weight of the population ($\text{g}/\text{ind.}$). [Patrones estacionales de la abundancia de *Lutjanus apodus*, *L. griseus*, *L. jocu* y *Ocyurus chrysurus* en el sistema arrecifal de Cozumel: densidad ($\text{Ind.} \cdot \text{m}^{-2}$), biomasa ($\text{g} \cdot \text{m}^{-2}$) y peso promedio de la población ($\text{g}/\text{ind.}$).]

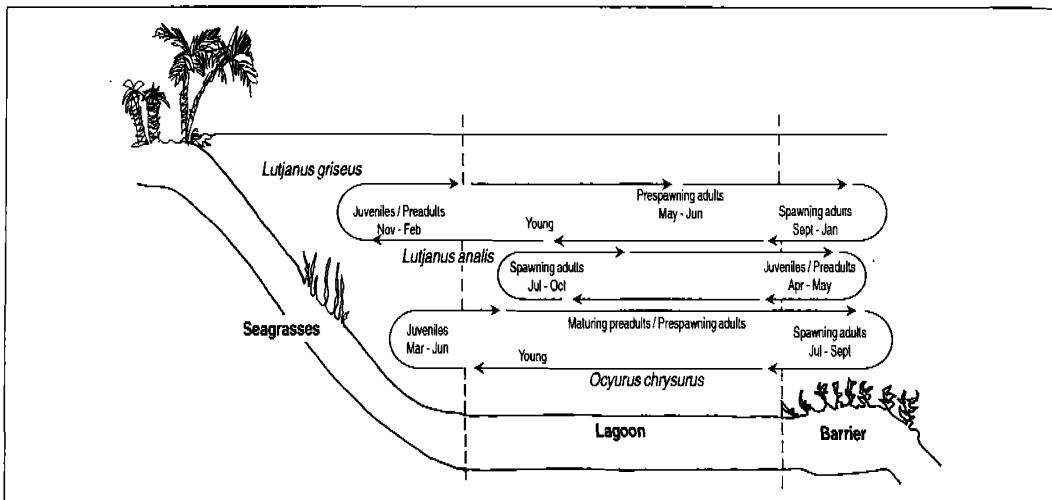


Fig. 3. Life cycles of three species of snappers based on their abundance and biomass in different areas of a reef system. [Ciclos de vida de tres especies de pargo basado en su abundancia y biomasa en diferentes áreas del sistema arrecifal.]

the search for food (Parrish and Zimmerman 1977; Luckhurst and Luckhurst 1978; Munro 1983; Ogden and Gladfelter 1983; Sale and Sharp 1983; Victor 1983; Williams and Hatcher 1983; Ogden and Quinn 1984; Acero and Garzon 1985; Berrios et al. 1985; Shulman 1985; Leis 1987; Sale 1988; Heck and Weinstein 1989; Sale and Steel 1989; Díaz-Ruiz and Aguirre-León 1991, 1993).

Acknowledgements

This research was supported by grants from the Universidad Autónoma Metropolitana-Iztapalapa through the Departamento de Hidrobiología (CBS/UAM-I). It was also supported by grants from the Dirección General de Investigación Científica y Superación Académica (DGICSA-SEP) through the project UAM-I /DGICSA "Ecología de los Recursos Ictiológicos del Arrecife Palancar en el Caribe Mexicano" C90-01-0287 /C91-09-00239.

References

- Alvarez-Guillén, H., M.C. García-Abad, M. Tapia, G.J. Villalobos and A. Yañez-Arancibia. 1986. Prospección ictiológica en la zona de pastos marinos de la laguna arrecifal de Puerto Morelos, Q. R. (verano 1984). An. Inst. Cienc. Mar Limnol. UNAM 13 (3):317-336.
- Acero, A. and J. Garzon. 1985. Los pargos (Pisces: Perciformes: Lutjanidae) del Caribe Colombiano. Actual. Biol. 14(53):89-99.
- Bannerot, S., W.W. Fox, Jr. and J.E. Powers. 1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and Caribbean, p. 561-603. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Basurto-Origel, M. 1988. Actual state of the demersal fish fishery of the north zone of Quintana Roo, Mexico, p. 479-496. In Secretaría de Pesca (ed.) Los Recursos Pesqueros del País. Inst. Nal. Pesca Press, Mexico.

- Berrios, J., J.K. Gonzalez and I. Díaz. 1985. Fish population studies of the seagrass beds and coral reefs of Cayo Berberia and Cayo Ratones, Ponce, P.R. Puerto Rico Sport Fish. Res. Survey, 57 p.
- Brusher, H.A. and B.J. Palko. 1987. Results from the 1984 and 1985 charterboat surveys in southeastern U.S. waters and the U.S. Caribbean Sea. Mar. Fish. Rev. 49(2):109-117.
- Dennis, G.D. 1991. The validity of length-frequency derived growth parameters from commercial catch data and their application to stock assessment of the yellowtail snapper (*Ocyurus chrysurus*). Proc. Gulf Carib. Fish. Inst. 40:126-138.
- Díaz-Ruiz, S. and A. Aguirre-León. 1991. Fish assemblages and patterns of fish habitat utilization from the Cozumel coral reef system, Mexican Caribbean. Bull. Zool. Mus. Univ. Amst., 98 p.
- Díaz-Ruiz, S. and A. Aguirre-León. 1993. Diversidad e ictiofauna de los arrecifes del sur de Cozumel, Quintana Roo, p. 817-832. In S.I. Salazar and N.E. González (eds.) Biodiversidad Marina y Costera de México. Com. Natl. Biodiversidad/CIQRO, México.
- Díaz-Ruiz, S., C. Macuitl, A. Aguirre-León, E. Núñez, J.R. Ramos and J. Chávez, 1993. Ecología de los peces arrecifales coralinos del Caribe Mexicano: Un perfil de comunidad. Informe Final, Proyecto de Investigación: Ecología y recursos Ictiológicos del Arrecife Palancar en el Caribe Mexicano (C91-09-00239) Convenio UAM-I/DGICSA, 85 p.
- Fenner, D.P. 1988. Some leeward reefs and corals of Cozumel, Mexico. Bull. Mar. Sci. 42(1):133-144.
- García, E. 1987. Modificación al sistema de clasificación climática de Köppen. Inst. Geogr. Univ. Nal. Autón, México. 346 p.
- Heck, K.L. and M.P. Weinstein. 1989. Feeding habits of juvenile reef fishes associated with Panamanian seagrass meadows. Bull. Mar. Sci. 45(3):629-636.
- Jordán, D.E. 1988. Arrecifes profundos en la Isla Cozumel, México. An. Cienc. Mar Limnol. Univ. Autón, México 15(2):195-208.
- Leis, J. M. 1987. Review of the early life history of tropical groupers (Serranidae) and snappers (Lutjanidae), p. 189-237. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Lewis, S.M. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. Ecol. Monogr. 56(3):183-200.
- Luckhurst, B.E. and K. Luckhurst. 1978. Diurnal space utilization in coral reef fish communities. Mar. Biol. 49:325-332.
- Meyer, J.L. and E.T. Shultz. 1985. Migrating haemulid fishes as a source of nutrients and organic matter on coral reefs. Limnol. Oceanogr. 30(1):146-156.
- Munro, J.L., Editor. 1983. Caribbean coral reef fishery resources. ICLARM Stud. Rev. 7, 276 p.
- Munro, J.L. 1987. Workshop synthesis and directions for future research, p. 639-659. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Ogden, J.C. and E.H. Gladfelter. 1983. Coral reef, seagrass beds and mangroves: their interaction in the coast zones of the Caribbean. UNESCO Rep. Mar. Sci. (23):1-133.
- Ogden, J.C. and T.P. Quinn. 1984. Migration in coral reef fishes: ecological significance and orientation mechanisms, p. 293-308. In J.D. McCleave, G.P. Arnold, J.J. Dodson and W.H. Neill (eds.) Mechanisms of migration in fishes. Plenum Press, New York.
- Parrish, J.D. and R.J. Zimmerman. 1977. Utilization by fishes of space and food resources on an offshore Puerto Rican coral reef and its surroundings. Proc. 3rd Int. Coral Reef Symp. 3:297-303.
- Polovina, J.J. and S. Ralston, Editors. 1987. Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder. 659 p.
- Sale, P.F. 1988. Perception, pattern, chance and the structure of the reef fishes communities. Env. Biol. Fish. 21:3-15.
- Sale, P.F. and B.I. Sharp. 1983. Correction for bias in visual transect censuses of coral reef fishes. Coral Reefs 2:37-42.
- Sale, P.F. and W.J. Steel. 1989. Temporal variability in patterns of association among fish species on coral patch reefs. Mar. Ecol. Prog. Ser. 51:35-47.
- Sano, M. 1991. Patterns of habitat and food utilization in two coral-reef sandperches

- (Mugiloididae): competitive or non-competitive coexistence? *J. Exp. Mar. Biol. Ecol.* 140:209-223.
- Shulman, M.J. 1985. Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* 66: 1056-1066.
- Shulman, M.J., J.C. Ogden, J.P. Ebersole, W.N. McFarland, S.L. Miller and N.G. Wolf. 1983. Priority effects in the recruitment of juvenile coral reef fishes. *Ecology* 64:1508-1513.
- Smith, G.B. 1988. Abundance and potential yield of groupers (Serranidae), snappers (Lutjanidae) and grunts (Haemulidae) on the Little and Great Bahama Banks. WCAFC Nat. Rep. COPACO 376:84-105.
- Victor, B.C. 1983. Recruitment and population dynamics of a coral reef fish. *Science* 219:419-420.
- Williams, D.M. and A.I. Hatcher. 1983. Structure of fish communities on the outer slopes of inshore, mid-shelf and outer-shelf reefs of the Great Barrier Reef. *Mar. Ecol. Prog. Ser.* 10:239-250.

ENTERED IN NAGA

APR 14 1998

Biological Aspects of the Yellow Eye Snapper (*Lutjanus vivanus*) (Pisces: Lutjanidae) from the Los Hermanos Islands, Eastern Venezuela

G.J. GÓMEZ
R.A. GUZMÁN
L.A. MARCANO

FONAIAP, Centro Invest. Agrop. Pesq. Sucre
P. O. Box. 236, Cuman 6101, Venezuela

GÓMEZ, G.J., R.A. GUZMÁN and L.A. MARCANO. 1996. Biological aspects of the yellow eye snapper (*Lutjanus vivanus*) (Pisces: Lutjanidae) from Los Hermanos Islands, Eastern Venezuela [Aspectos biológicos del "pargo ojo amarillo" (*Lutjanus vivanus*) (Pisces: Lutjanidae), de las Islas Los Hermanos, Este de Venezuela], p. 51-58. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Biometric and reproductive aspects of the yellow eye snapper, *Lutjanus vivanus*, a species of great commercial interest to the artisanal fishers of the eastern region of Venezuela, are analyzed. A total of 592 fish were captured with Antillean fish traps between January and December 1992, in the vicinity of the Los Hermanos Islands, near Margarita Island, eastern Venezuela. Size structure showed that the most frequent group was 350-510 mm, followed by the groups 250-330 mm and 530-790 mm. The length-weight relationship did not show a significant difference between males and females ($p>0.05$), thus a common equation was estimated ($W = 1 \times 10^{-5} \times TL^{3.0218}$). The estimated sex ratio from the sample was 1.03:1 ($p>0.05$). Mean length at first maturity for males and females was estimated at 565 and 540 mm, respectively. Reproductive activity was more intense during May and June, and August to November.

Resumen

Se analizan aspectos biométricos y reproductivos del "pargo ojo amarillo" *Lutjanus vivanus*, una especie de gran interés comercial para pescadores artesanales de la región oriental de Venezuela. Un total de 592 peces fueron capturados con trampas para peces tipo Antillano entre Enero y Diciembre de 1992, en los alrededores de las Islas Los Hermanos, cerca de Isla Margarita, al este de Venezuela. La estructura por tamaños mostró que los grupos más frecuentes estuvieron comprendidos entre los 350 y 510 mm, seguidos por los grupos de 250 a 330 mm, y 530 a 790 mm. La relación peso - longitud no mostró diferencia significativa entre machos y hembras ($p>0.05$), por lo cual una ecuación para ambos性es fue estimada ($W = 1 \times 10^{-5} \times TL^{3.0218}$). La proporción de sexos en la muestra fue de 1.03:1 ($p>0.05$). La longitud media de primera madurez para machos y hembras fue estimada en 565 mm y 540 mm, respectivamente. La actividad reproductiva fue más intensa durante Mayo y Junio, y Agosto a Noviembre.

Introduction

The yellow eye snapper (*Lutjanus vivanus*) occurs over hard bottom (rocky, gravel, coralline or sandy), at depths between 90 and 170 m, from North Carolina and Bermuda, to the southern Amazon river delta in Brazil, and is particularly abundant near the Antilles and Bahamas. In Venezuela it has been reported for the southwest and southeast of Los Hermanos Island (Cervigón 1966; Fisher 1978; Gómez et al. 1992).

L. vivanus is one of the most important species of the genus *Lutjanus* exploited by the Venezuelan offshore fishery and distant water fishery (off Surinam and French Guiana) (see Cuellar et al., this vol.). However, there are no studies on the biology and fishery of this species in Venezuela.

This study was undertaken in order to evaluate some important biological aspects of the species (biometry and reproduction), which may provide a basis for the future management of the fishery.

Materials and Methods

The Los Hermanos Islands are located to the northeast of Margarita Island (11°40' N; 64°23' W; Fig. 1). The area is characterized by hard bottom, either rocky, coralline or sandy, which makes it an ideal habitat for fish of the families Lutjanidae and Serranidae (Gines 1972).

Samples were obtained using Antillean traps during exploratory fishing trips on board FONAIAP's *R/V Golfo de Cariaco*. Twelve trips of 8 days were executed during 1992. Twenty traps were placed at a depth of 20-70 fathoms, and baited with fresh sardine. The traps were baited every 24 hours between 0500 and 0600 hours, after removing the fish caught, for a period of five days.

Samples were kept iced during the trip and were thawed and processed in Cumaná. Total length (TL) and weight of each fish

were estimated using an ichthyometer (1-mm accuracy) and a balance of 1-g accuracy, respectively. The gonads were removed through a ventral incision in each fish, weighed and kept iced for further studies.

Size distribution was assessed using frequency histograms with 20-mm TL intervals. Size/weight relationships were estimated for males, females and both sexes combined, using log-transformed values of TL and W, and least square regressions (Sokal and Rohlf 1981). The comparison between male and female relationships was performed using covariance analyses (Snedecor and Cochran 1971). The deviation of the slopes "b" from a value of 3.0 (which would imply that body weight increases as a cubic function of size), was estimated using a Student t-test (Sokal and Rohlf 1981).

Sex identification and sexual maturity were assessed by visual examination of the gonads' external morphology, size and color, according to Holden and Raith (1975). The estimation of the monthly proportion of fish with mature gonads served as an index of reproductive activity for the species under study. The deviation of the sex ratio from a 1:1 proportion was estimated through a chi-square test (Sokal and Rohlf 1981).

Size at maturity is defined as the smallest length at which 50% of the males or females sampled are reproductively active (stage IV). Size at maturity was estimated by plotting the relative cumulative frequency of mature fish against total length. The observed values were fitted to the logistic equation:

$$Y = 1/(1 + a \cdot e^{bx}) \quad ...1$$

linearized by the function $\log_e(a) + bx = \log_e(1-Y/Y)$. The constants "a" and "b" were estimated by regression analysis between the size classes and $\log_e(1-Y/Y)$, where Y is the relative cumulative frequency of each size class. Replacing the values of these

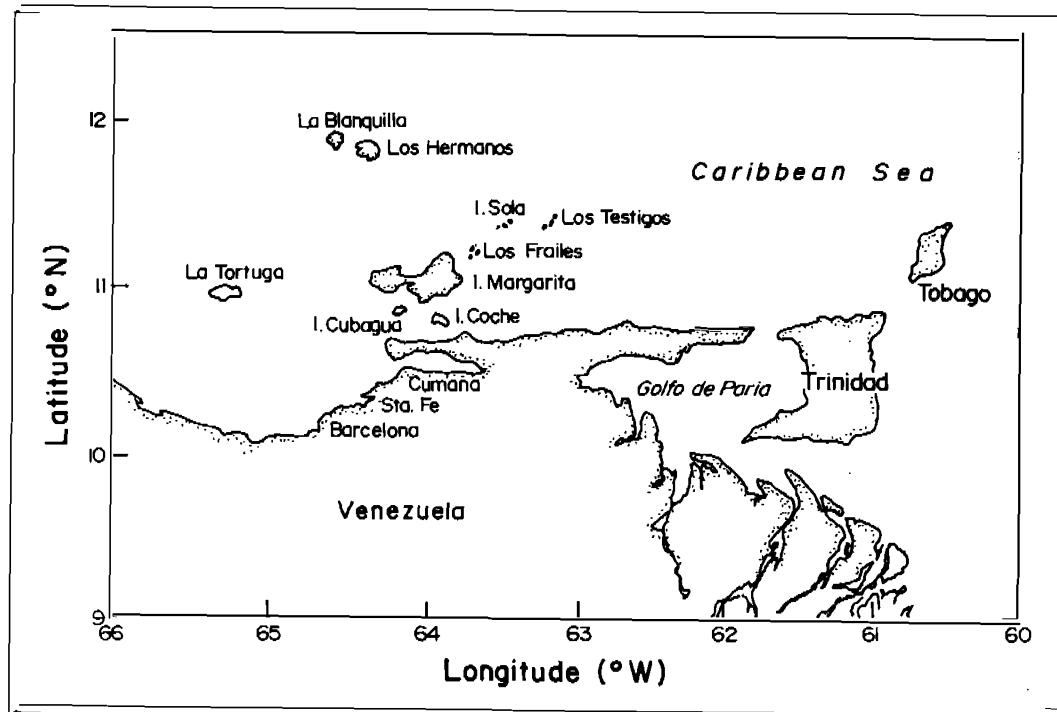


Fig. 1. Map showing the study area, the Los Hermanos Islands, eastern Venezuela. [Mapa mostrando el área de estudio, Islas Los Hermanos, Este de Venezuela.]

constants in equation (1) allowed the estimation of size at maturity of 50% of the population, according to the equation:

$$X_{0.5} = (-\log_e a)/b \quad ...2)$$

as suggested by Somerton (1980) and by Gaertner and Laloe (1986). The slopes and intercepts of the linearized logistic equation, by sex, were compared by covariance analysis (Snedecor and Cochran 1971).

Results

Biometry

Population Size Structure

A sample of 592 red eye snappers (*Lutjanus vivanus*) were obtained, consisting of 292 females (49.3%) and 300 males (50.7%). Females ranged from 260 to 750 mm TL,

with a mean value of 443 mm TL, while males ranged from 265 to 760 mm TL, with a mean of 442 mm TL (Fig. 2). No differences in size were observed between males and females (Student t-test, $p>0.05$). The mode was located between 350 and 510 mm TL (73% of the population). The smallest animals, fish between 250 and 330 mm TL, corresponded to 11% of the population, while the largest animals, with TL of 530 to 790 mm, represented 16% of the population.

The monthly size structure analysis indicated several modal groups (Fig. 3), with most 250 and 400 mm TL.

Length-weight Relationship

The equations describing the relationship between weight (W) and TL was estimated for males and females (Fig. 4). The slopes and intercepts were not significantly

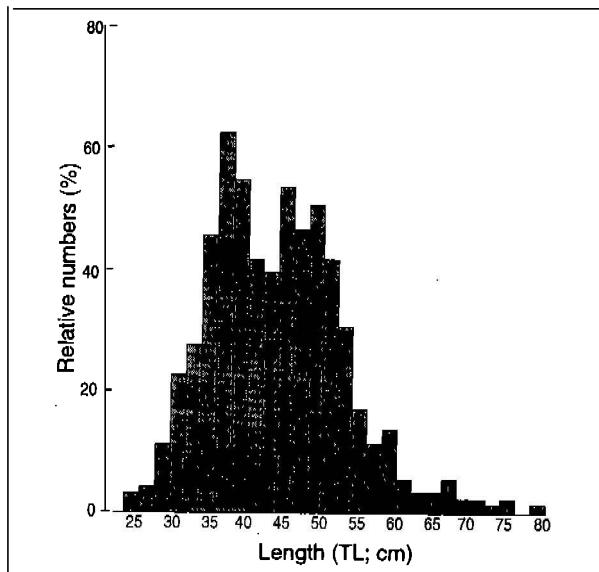


Fig. 2. Size structure of the sampled population of *Lutjanus vivanus* from Los Hermanos Islands, Venezuela, January–December 1992. [Estructura por tamaños de la población de *Lutjanus vivanus* de las Islas Los Hermanos, Venezuela, de Enero a Diciembre de 1992.]

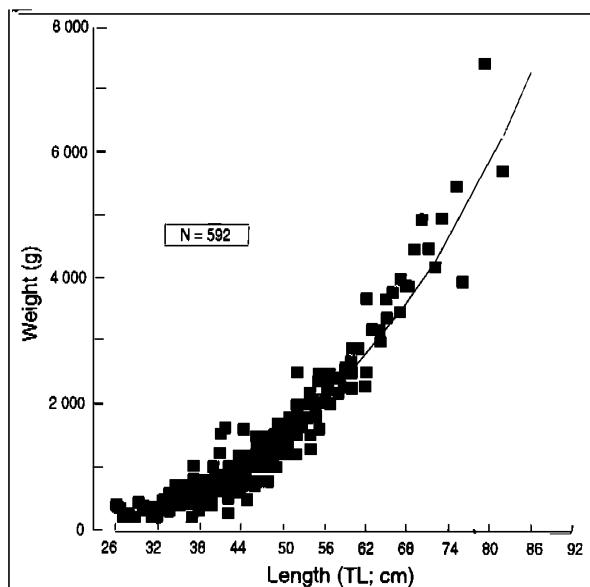


Fig. 4. Length-weight relationship for *Lutjanus vivanus* from Los Hermanos Islands, Venezuela, January–December 1992. [Relación peso longitud para *Lutjanus vivanus* de las Islas Los Hermanos, Venezuela, de Enero a Diciembre de 1992.]

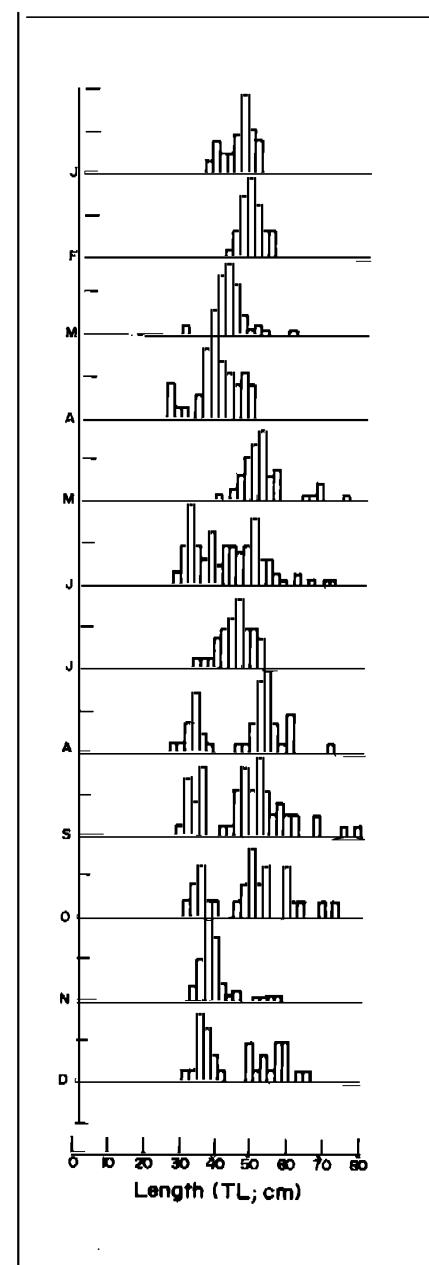


Fig. 3. Monthly size structure of the sampled population of *Lutjanus vivanus* from Los Hermanos Islands, Venezuela, January–December 1992. [Estructura mensual por tamaños de la población de *Lutjanus vivanus* de las Islas Los Hermanos, Venezuela, de Enero a Diciembre de 1992.]

different, hence a common equation was estimated for both sexes:

$$W = 1 \cdot 10^{-5} \cdot TL^{3.02}$$

The slope of 3.02 was not significantly different from 3 which suggests isometric growth in weight for this species.

Reproduction

Sex Ratio

In the sample of 592 snappers, the sex ratio was 49.3% males and 50.7% females, which did not differ significantly from 1:1 (chi-square test, $p>0.05$).

Sexual Maturity and Reproductive Season

Mature individuals were observed at the beginning of May, with two periods of increased gonadal activity, May-June and

August-November (Fig. 5). No spent individuals were observed.

The size at which 50% of the individuals are able to reproduce was estimated for males at 565 mm TL and the smallest mature individual was 450 mm TL. For females, the size of 50% maturity was estimated at 540 mm TL, and the smallest mature female was 420 mm TL. The comparison of the equations for size at maturity of 50% of the population indicated that intercepts for males and females were significantly different (covariance analysis, $p<0.05$); thus separate equations are reported for males and females (Fig. 6).

Discussion

Biometry

In this study the largest *L. vivanus* found was 790 mm TL, while the largest female was 760 mm TL. These sizes are larger than what have been reported by other authors

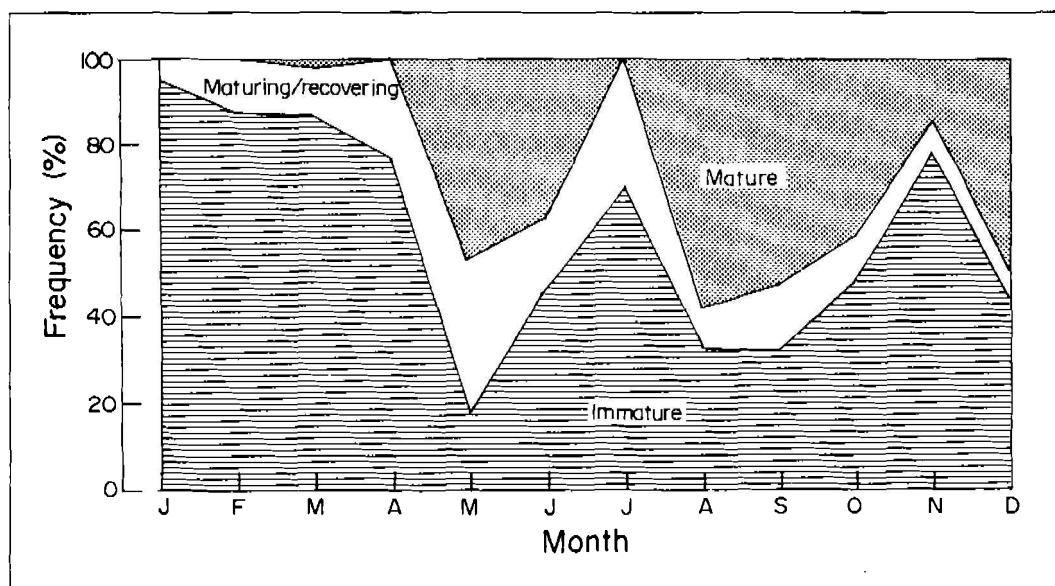


Fig. 5. Monthly variation in maturity stages of *Lutjanus vivanus* from Los Hermanos Islands, Venezuela, January-December 1992. [Variación mensual de los estadios de madurez de *Lutjanus vivanus* de las Islas Los Hermanos, Venezuela, de Enero a Diciembre de 1992.]

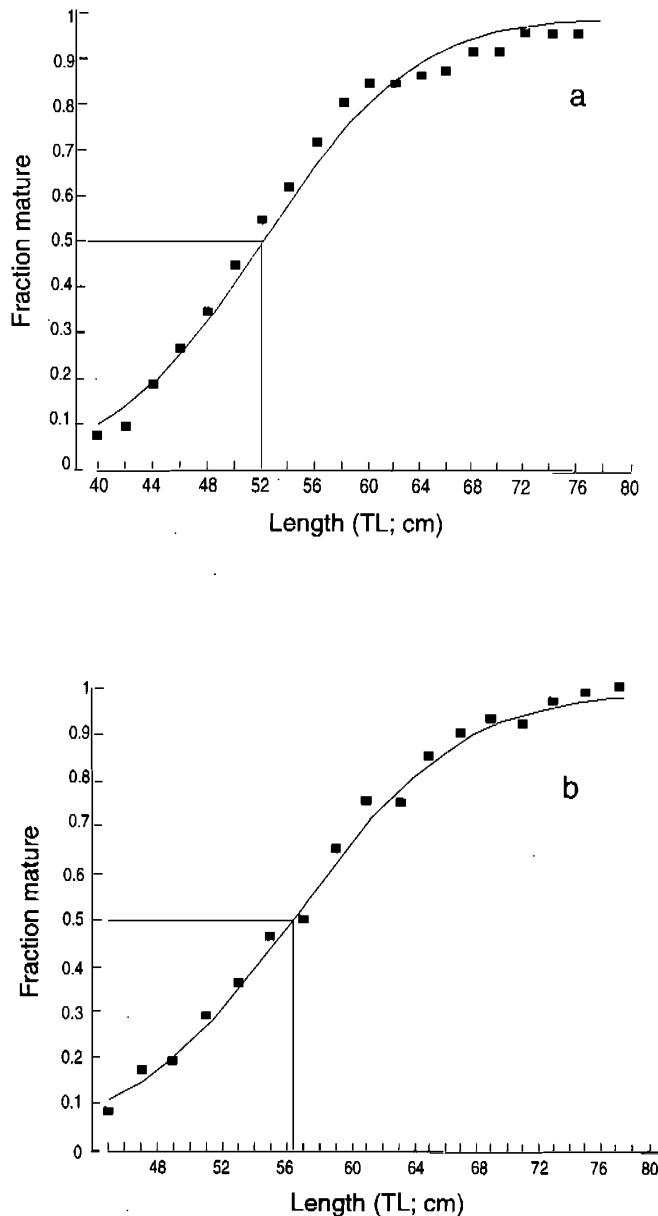


Fig. 6. Size at maturity of 50% of the population of (a) male and (b) female *Lutjanus vivanus* from Los Hermanos Islands, Venezuela, January–December 1992. [Tamaño de primera madurez (50%) de la población de (a) machos y (b) hembras de *Lutjanus vivanus* de las Islas Los Hermanos, Venezuela, de Enero a Diciembre de 1992.]

in the Caribbean area. Fischer (1978) reported a maximum size for *L. vivanus* of 690 mm total length, while Pozo and Espinoza (1982) found that the maximum size in Cuba was 560 mm fork length. The latter authors, in their study on age and growth of *L. vivanus*, estimated an asymptotic size (L_{∞}) of 756 mm. Cervigón and Fischer (1979) indicated that specimens of this species in the region average around 450 mm total length, which is slightly larger than that reported in the present study (443 mm and 442 mm, for females and males, respectively).

There is evidence that, according to the fishing method adopted for the exploitation of a resource, its population can undergo changes in age or size structures, in growth rate, or in reproductive capacity (Csirke 1980). One of the most noticeable changes is the reduction in the mean size of the fish in the population, as a result of a decrease in the proportion of older individuals. This situation was observed in the population studied. Analyzing its size structure, it was observed that 73% of the individuals were found in the range 350 to 510 mm TL, and only 16% were larger than 530 to 790 mm TL.

The presence of modal groups between 250 and 400 mm TL observed in the monthly distribution analysis (Fig. 3), suggests that recruitment to the fishing area is taking place at these sizes. However, a precise recruitment period for *L. vivanus* could not be established without more detailed studies.

The similarity of the length-weight regression equations for male and female *L. vivanus*, and the proximity of the slope value to 3, suggest that both sexes have isometric growth. Other authors have reported near-isometric growth for snapper species. Rubio et al. (1985) reported for *L. synagris* in Cuba; Pozo and Guardiola (1983), and Gómez et al. (1991) for *L. buccanella*. However, Pozo (1979) found in Cuba "b" values of 2.59 and 2.53, respectively, for male and female *L. analis*.

Reproductive aspects

Sex ratio can change considerably among species, or it can differ between populations, or even among different years for the same population. However, in most populations, the ratio is usually close to unity (Nikolsky 1963) as observed in this study.

Christiansen and Cousseau (1971) indicated that sex ratios can show variations according to the reproductive period and to the size groups under consideration. Margalef (1977) proposed that the optimal ratio between males and females is the result of selective pressure, which acts under different circumstances depending upon the distribution and the social organization of the species.

Reproduction of *L. vivanus* seems to take place only during the second half of the year, since mature fish were only found during this period and no mature fish were found during the first four months of the year. Thompson and Munro (1983) found that this species reproduces during a prolonged period of the year in Jamaican waters, with three main seasons: March/May, August/September and November. The absence of spent fish in the present study could suggest that the fishing area does not coincide with the reproductive area for this species, which would thus have to migrate elsewhere to spawn.

The size at 50% maturity of 50% of the *L. vivanus* population was established at 540 mm TL and 565 mm TL for females and males, respectively, suggesting that females mature before males do. Similar results were found by Thompson and Munro (1983) who reported that, in Jamaican waters, mean maturity size was 550-600 mm for males and 500-550 mm for females. These authors explained this difference in size at maturity, under the assumption that either growth rate is faster in males, or that males mature later than females.

Acknowledgements

We wish to acknowledge R. Chacón, A. Urbaneja and G. Vizcaino for their enthusiastic participation in the sampling program, J. Alió and F. Arocha for the translation and T. Ramírez for the typing of the manuscript. We also wish to recognize the help provided by the crew of the *R/V Golfo de Cariaco*. Funds to support this work were provided by Fondo Nacional de Investigaciones Agropecuarias of the Venezuelan Government.

References

- Cervigon, F. 1966. Los peces marinos de Venezuela. Fundación La Salle de Ciencias Naturales. Tomo II. Caracas, Venezuela. 994 p.
- Cervigon, F. and W. Fischer. 1979. Catálogo de especies marinas de interés económico actual o potencial para América Latina. Parte I. Atlántico Centro y Sur Occidental. FAO/UNDP. Sic/79/1372 p.
- Christiansen, H.E. and M.B. Cousseau. 1971. La reproducción de la merluza y su relación con otros aspectos biológicos de la especie. Bol. Inst. Biol. Mar. 20:44-73.
- Csirke, S. 1980. Introducción a la dinámica de población de peces. FAO Doc. Tec. (Pesca) 192, 82 p.
- Fischer, W., Editor. 1978. FAO species identification sheets for fishery purposes, Western Central Atlantic (Fishing Area 31). FAO, Rome.
- Gaertner, D. and F. Laloe. 1986. Etude biométrique de la taille à première maturité sexuelle de *Geryon maritae*, Manning et Holthuis, 1981 du Sénégal. Oceanol. Acta 9(4):479-487.
- Ginez, H., Editor. 1972. Carta pesquera de Venezuela. I. Áreas del nororiente y Guayana. Fund. La Salle de Cienc. Nat. Caracas. Monogr. 16, 319 p.
- Gomez, G., A. Urbaneja, R. Chacon and G. Vizcaino. 1991. Algunos aspectos biológicos del pargo aleta negra, *Lutjanus buccanella* (Cuvier, 1828) (Pisces: Lutjanidae), de las Islas Los Hermanos, Venezuela. AsoVAC. XLI Conv. Anual. Acta Cient. 42(1):293.
- Gomez, G., A. Urbaneja, R. Chacon and G. Vizcaino. 1992. Aspectos preliminares de la biología del pargo ojo amarillo *Lutjanus vivanus* (Cuvier, 1828) (Pisces: Lutjanidae), del sureste de las Islas Los Hermanos, Venezuela. AsoVAC. XLII Con. Anual. Acta Cient. vol. 43(1):279.
- Holden, M.J. and D.F.S. Raitt. 1975. Manual de ciencia pesquera. Parte 2. Métodos para investigar los recursos y su aplicación. FAO Doc. Tec. Pesca (115) Rev. 1:211 p.
- Margalef, R. 1977. Ecología. Omega S.A., Barcelona, España. 591 p.
- Nikolsky, G. 1963. The ecology of fishes. Academic Press, New York.
- Pozo, E. 1979. Edad y crecimiento del pargo *Lutjanus analis* (Cuvier, 1828) en la plataforma nororiental de Cuba. Rev. Cub. Inv. Pesq. 4(2):1-24.
- Pozo, E. and L. Espinoza. 1982. Estudio de la edad y crecimiento del pargo del alto *Lutjanus vivanus* (Cuvier, 1828) en la plataforma suroriental de Cuba. Rev. Cub. Invest. Pesq. 7(2):1-24.
- Pozo, E. and M. Guardiola. 1983. Aspectos preliminares de la biología del sesi *Lutjanus buccanella* (Cuvier, 1828) en la plataforma suroriental de Cuba. Rev. Cub. Inv. Pesq. 8(3):1-28.
- Rubio, R., P. Salahange and M. Betancourt. 1985. Relaciones de la edad con el largo, el peso y la fecundidad de la biajaiba *Lutjanus synagris* de la plataforma suroriental de Cuba. Rev. Invest. Pesq. 10(1-4):78-90.
- Snedecor, G. and W. Cochran. 1971. Statistical methods. The Iowa State University Press, Ames, Iowa. 593 p.
- Sokal, R. and F. Rohlf. 1981. Biometry. Freeman and Co., San Francisco. 859 p.
- Somerton, D.A. 1980. A computer technique for estimating the size of sexual maturity in crabs. Can. J. Fish. Aquat. Sci. 47:1488-1494.
- Thompson, R. and J.L. Munro. 1983. The biology, ecology and bioeconomics of the snapper, Lutjanidae, p. 94-109. In J.L. Munro (ed.) Caribbean coral reef fisheries resources. ICLARM Stud. Rev. 7, 276 p.

ENTERED IN MAGA

APR 14 1998

Species Composition, Distribution and Trends in Abundance of Snappers of the Southeastern USA, Based on Fishery-Independent Sampling

**N. CUELLAR^a
G.R. SEDBERRY^b
D.J. MACHOWSKI^b
M.R. COLLINS^b**

^a*Grice Marine Biological Laboratory
University of Charleston, South Carolina
205 Ft. Johnson Rd.
Charleston, South Carolina 29412, USA*

^b*Marine Resources Research Institute
South Carolina Wildlife and Marine Resources Management
P.O. Box 12559
Charleston, South Carolina 29412, USA*

CUELLAR, N., G.R. SEDBERRY, D.J. MACHOWSKI and M.R. COLLINS. 1996. Species composition, distribution and trends in abundance of snappers of the southeastern USA, based on fishery-independent sampling [*Composición por especies, distribución y tendencias en la abundancia de pargos en la ensenada del Atlántico Sur, basado en muestreos independientes de la pesquería*], p. 59-73. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) *Biology, fisheries and culture of tropical groupers and snappers*. ICLARM Conf. Proc. 48, 449 p:

Abstract

Routine Marine Monitoring and Assessment Program (MARMAP) sampling (1973-1992) with trawls, traps and hook-and-line between Cape Lookout, North Carolina and Cape Canaveral, Florida (9-366 m depths) collected 12 species of snappers (*Etelis oculatus*, *Ocyurus chrysurus*, *Pristipomoides aquilonaris*, *P. freemani*, *Rhomboplites aurorubens*; seven species of *Lutjanus*). Vermilion snapper (*R. aurorubens*) and red snapper (*L. campechanus*) were the most abundant and widely distributed species, and were collected over the continental shelf and shelf break throughout the region. Annual monitoring of abundance and length frequency indicated declines in vermillion snapper. Other species of *Lutjanus* were represented by occasional captures of juveniles in inshore waters (*L. analis*, *L. purpureus*, *L. synagris*) or rare occurrences at the shelf edge, under the influence of Gulf stream waters (*L. buccanella*, *L. griseus*, *L. vivanus*). Other snappers (*E. oculatus*, *O. chrysurus*, *P. aquilonaris*) were occasionally taken at the shelf edge.

Resumen

Los muestreos de rutina MARMAP (1973-1992) con redes de arrastre, trampas y palangres, entre Cabo Lookout, Carolina del Norte y Cabo Cañaveral, Florida (9-366 m de profundidad) colectaron 12 especies de pargo (Etelis oculatus, Ocyurus chrysurus, Pristipomoides aquilonaris, P. freemani, Rhomboplites aurorubens; y siete especies de Lutjanus). El pargo cunaro (R. aurorubens) y el pargo del Golfo (L. campechanus) fueron las especies más ampliamente distribuidas, y fueron colectadas sobre y al borde de la plataforma continental, a lo largo de la región mencionada. El monitoreo anual de abundancia y frecuencia de longitudes indicaron la declinación del pargo cunaro. Otras especies de Lutjanus estuvieron representadas por capturas ocasionales de juveniles en aguas interiores (L. analis, L. purpureus, L. synagris) y ocurrencias raras en el borde de la plataforma, bajo la influencia de las aguas de la corriente del Golfo (L. buccanella; L. griseus; L. vivanus). Otros pargos (E. oculatus; O. chrysurus; P. aquilonaris) fueron ocasionalmente colectados en el borde de la plataforma.

Introduction

The continental shelf of the southeastern USA (known in the USA as the South Atlantic Bight and extending from Cape Hatteras, North Carolina to Cape Canaveral, Florida) consists mainly of a sand bottom that gently slopes seaward to a series of ridges and scarps at the shelf edge. Scattered relatively infrequently throughout most areas of the shelf are rock outcrops, ledges, ridges and other exposed hard calcareous substrata. These areas, often referred to as hard bottom (Wenner et al. 1983; Sedberry and Van Dolah 1984; Wenner et al. 1984), live bottom (Struhsaker 1969), or sponge-coral habitat (Powles and Barans 1980; Wenner 1983) support dense populations of tropical, subtropical and warm temperate organisms including several species of snappers (Miller and Richards 1980; Wenner 1983; Sedberry and Van Dolah 1984).

Struhsaker (1969) summarized existing data from exploratory trawling in the region and divided the continental shelf and upper slope off the southeastern US into five habitat types, based on depth, bottom type, and catches of economically valuable fishes (Sedberry et al., in prep.). These five regions consisted of: 1) coastal areas; 2) open shelf; 3) live bottom; 4) shelf edge; and 5) lower shelf. Coastal habitat in this area is shallow (<9 m) and is greatly affected by seasonal temperature changes

and terrestrial runoff. It has turbid, lower salinity water and is primarily a decapod shrimp and sciaenid habitat. Open shelf habitat (19-55 m) consists of a smooth, sandy bottom where occasional large catches of sparids (e.g., *Stenotomus chrysops*), haemulids (e.g., *Haemulon aurolineatum*), and balistids (e.g., *Monacanthus hispidus*) are found (Sedberry et al., in prep.). Live bottom habitat (19-55 m) is interspersed with rocky outcroppings which support luxurious epifaunal growth. This habitat is ideal for lutjanids, serranids, sparids and haemulids (Sedberry and Van Dolah 1984). The shelf edge habitat (55-110 m) has smooth bottom to rocky high relief areas along the edge of continental shelf. Rocky reef habitats at the shelf edge have numerous warmwater invertebrates (Wenner et al. 1983) and reef fishes, including lutjanids (Struhsaker 1969; Sedberry and Van Dolah 1984). Lower shelf habitat (111-183 m) consists of a smooth, hard bottom with some areas of rocky outcrops. Deep reef fishes such as some species of snappers and snowy grouper (*Epinephelus niveatus*) utilize rugged habitat found at lower shelf depths.

Snappers (family Lutjanidae) of the Western Atlantic are percoid fishes most commonly found on coral reefs and adjacent tropical habitats (e.g., Sedberry and Carter 1993). However, some species are found in warm-temperate waters, such as those of the southeastern US (Robins and Ray 1986).

Most snappers are demersal; however, some are pelagic. Snappers are predators, usually feeding at night on demersal organisms such as crustaceans and fishes (Parrish 1987; Sedberry and Cuellar 1993). Most species of snappers are highly prized for their flesh and are very important in many commercial fisheries around the world (Fischer 1978).

Snappers in the southeastern US, especially the vermillion snapper (*Rhomboplites aurorubens*) and the red snapper (*Lutjanus campechanus*), are an important component of the commercial and recreational fisheries (see Chapman et al.; Collins et al.; Mendoza and Lárez, this vol.). In 1991, the South Carolina commercial landings for vermillion snapper were 227 t and the recreational headboat landings were about 50 t (Low 1992). An average vermillion snapper captured in the commercial fishery was 31.1 cm long and weighed 0.29 kg (Low 1992). In South Carolina a vermillion snapper sells for approximately US\$ 1.13-1.36 per kg. Reported landings in the red snapper commercial fishery were 16.8 t and in the recreational fishery were 10 t in South Carolina in 1991 (Low 1992). An average red snapper captured in the 1991 commercial fishery was 47.2 cm long and weighed 3.0 kg (Low 1992). Red snapper in the commercial fishery of South Carolina sell for approximately US\$ 1.60 per kg.

Since 1973, the Marine Resources Monitoring, Assessment and Prediction Program (MARMAP) has monitored offshore fish populations by conducting annual surveys of coastal, shelf and slope habitats between Cape Lookout and Cape Canaveral, Florida. MARMAP is a cooperative program between the National Marine Fisheries Service (NMFS) and the South Carolina Wildlife Marine Resources Department (SCWMRD). MARMAP has sampled all bottom habitats of the continental shelf with a variety of gears, including trawl nets, traps, and hook-and-line. Reef habitats have additionally been surveyed by divers, underwater video,

submersible and still cameras (e.g., Powles and Barans 1980; Sedberry and Cuellar 1993). During these surveys several species of snappers were collected. The purpose of this paper is to present data on the composition, distribution and trends in abundance of snappers collected during MARMAP surveys over the past 20 years.

Methods

Several surveys were conducted during 1973-1992, using a variety of vessels and types of gear. The first survey was the continental shelf trawl survey using the 32 m *R/V Dolphin*. Survey cruises were conducted at least once annually from Cape Fear, North Carolina to Cape Canaveral, Florida. A stratified random sampling design (Grosslein 1969; Wenner et al. 1979a) was used from 1973 to the winter of 1977; whereas from summer 1977 to 1980, a systematic sampling design of 180 preselected stations along seven transects were trawled (Sedberry et al., in prep.). At each station a 3/4 scale version of a #36 *Yankee* trawl was used in a standard trawl tow of 30 min at a speed of 6.5 km hour⁻¹ (3.5 knots) (Wenner et al. 1983). Fishes from catches were sorted to species, counted, weighed and measured to the nearest cm (fork length, FL, for snappers).

A second survey, the coastal trawl survey, was conducted from Cape Fear, North Carolina to Cape Canaveral, Florida, in 1980 to 1982 on the *R/V Atlantic Sun* or the *R/V Lady Lisa*. These vessels were 20-m double-rigged trawlers formerly used in the commercial shrimp industry. The stratified random sampling design consisted of 13 latitudinal strata (7 486 to 31 661 ha) in a depth zone of 4.6-9.1 m within this area (Wenner and Sedberry 1989). At each station within a stratum, paired (one towed from each outrigger) four-seam Gulf of Mexico shrimp trawl nets were used for 20 minutes at a speed of 4.4 km hour⁻¹ (Wenner and Sedberry 1989). Contents of each net

were combined, with fishes being sorted to species, counted, weighed (g) and measured to the nearest cm (Wenner and Sedberry 1989).

A third survey, the reef fish survey, was conducted from Cape Fear, North Carolina to Jacksonville, Florida, beginning in 1978 and continuing through 1992. From 1978 to 1987, nine reef areas were selected for annual sampling, although each area was not sampled during each year. During this period, reefs were sampled with Florida snapper traps, trawls and hook-and-line. From 1987 through 1992, randomly chosen reef sites were sampled with fish traps and hook-and-line. Sampling was generally conducted from late spring to mid-summer. Each station was surveyed and mapped with underwater television, fathometer and Loran-C. During mapping, a tethered underwater television camera was towed across the bottom. The area viewed, as well as fathometer traces, were continuously monitored by observers viewing a 46-cm monitor and white line depth recorder or color video fathometer aboard the research vessel. Observations regarding bottom type (reef vs. nonreef) and the distribution and abundance of reef invertebrates and fishes were continuously recorded. From these reconnaissance television transects, maps of the reef areas were drawn. All subsequent samplings were attempted over known reef areas.

From 1978 to 1988, the reef fish survey cruises were conducted aboard the *R/V Oregon* using trawl nets (except 1988), traps and hook-and-line gear. The *R/V Palmetto* was used from 1989 to 1992 using only traps and hook-and-line gear. Two designs of trawl gear were used in this survey, the 3/4 scale version of a #36 *Yankee* trawl (Wenner 1983) and the 40/54 High Rise

Net (Sedberry and Van Dolah 1984). Trawl sampling for fishes consisted of 1-km tows with the trawl. Two types of fish traps used in the reef survey were used in the present analysis: a Florida snapper trap and a chevron trap (Collins 1990). Standard hook-and-line gear was also used in the reef survey (Collins and Sedberry 1991). Fishes collected in all gear types were sorted to species, counted, weighed (nearest gram) and measured to the nearest cm.

Snappers were ranked by abundance from the 1 680 MARMAP collections that collected snappers. Percent number was calculated as a percentage of the total number of snappers caught comprised by each species.

For each snapper species, a map was constructed showing the mean number of individuals per collection in the survey area. To calculate means, the survey area was divided by one-minute latitudinal, by one-minute longitudinal units, and the mean number per collection in each unit calculated.

Additional data analysis was conducted on the vermillion snappers and the red snappers due to their high abundance and economic importance in the region. Abundance by depth, mean length by depth, and mean length by year were compared for those species.

Results and Discussion

Species composition, distribution and abundance

Twelve species of snappers were caught in the MARMAP surveys (Table 1). Vermilion snappers and red snappers dominated the catches with the remaining species

being captured very rarely. The rare snapper species in descending order included: mutton snapper (*Lutjanus analis*), lane snapper (*Lutjanus synagris*), wenchman (*Pristipomoides aquilonaris*), gray snapper (*Lutjanus griseus*), Caribbean red snapper (*Lutjanus purpureus*), blackfin snapper (*Lutjanus buccanella*), yelloweye wenchman (*Pristipomoides freemani*), yellow-tailed snapper (*Ocyurus chrysurus*), silk snapper (*Lutjanus vivanus*) and queen snapper (*Etelis oculatus*).

Vermilion snapper (*Rhomboplites aurorubens*) was the most abundant snapper species in the MARMAP surveys (Table 1). Vermilion snappers were quite common across the continental shelf in the region, and also occur in the Gulf of Mexico south to southeastern Brazil (Bohlke and Chaplin 1968). Vermilion snapper captured in the MARMAP surveys occurred throughout the

region from 14 to 92 m (Fig. 1), which is similar to Grimes' (1976) findings that vermillion snapper was associated with two distinct habitats on the southeastern shelf, the shelf-edge habitat (64-183 m) and inshore live bottom habitat (26-56 m). The size of vermillion snapper captured in MARMAP surveys ranged from 3 to 51 cm. Maximum size for a vermillion snapper is approximately 60 cm TL (Grimes 1978). Vermilion snappers were caught with all gear types used in MARMAP surveys (Table 1).

Red snapper (*Lutjanus campechanus*) were the second most abundant lutjanid captured in MARMAP surveys. Although not as abundant as vermillion, red snappers occurred 124 times (322 individuals) from depths of 7-68 m (Table 1, Fig. 1). Red snappers were also broadly distributed across the shelf and are found throughout the region to Key West and around the Gulf coast

Table 1. Rank by abundance of snappers in 1 680 MARMAP collections, Cape Lookout to Cape Canaveral. Percent number (%N) is based on percentage of total snappers caught, and percent frequency (%F) is based on percentage of the total number of stations where snappers occurred. [*Ordenamiento de pargos por su abundancia en 1 680 colectas de MARMAP, desde Cabo Lookout a Cabo Cañaveral. El porcentaje del número (%N) está basado en el porcentaje de pargos totales capturados; y el porcentaje de frecuencia (%F) basado en porcentaje del número total de estaciones donde los pargos estuvieron presentes.*]

Species	Number	%N	Freq.	%F	Depth range (m)
<i>Rhomboplites aurorubens</i>	20 254 ^a	98.19	1 573	93.63	14-92
<i>Lutjanus campechanus</i>	322 ^b	1.56	124	7.38	7-68
<i>Lutjanus analis</i>	13 ^c	0.06	5	0.30	7-28
<i>Lutjanus synagris</i>	13	0.06	12	0.71	5-16
<i>Pristipomoides aquilonaris</i>	11	0.05	7	0.42	64-179
<i>Lutjanus griseus</i>	5	0.02	3	0.18	28-37
<i>Lutjanus purpureus</i>	3	0.01	3	0.18	12-35
<i>Lutjanus buccanella</i>	2	0.01	2	0.12	22-31
<i>Pristipomoides freemani</i>	1	<0.01	1	0.06	121
<i>Ocyurus chrysurus</i>	1	<0.01	1	0.06	28
<i>Lutjanus vivanus</i>	1	<0.01	1	0.06	79
<i>Etelis oculatus</i>	1	<0.01	1	0.06	59

^a Number caught by trawl: 7 767; by traps: 10 261; by hook-and-line: 2 201

^b Number caught by trawl: 131; by traps: 111; by hook-and-line: 80

^c All by trawl (also for all subsequent species).

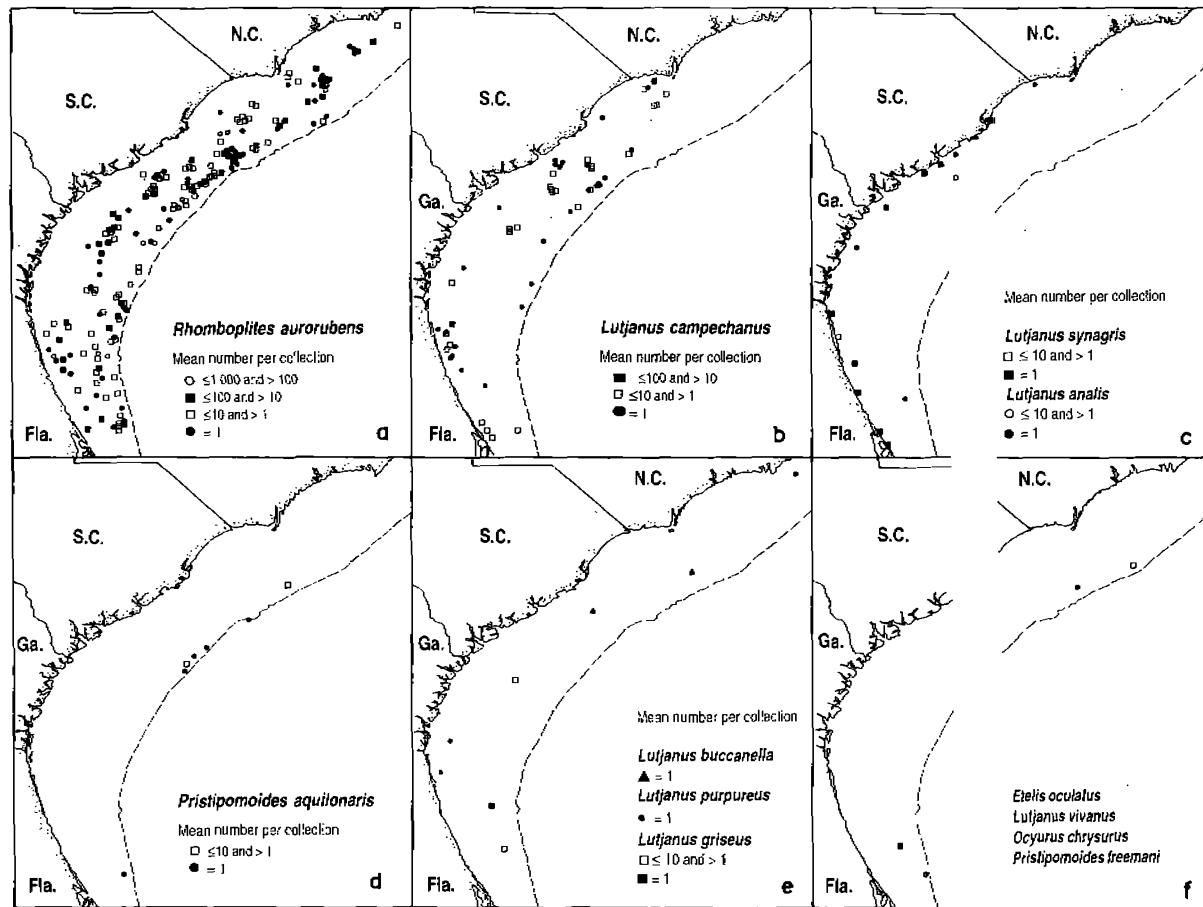


Fig. 1. Distribution of snappers from Cape Fear, North Carolina to Cape Canaveral, Florida, in *M. vermillion* snapper (*Rhomboplites aurorubens*); b) red snapper (*Lutjanus campechanus*); c) *Lutjanus . aquilonaris*; e) *L. griseus*, *L. purpureus* and *L. buccanella*; f) *Etelis oculatus*, *L. vivanus*, *Ocyurus c. surus* and *Pristipomoides freemani*.

[*Distribución de pargos desde Cabo Fear a Cabo Cañaveral, Florida; a partir de muestras experimentales MARMAP, de 1973 a 1992: a) pargo cunaro (*Rhomboplites aurorubens*), b) pargo del Golfo (*Lutjanus campechanus*), c) pargo criollo (*Lutjanus synagris*), d) panchito voraz (*Pristipomoides aquilonaris*), e) pargo prieto (*L. griseus*), pargo cebo (*L. buccanella*), f) pargo cachucero (*Etelis oculatus*), pargo de lo alto (*L. vivanus*), rabirrubia (*Ocyurus chrysosomus*) y panchito menudo (*Pristipomoides freemani*).*]

MAP surveys from 1973 to 1992: a) *L. synagris*; d) *Pristipomoides aquilonaris* and *Pristipomoides freemani*. b) *Lutjanus analis* and *pargo blajalba* (*L. analis* (*L. purpureus*) y *pargo seso* (*L. analis*)) and *panchito menudo* (*Pristipomoides* *freemani*).

to the Campeche Banks (Grimes et al. 1977). Adult fish are commonly found at 30 to 130 m (Fischer 1978), but in the Carolinas they are usually found at depths of 46 to 91 m over both high and low relief areas (Grimes et al. 1977). Red snappers captured in MARMAP surveys ranged in length from 2 to 85 cm. The maximum size of a red snapper is approximately 91 cm (Robins and Ray 1986). Red snappers were captured with all gear types in these surveys (Table 1).

Mutton snapper (*Lutjanus analis*) ranked third in abundance and were captured with the Yankee and shrimp trawl nets in the continental shelf and coastal trawl surveys (Table 1). Mutton snappers occurred south of North Carolina in five collections, some of which contained more than one individual (13 total individuals). Mutton snapper occurred across the shelf, out to 28 m depths (Fig. 1). Mutton snappers are found occasionally from Massachusetts to Brazil (Bohlke and Chaplin 1968), but are most abundant in southern Florida, the Bahamas and the Antilles (Fischer 1978). Habitats preferred by this species are shallow coastal waters over coral reefs and vegetated sand and mud bottoms, often surrounded by mangrove thickets (Fischer 1978). Mutton snappers captured in MARMAP surveys ranged in FL from 3 to 46 cm. Mutton snappers are commonly found around 50 cm (Fischer 1978; Mason and Manooch 1985), but can grow as large as 86 cm TL (Mason and Manooch 1985).

Lane snapper (*Lutjanus synagris*) are ranked fourth and were captured with the Yankee and shrimp trawl nets in the coastal and continental shelf trawl surveys (Table 1). This snapper species was rare in the collections, found in shallow waters along the coast from South Carolina to Cape Canaveral, Florida (Table 1, Fig. 1). Lane snappers commonly occur in the Western Atlantic from the north coast of Florida to southeastern Brazil, often in reef areas (Manooch and Mason 1984). According to Manooch and Mason (1984), juveniles are

occasionally found as far north as the North Carolina area due to transportation of eggs and larvae by the Gulf stream. Fish captured in the MARMAP surveys were mostly juveniles ranging in length from 2 to 23 cm and found in coastal waters. Smaller lane snappers are generally found in coastal waters or estuaries whereas adults are generally found offshore (Starck and Schroeder 1971). Lane snappers are commonly reached at 25 cm (Fischer 1978), but a large fish can reach up to 51 cm (TL) (Manooch and Mason 1984).

Wenchman (*Pristipomoides aquilonaris*) ranked fifth, but occurred seven times (11 individuals) in the Yankee trawl data during the continental shelf trawl survey (Table 1). The wenchman is found from North Carolina to Brazil, but more commonly off the northern coast of the Gulf of Mexico, in the Gulf of Campeche, and off the Guyanas (Robins and Ray 1986). The depth range in the MARMAP surveys was mainly along the shelf edge (Table 1, Fig. 1). Anderson (1972) found the depth range to be 24 to 366 m. Wenchman commonly grows to 20 cm (Fischer 1978) and in the MARMAP surveys the fish ranged from 2 to 22 cm.

The gray snapper (*Lutjanus griseus*) ranked sixth and was caught by the Yankee trawl in the continental shelf trawl survey (Table 1). Gray snappers occurred in three collections (five individuals) at the middle shelf off Georgia and Florida (Table 1, Fig. 1). It is mainly a tropical and subtropical species, found from Massachusetts (rarely) to Florida to southeastern Brazil, but it is most common around southeastern Florida and the Antilles (Starck and Schroeder 1971). Gray snappers in the MARMAP surveys were captured at middle shelf depths and ranged in length from 23 to 56 cm. These were adults, caught offshore in trawls (Table 1, Fig. 1); juveniles are usually found in estuarine waters and shallow coastal waters not sampled by the MARMAP surveys (Manooch and Matheson 1983). They frequently grow to approximately 35 cm, but can grow as large as a 21-year-old fish

of 77 cm TL captured by Manooch and Matheson in 1983.

Caribbean red snappers (*Lutjanus purpureus*) ranked seventh and were caught by the *Yankee* trawl in the continental shelf trawl survey (Table 1). They occurred in three collections off Cape Lookout, North Carolina and near the Georgia/Florida border, at inner and middle shelf depths (Table 1, Fig. 1). This species is very similar in morphology to the red snapper, but it has a more southerly distribution. It is found around Cuba and from the Yucatan Peninsula along continental shelves to northeastern Brazil, and is most common on the continental shelf off Honduras and Guyanas (Fischer 1978). Caribbean red snappers are commonly found at depths between 70 and 120 m and at a size up to 65 cm (Fischer 1978). In MARMAP surveys this species had a length range of 3-32 cm.

Blackfin snappers (*Lutjanus buccanella*) ranked eighth and occurred only twice in collections in the *Yankee* trawl in the continental shelf trawl survey (Table 1). Blackfin snappers are found from North Carolina, Bermuda, and the Gulf of Mexico through the Antilles to northeast Brazil (Fischer 1978). According to Grimes et al. (1977), exploratory trawling in the 1960s found blackfin snapper to be very rare in the southeastern United States and only seven fish were reported from the headboat catches in the Carolinas from 1972 to 1975. Headboat fishers rarely recognized this species and this might explain the low catches for the blackfin snapper in the Carolinas during this period (Grimes et al. 1977). Blackfin snappers were found at the middle shelf off South Carolina during the MARMAP survey (Fig. 1). Usual habitat for the blackfin snapper is the shelf edge or live bottom areas from 9 to 219 m (Grimes et al. 1977). This species is common up to 50 cm, but is found up to 75 cm (Robins and Ray 1986).

Pristipomoides freemani (yelloweye wenchman) occurred only once, in the *Yankee* trawl in the continental shelf trawl survey

(Table 1). It was a small specimen (10-cm FL) and was found in deepwater off Florida (Table 1, Fig. 1). Little is known about the life history of this fish. This species is found off Panama, Colombia, Venezuela, Barbados, Surinam, southern Brazil and Uruguay from 87 to 220-m water depths (Anderson 1972). This deepwater snapper reaches a maximum size of approximately 20 cm SL (Anderson 1972).

Ocyurus chrysurus (yellowtail snapper) occurred only once, in the *Yankee* trawl in the continental shelf trawl survey (Table 1). Its fork length was 36 cm and it was found on the middle shelf off Florida (Fig. 1). Yellowtail snappers are commonly found in the Bahamas, off southern Florida, and throughout the Caribbean, but range from Massachusetts to southeastern Brazil (Fischer 1978). Their preferred habitat is coastal waters between 10 and 70 m around coral reefs (Fischer 1978). This species can reach approximately 75 cm, but is common to 40 cm (Robins and Ray 1986).

Silk snapper (*Lutjanus vivanus*) also occurred only once, and was collected in the *Yankee* trawl in the continental shelf trawl survey (Table 1). The fork length of this fish was 73 cm and it was captured at the shelf edge off South Carolina (Fig. 1). Silk snappers have been quite common in the Carolinas, making an important contribution to the headboat catches (Grimes et al. 1977) and are distributed from North Carolina and Bermuda to Trinidad and to Brazil, but are most common around the Antilles and the Bahamas (Fischer 1978). Generally, the silk snapper is found in waters that are deeper than the red or vermillion snapper. Ideal habitat for the silk snapper is rough bottom at 55 to 128 m (Grimes et al. 1977). An average silk snapper caught off the Carolinas is approximately 66 cm TL and 4.5 to 5 kg (Grimes et al. 1977).

Queen snapper (*Etelis oculatus*) occurred once, in the *Yankee* trawl in the continental shelf trawl survey (Table 1); it was captured at the shelf edge off Winyah Bay, South

Carolina (Table 1, Fig. 1). The queen snapper ranges from North Carolina and Bermuda to the Lesser Antilles and Brazil, and in the southern portion of the Gulf of Mexico (Anderson 1972). Ideal habitat for the queen snapper is rocky bottom from 135 to 450 m (Fischer 1978). This species is commonly found up to 52 cm, but can grow as large as 91 cm (Robins and Ray 1986).

Vermillion snapper and red snapper

Vermillion and red snappers are the most important lutjanids in South Carolina commercial landings (Fig. 2). Levels of commercial landings were compared with abundance of these two species in annual South Carolina MARMAP survey data and no correlations were found. Commercial landings of vermillion snapper and red snapper appear to be very similar from 1980 until 1990. This similarity probably reflects similar fishing effort for the two species. From 1980 to 1985, fishers concentrated on deepwater slope species such as tilefish and snowy groupers until they became overfished. In 1985, the fishers returned to the shelf snapper/grouper fishery and

commercial landings of red and vermillion snappers increased.

Mean number of vermillion snappers per sample in 10-m depth intervals (for each gear type) indicated that most vermillion snappers were captured between 30 and 60 m (Fig. 3). In the reef trawl survey, mean catch of vermillion snappers per tow was greatest in depths of 31-40 m (Sedberry and Machowski, unpubl.); however, in the shelf trawl survey (*Yankee* trawl, Fig. 3) mean catches were highest at 60-70 m depths. From southern Onslow Bay, North Carolina, to South Carolina, hard rocky bottom is scattered more over the continental shelf than at the shelf edge, and vermillion snappers occur more frequently in these areas from 33 to 64 m (Grimes et al. 1977).

Mean length of vermillion snappers increased with depth for each type of gear (Fig. 4). However, the mean length of vermillion snappers was less with the *Yankee* trawls in comparison to other gear types. Generally, the trawl is more efficient at sampling smaller individuals of this species prior to growth and recruitment to the baited fishing gear (Sedberry and Machowski, unpubl.), and larger fish may be able to avoid the trawl net. Hook-and-line gear captured the largest fish.

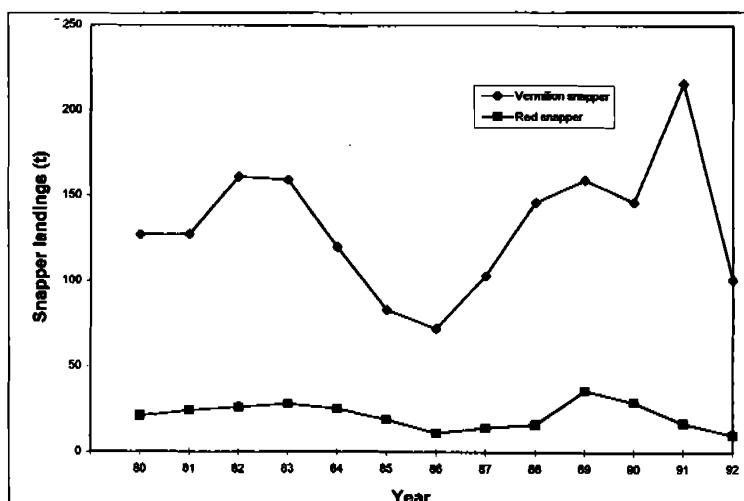


Fig. 2. South Carolina commercial landings for the vermillion snappers and red snappers landed by year (1980-1992). [Descargas comerciales anuales, en Carolina del Sur, del pargo cunaro y del pargo del Golfo (1980-1992).]

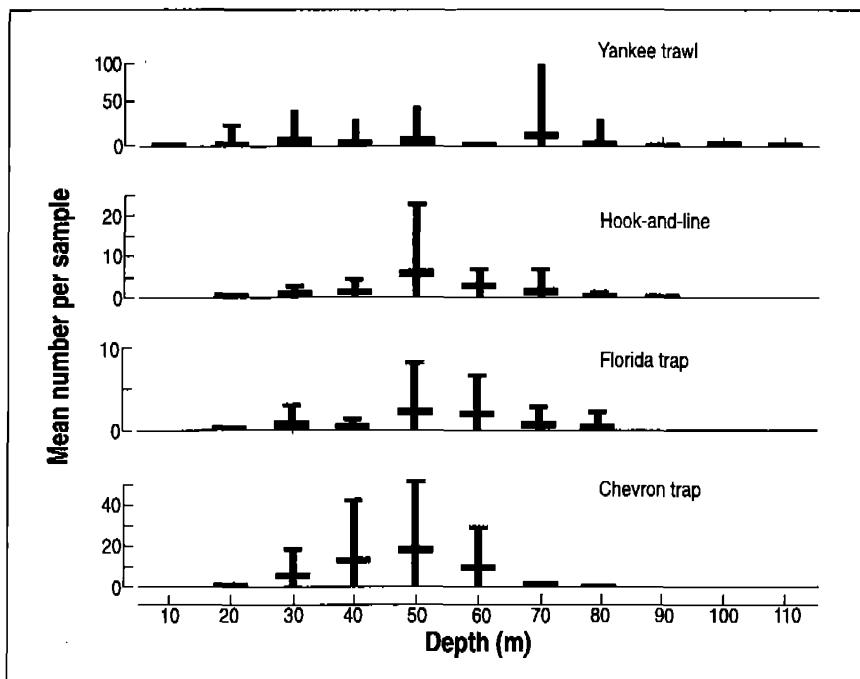


Fig. 3. Mean catch per sample by depth of vermilion snappers for the Yankee trawl, hook-and-line, Florida trap and chevron trap in MARMAP surveys. [Captura media por muestra por profundidad del pargo cunaro para el arrastre Yankee, palangre, trampa tipo Florida, y trampa tipo chevron en los cruceros MARMAP.]

Mean length and abundance of vermilion snappers were compared by year for certain gear types used during a period of expansion in the fishery (Figs. 5 and 6). From 1983 to 1987 there was a decrease in mean FL and abundance of vermilion snapper caught with fish traps and hook- and-line gear, and a decline in commercial landings (Fig. 2). Collins and Sedberry (1991) attributed the declines in abundance and mean length in fishery-independent samples to overfishing. Collins and Pinckney (1988) found that vermilion snappers in the SAB became reproductively mature earlier in life, than was previously reported prior to the expansion in the fishery.

Greatest catches of red snappers occurred between 20 and 50 m for all gear types (Fig. 7). Catches of red snappers were much lower than catches of vermilion snapper in the MARMAP surveys.

Mean FL of red snapper, compared by depth for all gear types (Fig. 8), indicated an increase in mean FL of red snapper with increasing depth in the Yankee trawl. Other gear types that caught red snapper in sufficient numbers to examine depth trends did not cover a great enough depth range to show any relationship between depth and abundance. Generally, the trawl was not effective in capturing large snappers of the genus *Lutjanus* (Sedberry and Machowski, unpubl.).

In conclusion, MARMAP surveys over the past 20 years have captured 12 species of snappers of the family Lutjanidae. Vermilion snappers and red snappers were the most abundant species found in the SAB. Both of these species are economically important to the commercial and recreational fisheries of this region. Overfishing might be

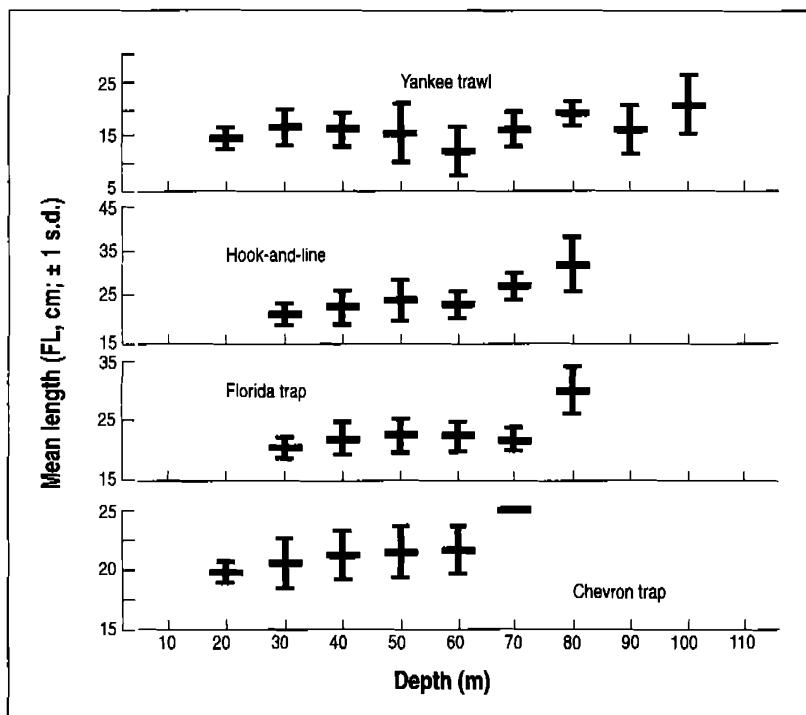


Fig. 4. Mean fork length by depth of vermillion snappers for the Yankee trawl, hook-and-line, Florida trap and chevron trap in MARMAP surveys. [Longitud furcal media por profundidad del pargo cunaro para el arrastre Yankee, palangre, trampa tipo Florida, y trampa tipo chevron en los cruceros MARMAP.]

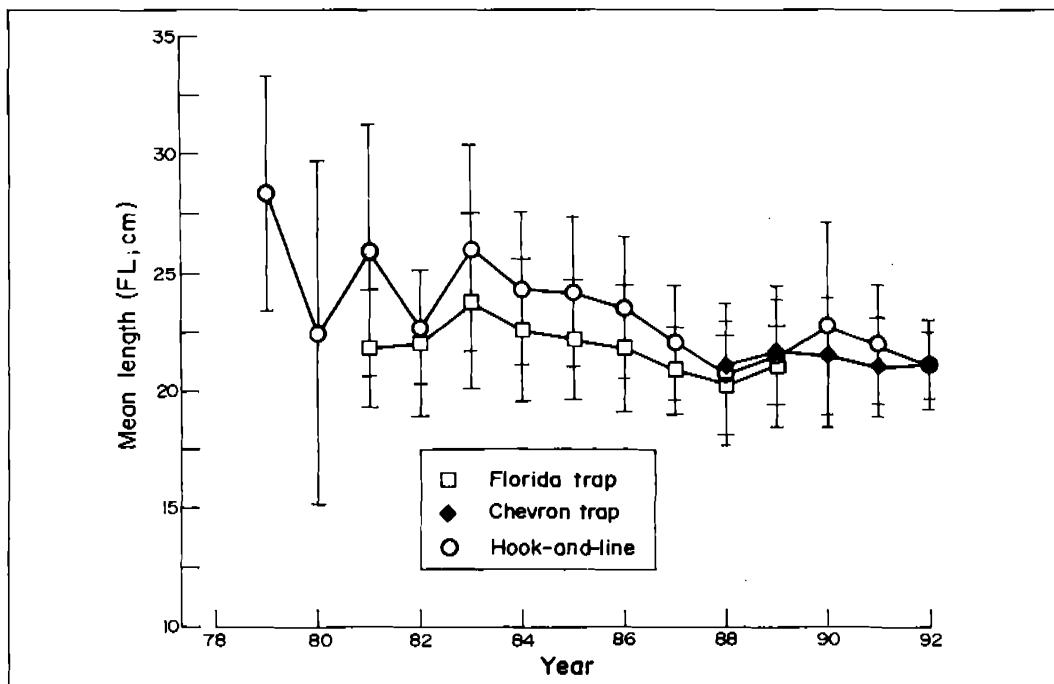


Fig. 5. Mean fork length by year of vermillion snapper for the Florida trap, chevron trap, and hook-and-line in MARMAP surveys. [Longitud furcal media por año del pargo cunaro para la trampa tipo Florida, trampa tipo chevron, y palangre de los cruceros MARMAP.]

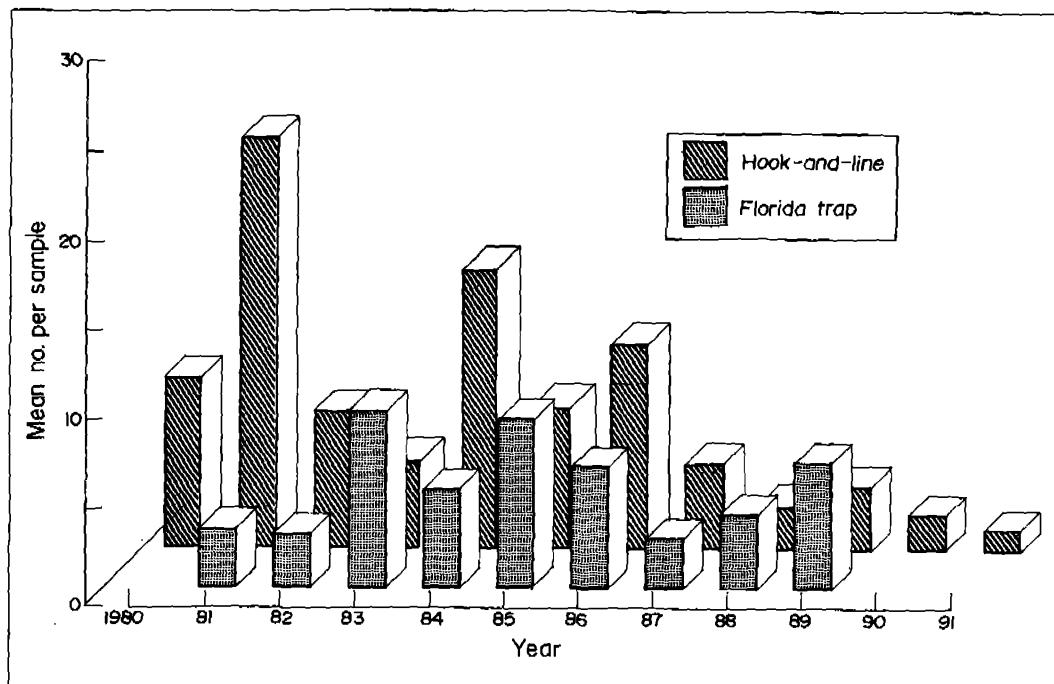


Fig. 6. Mean number per sample by year of vermilion snapper for the Florida trap and hook-and-line in MARMAP surveys. [Número medio por muestra por año del pargo cunaro obtenidos con trampas y palangre en los muestreos MARMAP.]

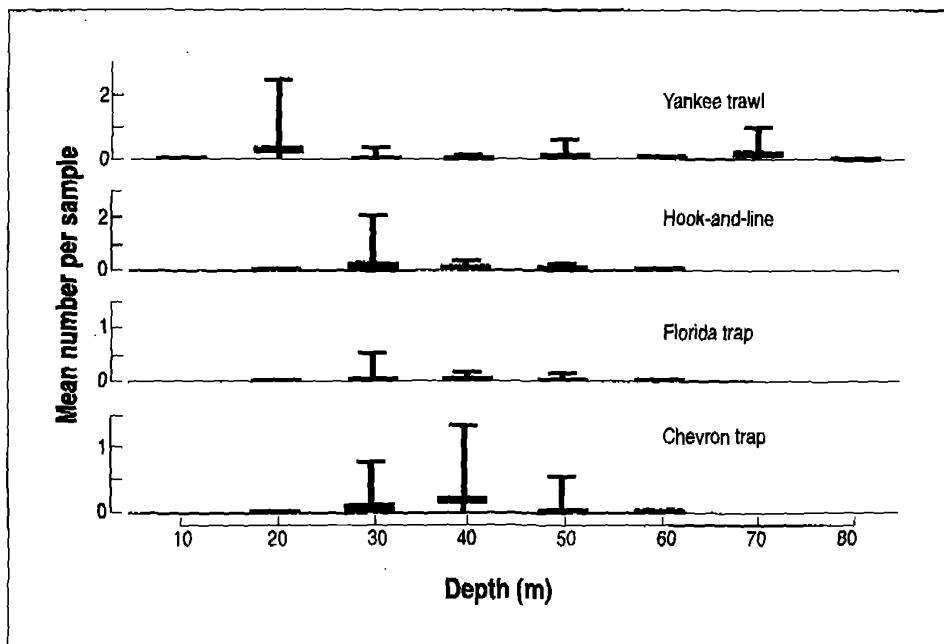


Fig. 7. Mean number per sample by depth of red snapper for the Yankee trawl, hook-and-line, Florida trap and chevron trap in MARMAP surveys. [Número medio por muestra por profundidad del pargo del Golfo para el arrastre Yankee, palangre, trampa tipo Florida, y trampa tipo chevron en los cruceros MARMAP.]

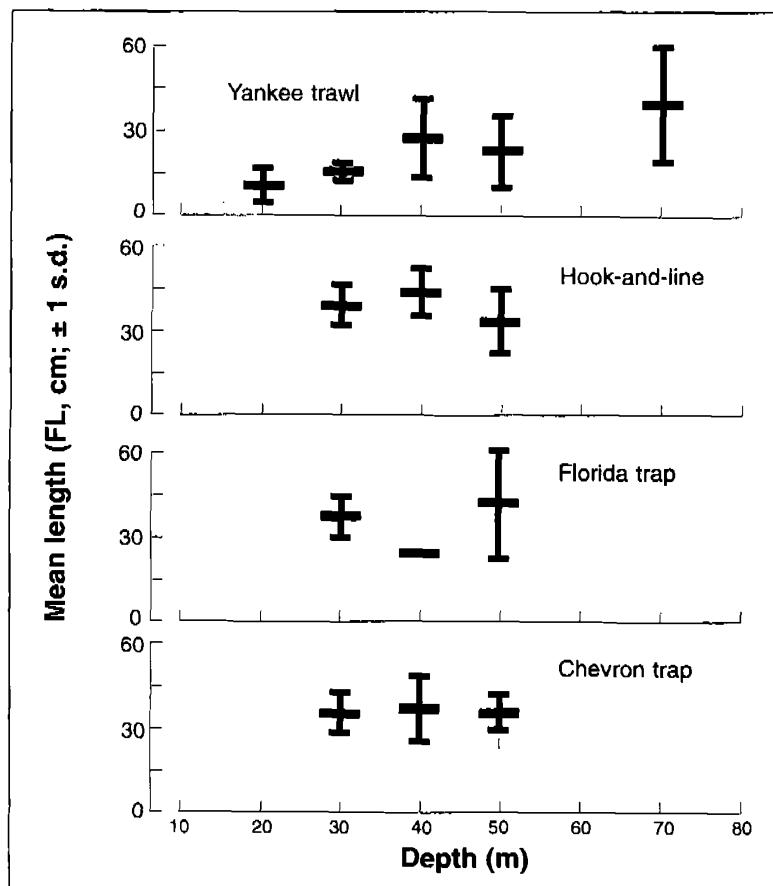


Fig. 8. Mean fork length by depth of red snapper for the Yankee trawl, hook-and-line, Florida trap and chevron trap in MARMAP surveys. [Longitud furcal media por profundidad del pargo del Golfo para el arrastre Yankee, palangre, trampa tipo Florida y trampa tipo chevron en los cruceros MARMAP.]

be affecting populations of vermillion snappers in the SAB, as evidenced by decreasing the mean length of the fish and younger age at maturity.

Acknowledgements

We thank all past and present personnel of the Marine Resources Research Institute who participated in the MARMAP groundfish and reef fish surveys, for their assistance in the field and in data reduction. We especially thank C.A. Barans and C.A. Wenner, who supervised the scientific

parties at sea on many cruises, and who were responsible for much of the data reduction and quality control. We also thank the captains and crew members who skillfully manned the research vessels used in the MARMAP surveys. This work was supported through various MARMAP contracts between the South Carolina Wildlife and Marine Resources Department, and the U.S. National Marine Fisheries Service. This is Contribution Number 385 from the South Carolina Marine Resources Center, and Contribution Number 136 from the Grice Marine Biological Laboratory.

References

- Anderson, W.D., Jr. 1972. Notes on western Atlantic lutjanid fishes of the genera *Pristipomoides* and *Etelis*. Copeia 1972(2):359-362.
- Böhlke, J.E. and C.C.G. Chaplin. 1968. Fishes of the Bahamas and adjacent tropical waters. Livingstone Publ. Co., Wynnewood, Pennsylvania. 771 p.
- Collins, M.R. 1990. A comparison of three fish trap designs. Fish. Res. 9:325-332.
- Collins, M.R. and J.L. Pinckney. 1988. Size and age at maturity for vermilion snapper (*Rhomboptilus aurorubens*) (Lutjanidae) in the South Atlantic Bight. Northeast Gulf Sci. 10(1): 51-53.
- Collins, M.R. and G.R. Sedberry. 1991. Status of vermilion snapper and red porgy stocks off South Carolina. Trans. Am. Fish. Soc. 120:116-120.
- Fischer, W. 1978. FAO species identification sheets for fishery purposes. Western Central Atlantic (fishing area 31). Vol. 3. Food and Agriculture Organization of the United Nations, Rome, pag. var.
- Grimes, C.B. 1976. Certain aspects of the life history of the vermilion snapper *Rhomboptilus aurorubens* (Cuvier) from North and South Carolina. University of North Carolina, Chapel Hill, North Carolina. 240 p. Ph.D. dissertation.
- Grimes, C.B. 1978. Age, growth, and length-weight relationships of vermilion snapper, *Rhomboptilus aurorubens*, from North and South Carolina. Trans. Am. Fish. Soc. 107(3): 454-456.
- Grimes, C.B., C.S. Manooch, G.R. Huntsman and R.L. Dixon. 1977. Red snappers of the Carolina coast. Mar. Fish. Rev. Pap. 1229(39):12-15.
- Grosslein, M.D. 1969. Groundfish survey program of BCF Woods Hole. Comm. Fish. Rev. 31(8-9):22-30.
- Low, R.A. 1992. South Carolina Marine Fisheries, 1991. Marine Resources Division, Office of Fisheries Management, Fisheries Statistics Section. Data Report 13, 50 p.
- Manooch, C.S. III and D.L. Mason. 1984. Age, growth, mortality of lane snapper from southern Florida. Northeast Gulf Sci. 7:109-115.
- Manooch, C.S. III and R.H. Matheson III. 1983. Age, growth, and mortality of gray snapper collected from Florida waters. Proc. Ann. Conf. S.E. Assoc. Fish & Wildl. Agencies 35:331-344.
- Mason, D.L. and C.S. Manooch III. 1985. Age and growth of mutton snapper along the east coast of Florida. Fish. Res. 3:93-104.
- Miller, G.C. and W.J. Richards. 1980. Reef fish habitat, faunal assemblages and factors determining distributions in the South Atlantic Bight. Proc. Gulf Caribb. Fish Inst. 32:114-130.
- Parrish, J.D. 1987. The trophic biology of snappers and groupers, p. 405-463. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Powles, H. and C.A. Barans. 1980. Groundfish monitoring in sponge-coral areas off the southeastern United States. Mar. Fish. Rev. 42:21-35.
- Robins, C.R. and G.C. Ray. 1986. Peterson field guide: Atlantic Coast Fishes. Houghton Mifflin Company, Boston. 354 p.
- Sedberry, G.R., J.C. McGovern, C.A. Barans and C.A. Wenner. The ichthyofauna of sandy bottom habitat on the continental shelf off the southeastern U.S. In prep.
- Sedberry, G.R. and N. Cuellar. 1993. Planktonic and benthic feeding by the reef-associated vermilion snapper, *Rhomboptilus aurorubens*. Fish. Bull. 91(4):699-709.
- Sedberry, G.R. and R.F. Van Dolah. 1984. Demersal fish assemblages associated with hard bottom habitat in the South Atlantic Bight of the USA. Env. Biol. Fish. 11(4):241-258.
- Sedberry, G.R. and H.J. Carter. 1993. The fish community of shallow lagoon habitats in Belize, Central America. Estuaries 16(2):198-215.
- Sedberry, G.R. and D.J. Machowski. 1987. Species composition, abundance, biomass and distribution of fishes trawled from reef habitat on the southeastern continental shelf, 1878-1987. South Carolina Wildlife and Marine Resources Department.
- Starck, W.B. III and R.E. Schroeder. 1971. Investigations on the gray snapper, *Lutjanus griseus*. University of Miami Stud. Trop. Oceanogr. 16, 224 p.

- Struhsaker, P. 1969. Demersal fish resources: composition, distribution and commercial potential of the continental shelf stocks off the south-eastern United States. *Fish. Ind. Res.* 4:261-300.
- Wenner, C.A. 1983. Species associations and day-night variability of trawl caught fishes from the inshore sponge-coral habitat, South Atlantic Bight. *Fish. Bull.* 81:537-552.
- Wenner, C.A. and G.R. Sedberry. 1989. Species composition, distribution, and relative abundance of fishes in the coastal habitat off the southeastern United States. *NOAA Tech. Rep. NMFS* 79, 49 p.
- Wenner, C.A., C.A. Barans, B.W. Stender and F.H. Berry. 1979. Results of MARMAP otter trawl investigations in the South Atlantic Bight. I: Fall 1973. *S.C. Marine Resources Center. Tech. Rep.* 33, 79 p.
- Wenner, E.L., D.M. Knott, R.F. Van Dolah and V.G. Burrell, Jr. 1983. Invertebrate communities associated with hard bottom habitats in the South Atlantic Bight. *Estuarine Coastal Shelf Sci.* 17:143-158.
- Wenner, E.L., P. Hinde, D.M. Knott and R.F. Van Dolah. 1984. A temporal and spatial study of invertebrate communities associated with hard-bottom habitats in the South Atlantic Bight. *NOAA Tech. Rep. NMFS* 18, 104 p.

ENTERED IN NASA

APR 14 1998

The Ecology of Shallow-Water Groupers (Pisces: Serranidae) in the Upper Florida Keys, USA

K.M. SULLIVAN^{a,b}

R. SLUKA^a

^a*University of Miami, Department of Biology
Coral Gables, Florida 33124, USA*

^b*The Nature Conservancy, Florida and Caribbean
Marine Conservation Science Center
P.O. Box 249118, Coral Gables, Florida 33124, USA*

SULLIVAN, K.M. and R. SLUKA. 1996. The ecology of shallow-water groupers (Pisces: Serranidae) in the upper Florida Keys, USA [La ecología de meros de baja profundidad (Pisces: Serranidae) en los Cayos Superiores de Florida, USA], p. 74-84. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

The density, diversity and home range size of groupers were studied at different reefs in the upper Florida Keys, USA. Visual transects were used to estimate density and diversity on four different reef community classes: reef ridge, low-relief spur-and-groove, high-relief spur-and-groove, and channel patch reefs. Mean reef community class densities ranged from 0.52 to 0.63 groupers·100 m⁻². There were significant differences between reefs in the eroded reef ridge and eroded spur-and-groove classes. There were also significant seasonal and/or season by reef interaction factors in these two reef classes. There were no significant differences among different reefs in the high-relief spur-and-groove and channel patch reef community classes. Seven different species of grouper were identified in the surveys: Nassau (*Epinephelus striatus*), red (*E. morio*), coney (*E. fulvus*), graysby (*E. cruentatus*), red hind (*E. guttatus*), black (*Mycteroperca bonaci*), and yellowfin (*M. venenosa*). At three sites a transect was surveyed at different times of the day to determine whether or not grouper density varies diurnally. There were no significant differences in the numbers of groupers seen, based on time of day. At one site, Conch Reef, the home range size of graysby was examined by following individuals over 20-minute intervals. The home range size of graysby was estimated as 23.7 m² for 5-15 cm individuals and 27.6 m² for 15-25 cm individuals. These were not significantly different. The amount of area the graysby was observed to occupy was significantly correlated to the amount of time the individual was observed.

Resumen

La densidad, diversidad y el tamaño del sitio donde viven los meros fueron estudiados en diferentes arrecifes de los Cayos superiores de Florida, USA. Transectos visuales fueron usados para estimar la densidad y la diversidad en cuatro clases diferentes de comunidades de arrecife: arrecife de borde, salientes y surcos de bajo relieve; salientes y surcos de alto relieve; y manchones de arrecife acanalados. Las densidades medias de las clases de comunidad de los arrecifes variaron de 0.52-0.63 meros por cada

100 m². Hubo diferencias significativas entre los arrecifes del borde erosionado y los arrecifes erosionados formados por salientes y surcos. También hubo estacionalidad y/o estación significativa por factores de interacción de arrecifes en estas dos clases de arrecife. No hubo diferencias significativas entre las comunidades de arrecifes deformadas por salientes y surcos de alto relieve y los manchones de arrecifes acanalados. Siete especies diferentes de meros fueron identificadas en los viajes de campo: la cherna criolla (*Epinephelus striatus*), mero americano (*E. morio*), cherna cabrilla (*E. fulvus*), cherna enjambre (*E. cruentatus*), mero colorado (*E. guttatus*), cuna bonaci (*Mycteroperca bonaci*) y el cuna de piedra (*M. venenosa*). En tres sitios diferentes un transecto fué sujeto a observación en tres momentos del día para determinar hasta donde o dónde la densidad de meros presenta variaciones diurnas. No hubo diferencias significativas en el número de meros observados tomando como base la hora del día. En un sitio, Conch Reef, el tamaño del sitio donde habita la cherna enjambre fué examinado siguiendo a los individuos por períodos de 20 minutos. El tamaño del sitio donde habita la cherna enjambre fué estimado en 23.7 m² para peces de 5-15 cm y de 27.6 m² para individuos de 15 a 25 cm. No hubo diferencias significativas. La magnitud del área observada que ocupó la cherna enjambre fué significativamente correlacionada con el período de tiempo que los peces fueron observados.

Introduction

Fisheries scientists and managers recognize that grouper stocks throughout the tropical Western Atlantic have been overfished and are declining (Beets and Freidlander 1992; Sadovy and Figueira 1992; Beets et al. 1994; Sadovy 1994). The Florida Keys, USA, are situated at the northern edge of the distribution of many tropical groupers. The catch composition in Florida is more similar to the tropical Western Atlantic (or wider Caribbean) than northern subtropical and temperate grouper fisheries in the Gulf of Mexico and the northeastern coast of Florida (see Arreguín-Sánchez and Valero; Brulé and Déniel, this vol.). A commercial fishery for groupers has existed at least since the 1830s off Key West, Florida (Allen and Tashiro 1976). Anecdotal evidence suggests that both the catch amount and composition have changed dramatically over the past 30 years (Bohnsack unpubl.). Nassau grouper (*Epinephelus striatus*) were once abundant throughout the Florida Keys, being seen on almost every dive (Stark 1968). In the late 1950s, the relative abundance of commercially caught Nassau grouper was almost equivalent to black grouper (*Mycteroperca bonaci*) (Springer and McErlean 1962).

US grouper landings were fairly consistent from 1949 (4 640 t) to 1974 (3 136 t) (Allen and Tashiro 1976). The majority of the US catch came from Florida (89% in 1973). Most of the catch in Florida originated off the western coast in the Gulf of Mexico (91%) (Allen and Tashiro 1976). The commercial catch off the eastern coast of Florida ranged from 272 t in 1969 to 341 t in 1971 to 238 t in 1973. Red grouper (*E. morio*) and black grouper were important components during these years (Allen and Tashiro 1976). Headboat catch-per-unit-effort (CPUE) of Nassau grouper in the Florida Keys decreased from 0.175 fish per trip in 1981 to 0.025 in 1989 (Bohnsack, unpubl.). Black grouper CPUE decreased from 0.45 fish per trip in 1980 to 0.2 in 1989 (Bohnsack, unpubl.). There was an overall decrease of 48.6% in grouper landings in the Florida Keys and southwest Florida in 1989 over the 5-year mean (Brown et al. 1991).

Current information on the habitat requirements of epinepheline groupers is sparse and mainly qualitative. This is especially true for juveniles. In general, groupers tend to be more abundant on wide shelf areas rather than narrow shelf areas (Bannerot et al. 1987). They tend to be secretive fish, occupying caves, crevices and ledges (Smith 1961). The juveniles tend to be more nearshore

than adults (Stewart 1989). Nassau grouper can be found in high-relief coral reef areas and over rocky bottoms (Bannerot et al. 1987; Stewart 1989). The larger fish tend to occupy deeper water (Thompson and Munro 1978). Red groupers are mainly caught over rocky bottoms with crevices, ledges and caverns (Moe 1969) (see Arreguín-Sánchez et al.; Brûlé and Déniel, this vol.). The juveniles are found over hard bottoms (Jory and Iverson 1989). Red groupers under 50 cm tend to inhabit nearshore reefs (Beaumariage and Bullock 1976). Coneys (*E. fulvus*) and red hinds (*E. guttatus*) were found to be most abundant in Curaçao on isolated patch reefs surrounded by sandy bottoms (Nagelkerken 1981). Graysbys (*E. cruentatus*) are most abundant on coral reefs with high vertical relief and numerous holes, crevices, and caves for shelter (Nagelkerken 1981) where they hide between and under the corals (Nagelkerken 1979). The abundance of graysbys in Curacao was related to the quantity of coral cover and more specifically associated with *Montastrea annularis* and *Agaricia* spp. (Nagelkerken 1979), although Thompson and Munro (1978) caught graysbys in turtle grass beds.

The objectives of this investigation were three-fold:

- 1) to investigate what species of groupers co-occur on Florida reefs and their relative abundance;
- 2) to relate grouper diversity and abundance to definable reef community classes; and
- 3) to begin examining diurnal, seasonal and sampling biases for the monitoring of groupers on shallow reefs.

This study examines the density and species composition among four reef community classes: reef ridges, low-relief (eroded) spur-and-groove reefs, high-relief spur-and-groove reefs and channel patch reefs. Seasonal and diurnal changes in the number and species of grouper recorded are reported. Home range size of the most abundant species, *E. cruentatus*, is estimated.

Methods

The study identified twelve reef sites that could be labeled as one of four image-definable reef community classes. The reef community classes had been both described in the literature and had unique geomorphological characteristics (Table 1). Geological surveys and reef research in the upper Florida Keys identified unique reef classes within the larger bank-barrier reef system (Shinn et al. 1989). The reef community class have been described by Dustan and Halas (1987), Jaap et al. (1989) and Jaap (1984).

A low-relief spur-and-groove reef is found seaward of high-relief spur-and-groove reefs or seaward of reef ridges. The low-relief spur-and-groove reefs represent "drowned" or relic reefs and are erosional features characterized by higher sediment accumulation, visual predominance of octocorals, and sparse coverage of algae. High-relief spur-and-groove reefs are found seaward of a reef flat or reef crest. High-relief spur-and-groove reefs are characterized by high surge and high relief (up to 4 m rise over 1 m run). All the spurs in these communities are dominated by *Acropora palmata* or *Montastrea annularis*. Reef ridge communities (sometimes referred to as "transitional reef communities" in Jaap 1984) were built by *A. palmata* and "drowned" with rapid rises in sea level. Reef ridges had previously been reef crests; they extend seaward to the low-relief spur-and-groove communities. Reef ridge communities occur at depths similar to high-relief spur-and-groove communities. There are over 8 000 channel patch reefs in the upper Florida Keys; the patch reefs are found in Hawk Channel, a seagrass-dominated channel (5–7 m depth) between the islands and outer bank reefs. Channel patch reefs can have large isolated coral heads of *Montastrea* spp., *Siderastrea siderea*, *Colpophyllia natans* and *Diploria* spp. Channel patch reefs are typically dome-shaped and can have

Table 1. Summary of survey sites and sampling effort by community class.
[Resumen de sitios observados y esfuerzo de muestreo por clase de comunidad.]

	CLASS 1	CLASS 2
Reef class designation	Reef ridge	Low-relief spur-and-groove reef
Survey sites	Conch Reef Ridge Davis Reef Ridge Alligator Reef Ridge	Pickles Reef The Elbow Reef Davis Reef
Reef community class characteristics	- octocorals common - moderate relief - "drowned" reef crest	- low relief - sparse benthos - relic relief
Area surveyed (m ²)	17 392	16 240
Number of species recorded at all sites	5	4

	CLASS 3	CLASS 4
Reef class designation	High-relief spur-and-groove reef	Channel patch reef
Survey sites	Elbow Reef French Reef Pickles Reef	Hens-and-Chickens Three Sisters TS1 Three Sisters TS2
Reef community class characteristics	- high surge - high relief - seaward of reef crest	- large coral heads - high relief - high coral cover
Area surveyed (m ²)	18 960	8 226
Number of species recorded at all sites	6	3

abundant soft coral coverage. These reefs are characterized by high relief and have the highest coral cover of all reef classes (Jones 1977; Jaap 1984).

Observers were trained to consistently and accurately estimate the lengths of fish using a technique modified from Bell et al. (1985). The length, species and number of groupers observed was recorded within transects either 20 m or 50 m long and 12 m wide. Observers swam over each portion of the transect and examined all holes, caves and crevices. This tends to reveal smaller size classes and is recommended for surveying grouper density (Craik 1981).

Surveys were conducted throughout the day in the periods 1-18 April, 16-17 May, and 1-18 September 1993 by two to six observers. A two-factor Analysis of Variance (ANOVA) model was used to test for significant differences in the mean density of grouper between reefs and seasons.

At three sites (Conch Reef, Tennessee Reef and Alligator Reef), transects were repeatedly sampled between dawn and dusk to examine the effects of time of day on survey results. Chi-square analysis tested the null hypothesis that there was no difference in the number of groupers observed on the same transect among different times

of day. Two observers surveyed each transect. The maximum number observed between the observers at each time of day was used in the analysis.

In order to estimate the home range size of graysbys (*E. cruentatus*), a circular grid was marked out at Conch Reef (eroded reef ridge community; 24°57.21N, 80°27.26W) using weights with flagging tape. Flags were positioned at 2.5-m intervals along the four main compass directions and centered around an area where a number of graysbys had been observed. This produced a circular grid 20 m in diameter within which the movement of individual graysbys could be tracked. Prior to the observations, four 20-minute intervals were chosen in each of two observation periods: 0600-0800 and 1540-1800 hours. These periods were at dawn and dusk, the time periods that groupers would most likely be traveling the farthest in their foraging. Within each 20-minute observation, the position of a graysby was plotted on a map of the grid at 30-sec intervals. The home range size of the graysby was estimated by connecting the outermost observation points to form a polygon enclosing the movement patterns of the fish. The point method (Maling 1989) was used to determine the area of the polygon. If the grouper did not move over the duration of the observation period, the home range size was recorded as 1 m² for statistical analyses.

Results

A summary of the sites surveyed and sampling effort within each reef community class is provided to illustrate overall experimental design (Table 1). The mean number of grouper observed per 100 m² was determined for each reef class (Table 2). There were significant differences in the density of groupers between reefs of moderate (reef ridges) and low relief

(low-relief spur-and-groove reefs) (Table 2). There were no significant differences between high relief reefs within the high-relief spur-and-groove and channel patch reef classes. Reefs were combined within their respective reef classes and tested for differences between the two reef classes. There were no significant differences in the density of grouper between high-relief spur-and-groove reefs and channel patch reefs ($t[0.05(2),86] = 0.390$, $p>0.05$).

There were significant seasonal effects and/or reef by season interactions in the low to moderate relief reef community classes (reef ridges and low-relief spur-and-groove reefs) (Table 3). The seasonal effects on reefs within the low-relief spur-and-groove reef class resulted from an unusually high density value of 2.332 grouper 100 m⁻² on the deeper portion (13-17 m) of The Elbow Reef during the September sampling season. The majority of these groupers observed were small (< 15 cm TL) graysby. The season by reef interaction effects occurred in the reef ridges due to the density of grouper being higher at Davis Reef during the April sampling period than the September period and vice versa for Conch Reef. The interaction effect for reefs in the low-relief spur-and-groove reefs occurred due to the density of grouper being higher on Pickles Reef during the April sampling period than the September period and vice versa for The Elbow Reef. There were no seasonal effects or season by reef interaction effects in the high-relief spur-and-groove and channel patch reef classes.

Seven species of groupers were observed at reefs in the Florida Keys (Table 4). The high-relief spur-and-groove reefs had the most: six species were observed. Only three species were observed on channel patch reefs. Graysbys were observed on all reefs with the exception of Hens-and-Chickens channel patch reef site. Black groupers were not observed at all reef sites, but were observed on at least one site within each community class.

Table 2. Mean density of grouper (# 100 m⁻²) on four different reef classes in the Florida Keys. Class 1 = reef ridge, Class 2 = low-relief spur-and-groove reef, Class 3 = high-relief spur-and-groove reef, Class 4 = channel patch reefs. [Densidad media de meros (# 100 m⁻²) de cuatro clases de arrecife diferente en los Cayos de Florida. Clase 1: arrecife de borde; Clase 2: arrecife de sallentes y surcos de bajo relieve; Clase 3: arrecife de sallentes y surcos de alto relieve; Clase 4: manchones de arrecifes acanalados.]

	Class 1	Class 2	Class 3	Class 4
n	71	55	65	23
mean density	0.603	0.627	0.564	0.520
s	0.611	0.736	0.448	0.533
95 % CI	0.145	0.199	0.111	0.231

Table 3. Summary of analysis of variance results comparing differences between reefs within classes and seasonal effects. Class 1 = reef ridge, Class 2 = low-relief spur-and-groove reef, Class 3 = high-relief spur-and-groove reef, Class 4 = channel patch reefs. ** = p<0.01, ns = not significant, NA = not applicable, no interaction term due to one way ANOVA. [Resumen de los resultados del análisis de varianza comparando diferencias entre arrecifes dentro de las clases y efectos estacionales. Clase 1= arrecife de borde; Clase 2= arrecife de sallentes y surcos de bajo relieve; Clase 3= arrecife de sallentes y surcos de alto relieve; Clase 4= manchones de arrecifes acanalados. **p<0.01, n.s.= no significativa, na= no aplicable. No hay término de interacción debido al ANOVA de una vía.]

Factor	Class 1	Class 2	Class 3	Class 4
Reef	**	**	ns	ns
Season	ns	**	ns	ns
Reef x	**	**	ns	NA

Two transects were repeatedly sampled at Conch Reef at 0700-1800 hours on 3 April 1993 (Table 5). There were no significant differences between the observed number of groupers at each time of day ($\chi^2_{0.05,7} = 6.636$ and $\chi^2_{0.05,7} = 2.66$, $p>0.05$). At Tennessee Reef and Alligator Reef one transect was surveyed between 0730 and 2100 hours (Table 5). There were no significant differences among time of day ($\chi^2_{0.05,3} = 2.00$ for Tennessee Reef and $\chi^2_{0.05,3} = 3.33$ for Alligator Reef, $p>0.05$).

The home range size of graysby 5-15 cm in total length was estimated as $23.73 \text{ m}^2 \pm 5.51$ and for 15-25 cm graysby as

$27.57 \text{ m}^2 \pm 12.24$ (Table 5). There were no significant differences in the mean home range size of the two size classes ($t_{0.05}(2),63 = -0.592$, $p>0.05$). The maximum area covered by a graysby in the 20-minute observation period was almost three times greater in the 15-25-cm size class when compared to the smaller size class. Most individual graysbys were not observed for the entire 20-minute observation period due to their cryptic appearance and behavior. The amount of area covered during an observation period was significantly correlated with the duration of the observation ($r = 0.31$ $p<0.01$).

Table 4. Species of grouper observed on four different reef classes in the Florida Keys. Class 1 = reef ridge, Class 2 = low-relief spur-and-groove reef, Class 3 = high-relief spur-and-groove reef, Class 4 = channel patch reefs. [Especies de mero observadas en cuatro clases de arrecife diferentes de los Cayos de Florida. Clase 1= arrecife de borde; Clase 2= arrecife de sallentes y surcos de bajo relieve; Clase 3= arrecife de sallentes y surcos de alto relieve; Clase 4= manchones de arrecifes acanalados.]

Species	Class 1	Class 2	Class 3	Class 4
<i>Epinephelus cruentatus</i>	+	+	+	+
<i>E. fulvus</i>	-	+	+	-
<i>E. guttatus</i>	-	+	-	-
<i>E. morio</i>	+	-	+	+
<i>E. striatus</i>	+	-	+	-
<i>Mycteroperca bonaci</i>	+	+	+	+
<i>M. venenosa</i>	+	-	+	-

Discussion

There appeared to be some significant differences in either the density or diversity of groupers observed on all four classes of reef communities, but community class alone is too coarse for segregating and defining grouper communities. Specific habitat requirements between species may be partially related to relief and reef morphology. The shallow-water reef communities in the Florida Keys are dominated by graysbys. This species is found on all reef classes and can occur in very high densities. These results agree with previous studies relating abundance to the availability of refuge (caves and crevices) available in high-relief reef sites (Smith 1961).

The fact that graysbys were found on all reef community classes, rather than just on coral reefs with high vertical relief (Nagelkerken 1981, 1979) raises the question of what biological constraints existed on grouper distribution prior to the decline in populations of certain species such as Nassau, red and black groupers. Changes in grouper community structure with exploitation of certain species or habitat degradation would need to be understood to effectively design and manage marine fisheries reserves (Plan Development Team

1990). The abundance and prevalence of graysbys in these surveys suggest that there has been a change in the grouper communities off Key Largo from either overexploitation or poor recruitment. Thompson and Munro (1978) found an abundance of graysbys in heavily fished areas. They suggested this might be due to a low catchability or desirability to fishers.

The objectives of this investigation were to gain a better understanding of habitat requirements of grouper in addition to defining relative abundance and co-occurrence of species in the upper Keys. Within the reef community classes, there were significant differences within and between low to moderate relief communities (reef ridges and low-relief spur-and-groove reefs). Clearly, there are other characteristics beyond relief that are important to groupers. These benthic parameters such as coral, sponge and algae coverage may be related to foraging base and food availability. The density and diversity of groupers were most variable between the moderate- and low-relief reef sites. High-relief communities (high-relief spur-and-groove reefs and channel patch reefs) were not significantly different in density, but had fewer or different species. Channel patch

Table 5. Number of groupers observed at each time of day at a transect repeatedly surveyed. Hours indicate the starting time of surveys and (-) indicates no surveys during this time interval. [Número de meros observados a cada hora del día en un transecto observado repetidas veces. La hora indica el momento en el cual se inició la observación y (-) indica que no hubo observaciones durante esas horas del día.]

COMMUNITY CLASS/Site	Time (Hours)											
	0700	0730	0800	0930	1000	1100	1230	1400	1530	1700	1800	2100
REEF RIDGE Conch Reef 1	3	-	3	2	-	6	1	3	1	3	-	-
REEF RIDGE Conch Reef 2	3	-	2	2	-	2	5	4	3	3	-	-
REEF RIDGE Alligator Reef	-	-	-	-	5	-	-	3	-	-	7	9
LOW-RELIEF SPUR-AND-GROOVE Tennessee Reef	-	-	-	-	-	2	-	-	0	-	-	3

reefs had the fewest number of species (3) seen in a given reef community class.

Seasonal changes in the numbers of groupers can be dramatic, particularly with recruitment events. An increase in the density of groupers was only noted for graysbys at one reef site. Most of the published ecological data on groupers in the Florida Keys are derived from catch data. Moe (1969) examined the biology of red grouper primarily in the Gulf of Mexico off western Florida. Moor and Labisky (1984) investigated snowy grouper (*E. niveatus*) in the Florida Keys and found that this species could not support an extensive and sustained fishery. A number of studies have examined age and growth of certain species including snowy grouper (Moore and Labisky 1984), black grouper and Warsaw grouper (*E. nigris*) (Manooch and Mason 1987), and Jewfish (*E. itajara*) (Bullock et al. 1992). Bullock et al. (1992) examined the spawning and sexual differences of Jewfish. Jory and Iverson (1989) summarized ecological data available on black, red and Nassau groupers.

Sullivan (1993) examined grouper physiology and home range size in an experimental tank at Long Key, Florida. Groupers were divided into dwarf (*E. guttatus* and *E. cruentatus*) and giant species (*E. striatus*, *E. itajara* and *E. morio*) based on differences in life history strategies including maximum total length and age at sexual maturity. The development of an energy budget indicated a decreased potential for growth during the summer months. The effect of removing a congener on home range size was to increase activity and mean distance travelled and to decrease home range size. Although more active early in the morning and late in the day, groupers were accurately surveyed throughout the day by trained observers.

The combination of laboratory investigations, catch records and ecological studies will begin to provide some information on what species of groupers are likely

to co-occur on specific reef community types and at what range of densities. This type of detailed data is critical for the management of grouper stocks as well as the design and evaluation of marine fisheries reserves.

Acknowledgements

The work was supported by funds from The Nature Conservancy's Florida and Caribbean Marine Conservation Science Center and by field logistical support from the National Oceanic and Atmospheric Administration National Underseas Research Center Grant UNCW-9316 to K.M. Sullivan. We wish to thank M. Chiappone, T. Potts and J. Levy for field assistance and thanks to Dr. J. Bohnsack, National Oceanic and Atmospheric Administration-National Marine Fisheries Service for discussions and information on grouper surveys.

References

- Allen, D.M. and J.E. Tashiro. 1976. Status of the US commercial snapper-grouper fishery, p. 41-76. In H.R. Bullis, Jr. and A.C. Jones (eds.) Proceedings: Colloquium on Snapper-Grouper Fishery Resources of the Western Central Atlantic Ocean. Florida Sea Grant Progr. Rep. 17, 333 p.
- Bannerot, S., W.W. Fox, Jr. and J.E. Powers. 1987. Reproductive strategies and the management of snappers and groupers, p. 561-603. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder, Colorado.
- Beaumariage, D.S. and L.H. Bullock. 1976. Biological research on snappers and groupers as related to fishery management requirements, p. 86-94. In H.R. Bullis, Jr. and A.C. Jones (eds.). Proceedings: Colloquium on Snapper-Grouper Fishery Resources of the Western Central Atlantic Ocean. Florida Sea Grant Progr. Rep. 17, 333 p.
- Beets, J. and A. Friedlander. 1992. Stock analysis and management strategies for red hind, *Epinephelus guttatus*, in the US Virgin

- Islands. Proc. Gulf Caribb. Fish. Inst. 42:66-79.
- Beets, J., A. Friedlander and W. Tobias. 1994. Stock analysis of coney, *Epinephelus fulvus*, in St. Croix, US Virgin Islands. Proc. Gulf Caribb. Fish. Inst. 43:403-416.
- Bell, J.D., G.J.S. Craik, D.A. Pollard and B.C. Russel. 1985. Estimating length-frequency distributions of large reef fish underwater. Coral Reefs 4:41-44.
- Brown, A., Jr., J.A. Bohnsack and D. Harper. 1991. Automated landings assessment for responsive management (ALARM): Gulf of Mexico commercial reef fish landings, September 1991. Coastal Resources Division, Contrib. No. MIA-90/91-80.
- Bullock, L.H., M.D. Murphy, M.F. Godcharles and M.E. Mitchell. 1992. Age, growth and reproduction of Jewfish *Epinephelus itajara* in the eastern Gulf of Mexico. Fish. Bull. 90(2):243-249.
- Craik, G.J.S. 1981. Underwater survey of coral trout *Plectropomus leopardus* (Serranidae) populations in the Capricorn section of the Great Barrier Reef Marine Park. Proc. 4th Int. Coral Reef Symp. 4(1):53-58.
- Dustan, P. and J.C. Halas. 1987. Changes in the reef-coral community of Carysfort Reef, Key Largo, Florida. Coral Reefs 2:91-106.
- Jaap, W.C., W.G. Lyons, P. Dustan and J.C. Halas. 1989. Stony coral (Scleractinia and Milleporina) community structure at Bird Key Reef, Fort Jefferson National Monument, Dry Tortugas. Florida Marine Research Institute Publ. No. 46, 31 p.
- Jaap, W.C. 1984. The ecology of south Florida coral reefs: a community profile. United States Fish and Wildlife Service Rep. FWS/OBS-82/08, 138 p.
- Jones, J.A. 1977. Morphology and development of southeastern Florida patch reefs. Proc. 3rd Int. Coral Reef Symp. 3(2):231-235.
- Jory, D.E. and E.S. Iverson. 1989. Special profiles: life histories and environmental requirements of coastal fishes and invertebrates (south Florida) - black, red, Nassau groupers. U.S. Fish Wildl. Serv. Biol. Rep. 82(11-110) and U.S. Army Corps of Engineers, TR EL-82-4 21 p.
- Maling, D.H. 1989. Measurements from maps: principles and methods of cartography. Pergamon Press, Oxford, UK. 577 p.
- Manooch, C.S. III and D.L. Mason. 1987. Age and growth of the Warsaw grouper and black grouper from the Southeast region of the United States. Northeast Gulf Sci. 9(2):65-75.
- Moe, M.A., Jr. 1969. Biology of the red grouper (*Epinephelus morio* Valenciennes) from the eastern Gulf of Mexico. Prof. Pap. Ser. Mar. Lab. Fla. No. 10, 95 p.
- Moore, C.M. and R.F. Labisky. 1984. Population parameters of a relatively unexploited stock of snowy grouper in the lower Florida Keys. Trans. Am. Fish. Soc. 113:322-329.
- Nagelkerken, W.P. 1979. Biology of the graysby, *Epinephelus cruentatus*, of the coral reef of Curaçao. Stud. Fauna Curaçao 60:1-118.
- Nagelkerken, W.P. 1981. Distribution of the groupers and snappers of the Netherlands Antilles. Proc. 4th Int. Coral Reef Symp. 4(2):479-484.
- Sadovy, Y. and M. Figuerola. 1992. The status of the red hind fishery in Puerto Rico and St. Thomas as determined by yield-per-recruit analysis. Proc. Gulf Caribb. Fish. Inst. 42:23-38.
- Sadovy, Y. 1994. Grouper stocks of the Western Central Atlantic: the need for management and management needs. Proc. Gulf Caribb. Fish. Inst. 43:43-64.
- Shinn, E.A., B.H. Lidz, R.B. Hulley, J.H. Hudson and J.L. Kindinger. 1989. Reefs of Florida and the Dry Tortugas: Field trip guide T176. 28th International Geological Congress, American Geophysical Union, Washington, DC. 53 p.
- Smith, C.L. 1961. Synopsis of biological data on groupers (*Epinephelus* and allied genera) of the Western North Atlantic. FAO Fish. Biol. Synop. 23, 61 p.
- Springer, V.G. and A.J. McErlean. 1962. A study of the behavior of some tagged South Florida coral reef fishes. Am. Mid. Nat. 67:386-397.
- Stark, W.A. II. 1968. A list of fishes of Alligator Reef, Florida with comments on the nature of the Florida reef fish fauna. Undersea Biology 1:5-36.
- Stewart, V.N. 1989. Grouper. Sea-Stats No.8. Fla. Dept. Nat. Res., St. Petersburg, Florida. 13 p.
- Sullivan, K.M. 1993. Animal welfare considerations in field and laboratory investigations of energetic strategies of tropical

reef fishes, p. 179-187. In D.O. Schaeffer, K.M. Kleinow and L. Krulisch (eds.) The care and use of amphibians, reptiles and fish in research. Scientists Center for Animal Welfare, Bethesda, Maryland.

Thompson R. and J.L. Munro. 1978. Aspects of the biology and ecology of Caribbean reef fishes: Serranidae (hinds and groupers). *J. Fish Biol.* 12:115-146.

ENTERED IN NASA

APR 14 1998

A Molecular Approach to Stock Identification and Recruitment Patterns in Red Snapper (*Lutjanus campechanus*)

R.W. CHAPMAN

*Marine Resources Research Institute
South Carolina Wildlife and Marine Resources Department
Charleston, South Carolina 29412, USA*

S.A. BORTONE

*Department of Biology
University of West Florida
11000 University Parkway
Pensacola, Florida 32504, USA*

C.M. WOODLEY

*National Marine Fisheries Service
Charleston Laboratory
217 Johnson Road
Charleston, South Carolina, USA*

CHAPMAN, R.W., S.A. BORTONE and C.M. WOODLEY. 1996. A molecular approach to stock identification and recruitment patterns in red snapper, *Lutjanus campechanus* [Una aproximación molecular a la identificación del stock y el patrón de reclutamiento en el pargo del Golfo (*Lutjanus campechanus*)], p. 85-91. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

The genetic structure of red snapper has been investigated by amplifying several regions of the mitochondrial DNA molecule via the polymerase chain reaction. The amplified regions were digested with four base restriction enzymes and the resulting fragments separated by polyacrylamide gel electrophoresis. Two conserved regions of the molecule, cytochrome b and the 16 rRNA genes, exhibited only one variant in 40 surveyed individuals. The D-loop region of the molecule which is known to be variable in some species was invariant in red snapper. Additional primer sets are being developed to amplify the NADH-I region which has been highly polymorphic in other species. Given the limited variation found to date in red snappers, it is doubtful that sufficient variation will be found in the NADH-I region to identify discrete stocks. An alternative approach using microsatellites is being pursued in hopes of finding more polymorphic markers.

Resumen

La estructura genética del pargo del Golfo ha sido investigada mediante la amplificación de varias regiones de la molécula de DNA mitocondrial a través de la reacción en cadena de la polimerasa. Las regiones amplificadas fueron digeridas con cuatro enzimas de restricción base y los fragmentos resultantes separados por electroforesis en gel de políacrilamida. Dos regiones conservadas de la molécula, citocromo b y los 16 genes de RNAr, mostraron solamente una variante en 40 individuos analizados. La región con "giro a la derecha" de la molécula, la cual se sabe que es variable en algunas especies, fué invariable en el pargo del Golfo. De manera adicional están desarrollándose algunas pruebas para amplificar la región NADH-1 la cual ha sido altamente polimórfica en otras especies. Debido a la poca variación encontrada hasta ahora en el pargo del Golfo, es dudoso que suficiente variación sea encontrada en al región NADH-1 como para identificar stocks discretos. Una aproximación alternativa usando microsatélites está siendo implementada con la esperanza de encontrar más marcadores genéticos polimórficos.

Introduction

Conservation and management of living marine resources require in-depth knowledge of the organisms' life history, including such parameters as mortality, fecundity, habitat preferences, population size, etc. In marine species, these parameters are often difficult to assess, because the organisms are free to move over a wide geographic area and many of them produce pelagic eggs permitting long distance dispersal. This complicates estimates of life history parameters as the data must be taken from a single population or stock in order to be reliable. To overcome this problem, genetic analyses of stock structure have become increasingly important tools for fisheries management (cf. Powers et al. 1990).

Red snappers (*Lutjanus campechanus*) are found from the southeastern US, throughout the Gulf of Mexico and Caribbean and southward to Brazil (Bortone 1986) (see Collins et al.; Cuellar et al., this vol.). It is one of the most sought-after demersal fishes in the Gulf of Mexico, for both commercial and recreational fisheries (Moran 1988). The alpha taxonomy of the species is relatively well known, except that some debate still exists over the status of southern populations, which have been considered as a distinct species, *L. purpureus* (cf. Bortone 1986; Allen 1987). In US waters in the subtropical Western Atlantic and Gulf of Mexico, *L.*

campechanus is currently managed as part of the reef fish management plans (SAFMC/NMFS 1983; GMFMC 1990) due to declines in abundance over the past two decades. The larvae of this species are thought to be widely dispersed by oceanic currents, leading to the belief that a single stock exists within the Gulf of Mexico and perhaps throughout the US portion of the range.

Previous efforts to define stocks of red snapper within the Gulf of Mexico (Camper et al. 1993) found no evidence supporting stock separation using traditional methods to assess genetic variation in mitochondrial DNA (mtDNA). Camper et al. (1993) found 29 haplotypes in 86 specimens, but only two haplotypes were found in more than two specimens and the remaining haplotypes were usually found only once. Camper et al. (1993) reported levels of interpopulation diversity in this species as relatively low compared to other marine species. It is possible that the absence of stock structure within the Gulf of Mexico reported by Camper et al. (1993) may result from the limited variation identified by their technical approach. In this report, we assess genetic variation in mtDNA from red snapper using the polymerase chain reaction to amplify four regions of the molecule and four base restriction digests of the amplified product. Studies on four alosid species using this approach found much more variation than traditional methods using

six base digestion of the total mtDNA molecule (Chapman et al. 1994). Our goal is to identify the region(s) of the molecule that reveal sufficient variation to discriminate stocks, should they exist.

Materials and Methods

Samples were collected from the Gulf of Mexico near Panama City, Florida, Orange Beach, Alabama and Freeport, Texas, and by sampling commercial catches. Liver samples were preserved in 95% ethanol and blood in 1% SDS and returned to the laboratory. Liver samples were dried, digested with Proteinase K and phenol-chloroform extracted. Nucleic acids were then collected by ethanol precipitation. The samples were rehydrated in 100 ml of sterile water and 1-15 ml were used in PCR reactions depending upon the DNA content.

Amplification of the 12s-16s rRNA (bases 1109-2510 on the human genome), cytochrome b-D-loop (15560-16498), 6-ATPase (8566-9139), NADH dehydrogenase I (2525-4410) and 16s rRNA (2500-3058) regions followed the protocol of Kocher et al. (1989). Oligonucleotide sequences for the primers are given in Meyer (1993). Unincorporated nucleotides and Taq polymerase were removed from the amplified products by either phenol chloroform extraction and ethanol precipitation or by Magic PCR preps (Promega Biotechnology). The products were then digested by a battery of four base restriction enzymes and the resulting fragments separated on polyacrylamide gels. The gels were stained with ethidium bromide and photographed under UV light following Chapman and Powers (1984). Molecular weight estimates of the restriction fragments were made using multiple regression procedures in Lotus 1-2-3.

Restriction fragment patterns were assigned a letter designation for each enzyme. The first pattern encountered was assigned the letter and subsequent variants

were assigned B, C, etc. Composite haplotypes for each individual were composed of these letter designations arranging the restriction enzymes in alphabetical order. The frequency distributions of composite haplotypes in each population were then compared using the Roff and Bentzen (1989) chi-square test.

Results

Of the five primer sets attempted in this survey only the ND I (2525-4410) set failed to amplify *L. campechanus* mtDNAs. This primer set has functioned well in partially purified mtDNAs from a variety of species. The remaining primer sets functioned well, generating consistent amplifications from either blood or liver derived DNA.

Molecular weight estimates for the restriction fragments obtained by digesting the 12s-16s regions of *L. campechanus* mtDNA are presented in Table 1. In general these estimates total about 1 600 bases and are consistent with the estimate of the total amplified region obtained from agarose gel electrophoresis. The exceptions to this are estimates obtained from Alu I and Hpa II digests which were less than those obtained for the other restriction enzymes. In the Alu I digests, several low molecular weight bands were noted in the photographs, but these bands were too faint to score reliably. The single variant pattern seen in this region of the mtDNA was generated by a Cfo I digest (Table 1) and this pattern was seen in only one individual. No variant haplotypes were seen in the forty individuals amplified for the cyt b-D-loop or 6 ATPase regions (Table 2).

Unlike the other regions amplified in this study the 16s rRNA segment revealed substantial variation using four base digestions. Of the five restriction enzymes employed, four showed two variants each (Table 3). Composite haplotypes based upon these variants (Table 4) for 52 individuals revealed a total of ten distinct lineages. Five of these

Table 1. Estimated molecular weights of fragments obtained by digestion with the indicated endonuclease for the 1109-2500 (12s to 16s rRNA) region of *Lutjanus campechanus* mtDNA. [Pesos moleculares estimados de los fragmentos obtenidos por digestión con la endonucleasa especificada para la 1109-2500 (12s a 16s rRNA) región del DNA mitocondrial de *Lutjanus campechanus*.]

Alu	Cfo I	Hae III	Msp	Rsa	Hpa II
A	A	B	A	A	A
335	1 254	581	750	581	539
229	410	410	410	383	390
164	-	324	229	347	351
141	-	320	121	263	272
131	-	-	103	116	126
112	-	-	-	-	73
-	-	-	-	-	54
-	-	-	-	-	43
-	-	-	-	-	37
1 112	1 664	1 635	1 613	1 690	1 751
					1 262

Table 2. Composite haplotypes for three regions of the mtDNA molecule taken from 40 red snappers. [Haplótipos compuestos para tres regiones de la molécula de DNA-mitocondrial tomada de 40 individuos de pargo del Golfo.]

Region	N
1109-2500 (12s-16s rRNA)	
AAAAAA	39
ABAAAA	1
15560-16498 (cyt b-D-loop)	
AAAAAA	40
8566-9139 (6-ATPase)	
AAAAAA	40

Table 3. Molecular weight estimates for fragments obtained by digesting the 16s rRNA portion of *Lutjanus campechanus* mtDNA molecule with the indicated enzyme. All estimates are accurate to within 5%. [Pesos moleculares estimados para fragmentos obtenidos por la digestión de la región 16s rRNA de la molécula de DNA-mitocondrial de *Lutjanus campechanus*, con la enzima indicada. Todas las estimaciones son precisas a un nivel 95%.]

Alu I		Cfo I		Hae III		Rsa I		Taq I	
A	B	A		A	B	A	B	A	B
213	241	361		220	410	610	349	628	519
164	213	138		184	122	-	201	-	90
140	140	115		122	88	-	60	-	-
90	-	-		88	-	-	-	-	-

Table 4. Composite haplotypes found in the 16s rRNA portion (2 500-3 058) of *Lutjanus campechanus* mtDNA. Composite haplotypes are based upon patterns produced by the restriction enzymes from Table 3 in alphabetical order. [Composición de haplotipos encontrados en la región 16s rRNA (2500-3058) de DNA mitocondrial de *Lutjanus campechanus*. La composición de haplotipos está basada en los patrones producidos por las enzimas de restricción de la tabla 3, en orden alfabético.]

Haplotype	Orange Beach Alabama	Freeport Texas	Panama City Florida	Total
AAAAA	4	-	-	4
AAAAB	8	-	12	20
AABAA	1	-	1	2
AABAB	1	-	-	1
BAABC	1	-	-	1
BAABB	2	-	-	2
BAABA	2	-	-	2
BABBB	-	5	-	5
BAAAB	6	-	2	8
BAAAA	8	-	-	8

haplotypes are common (i.e., found in more than two individuals), three haplotypes are represented by two individuals and the rest were seen only once.

Geographically the distribution of mtDNA haplotypes clearly distinguish the Texas population as different from

Panama City, Florida or Orange Beach, Alabama populations. All five of the Texas specimens shared a common haplotype that was not observed at the other locations. The chi-square tests also differentiated Orange Beach from Panama City ($p < 0.001$).

Discussion

The results of this study are important to our understanding of mtDNA evolution and to the population structure of red snapper. These issues will be discussed in some detail. The data should, however, be viewed with some reservations as the sample sizes are somewhat restricted.

The vast majority of data on mtDNA variation within and among species is based upon six base digestion of the entire molecule (cf. Meyer 1993). In most of these studies, restriction site losses and gains are not mapped to specific regions of the molecule and we cannot judge the relative rates of change among various regions. Despite this limitation some generalities have emerged from sequencing studies of portions of this genome. Meyer (1993) compared mtDNA sequences of cod and frog and reported that the 16s rRNA portion was among the most conserved regions. In addition, it is generally accepted that the D-loop region is subject to higher rates of change than most other segments. In some species, the D-loop appears to be constrained and may evolve at a pace consistent with the rest of the mitochondrial genome (Shedlock et al. 1992). In the present study, our limited survey of variation in the D-loop indicates a rate of evolution very much slower than the 16s rRNA. In addition, our results are not consistent with the conclusion that the 16s rRNA is one of the more conserved elements of *L. campechanus* mtDNAs. This should not be taken as a challenge to the general conclusion regarding rates of evolution in this region. Meyer (1993) compared only 207 bases of this region in frog and cod, where our study surveyed variation in approximately 610 bases. It is possible that we found variation in a part of the region that was not assessed by Meyer (1993). In addition, we have no doubts about the conservation of this region in some species. We found no restriction site differences in a comparison of dusky and

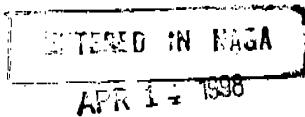
hammerhead sharks (two different families). This information was one of the reasons we did not examine the 16s rRNA region until recently. If the region is so highly conserved that one cannot differentiate families, there is little chance of finding intraspecific variation.

The geographic distribution of mtDNA haplotypes found in the 16s rRNA region clearly distinguishes populations of *L. campechanus* in the northern Gulf of Mexico. The data contrast markedly from those of Camper et al. (1993) where no evidence of population subdivision was observed. We believe that the difference is due to the distribution of mtDNA haplotypes in the two data bases. Most of the haplotypes reported by Camper et al. (1993) were represented by more than two individuals, permitting greater statistical power. In addition, the geographic distribution of common haplotypes was highly structured. All five of the BABBB haplotypes were found in the Texas specimens. These results should be viewed as provisional due to the limited number of individuals in the Texas specimens. Should further analyses of Texas specimens support the data presented here, a substantial revision of current plans for this species are in order.

References

- Allen, G.R. 1987. Synopsis of the circumtropical fish genus *Lutjanus* (Lutjanidae), p. 33-88. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder, Colorado.
- Bortone, S.A. 1986. State/Federal management of red snapper and gag, p. 103-111. In R.H. Shroud (ed.) Multi-jurisdictional management of marine fisheries. Marine Recreational Fisheries 11. National Coalition for marine Conservation, Inc., Savannah, Georgia, USA.
- Camper, J.D., R.C. Barber, L.R. Richardson and J.R. Gold. 1993. Mitochondrial DNA variation among red snapper (*Lutjanus*

- campechanus*) from the Gulf of Mexico. *Molec. Mar. Biol. Biotech.* 2:154-161.
- Chapman, R.W. and D.A. Powers. 1984. A method for the rapid isolation of mitochondrial DNA from fishes. *Maryland Sea Grant Tech. Rept.* No. UM-SG-TS-84-5.
- Chapman, R.W., J.C. Patton and B. Eleby. 1994. Comparisons of mitochondrial DNA variation in four alosid species as revealed by the total genome, the NADH dehydrogenase I and cytochrome b regions, p. 249-262. In A. Beaumont (ed.) *Genetics and evolution of aquatic organisms*. Chapman and Hall, London.
- GMFMC. 1990. Revised regulatory amendment of the reef fishery management plan. Gulf of Mexico Fishery Management Council, Tampa, Florida, USA.
- Kocher, T.D., W.K. Thomas, A. Meyer, S.V. Edwards, S. Paabo, F.X. Villablanca and A.C. Wilson. 1989. Dynamics of mitochondrial DNA evolution in animals. Amplification and sequencing with conserved primers. *Proceedings of the National Academy of Science* 86:6196-6200.
- Meyer, A. 1993. Evolution of mitochondrial DNA in fishes, p. 1-38. In P.W. Hochachka and T.P. Mommsen (eds.) *The biochemistry and molecular biology of fishes*. Vol. 2. Elsevier Science Publishers, Amsterdam.
- Moran, D. 1988. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (Gulf of Mexico) red snapper. *Biological Report* 82(11.83), 19 p. United States Army Corps of Engineers, TR EL-82-4.
- Powers, D.A., F.W. Allendorf and T.T. Chen. 1990. Application of molecular techniques to the study of marine recruitment problems, p. 104-121. In L.M. Alexander and B.D. Gold (eds.) *Large marine ecosystems; patterns, processes, and trends*. American Association for Advancement of Science, Washington, DC.
- Roff, D.A. and P. Bentzen. 1989. The statistical analysis of mitochondrial polymorphisms: chi-square and the problem of small samples. *Mol. Biol. Evol.* 6:539-545.
- SAFMC/NMFS. 1983. Fishery management plan for the snapper-grouper fishery of the South Atlantic Region. South Atlantic Fishery Management Council, Charleston, South Carolina and the National Marine Fisheries Service, Charleston, South Carolina.
- Shedlock, A.M., J.D. Parker, D.A. Crispin, T.W. Pietsch and G.C. Burmer. 1992. Evolution of the salmonid mitochondrial control regions. *Mole. Phylo. Evol.* 1:179-192.



Large Catches of Red Snappers by Tuna Purse Seiners off the West African Continental Shelf

A. CAVERIVIÈRE

Institut Français de Recherche Scientifique Pour le Développement en Coopération (ORSTOM) B.P. 1386 Dakar, Sénégal

CAVERIVIÈRE, A. 1996. Large catches of red snappers by tuna purse seiners off the West African continental shelf [*Grandes capturas del pargo colorado africano obtenidas por atuneros de cerco fuera de la plataforma continental del Oeste de África*], p. 92-95. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

This note reports summer catches of large (84-116 cm fork length) red snappers (*Lutjanus agennes*), often associated with tunas, by tuna purse seiners off Guinea Gulf coast (West Africa). Such high concentrations in surface schools beyond the continental shelf are surprising for a demersal coastal species but may be related to reproductive behavior.

Resumen

*Esta contribución reporta capturas de verano del gran pargo colorado africano (*Lutjanus agennes*), a menudo asociado con atunes, por barcos atuneros de cerco fuera de las Costas de Nueva Guinea (Oeste de África). Esas altas concentraciones en cardúmenes superficiales más allá de la plataforma continental son sorprendentes para una especie costera demersal. Esto podría estar, al menos parcialmente, relacionado a comportamiento reproductivo.*

On 27 October 1978, during daytime, the tuna purse seiner *Bougainville* caught 50 t of large red snappers (*Lutjanus agennes*) (Bleeker 1863). The catch location was 6°50'N-13°10'W (Fig. 1, location 1). Depth was more than 3 000 m and the nearest land (Cape St. Ann, Sherbro Island) was 45 nautical miles. As this refers to a demersal species known until then as littoral (Allen 1981), such a catch of about 2 500 specimens near the surface in open sea is

surprising. The purse seine also caught 2 or 3 t of yellowfin tuna (*Thunnus albacares*) weighing 30-40 kg each. The sea surface temperature was 27°C. Once landed in Abidjan, red snappers which were not deformed by freezing were measured (Fig. 2). All specimens were very large and exceeded the maximum length of 80 cm maximum suggested by Blache et al. (1970), and Séret and Opic (1981). Only three specimens were carried to the laboratory for

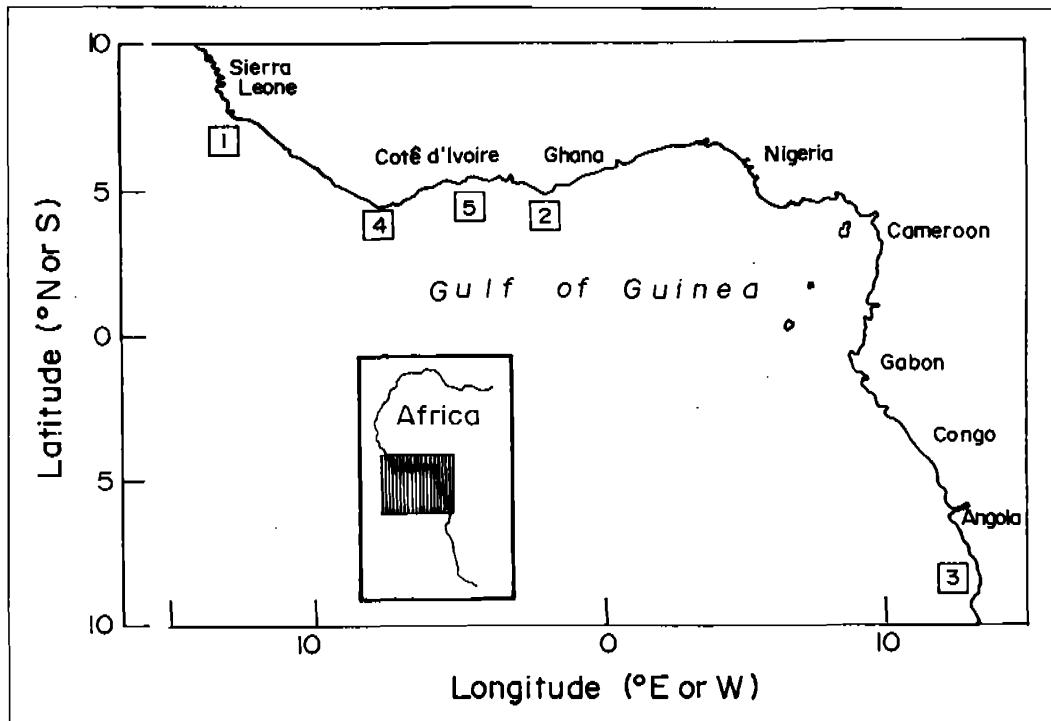


Fig. 1. Locations of red snapper fishing by tuna purse seiners. [Localidades de pesca del pargo colorado africano por barcos atuneros de cerco.]

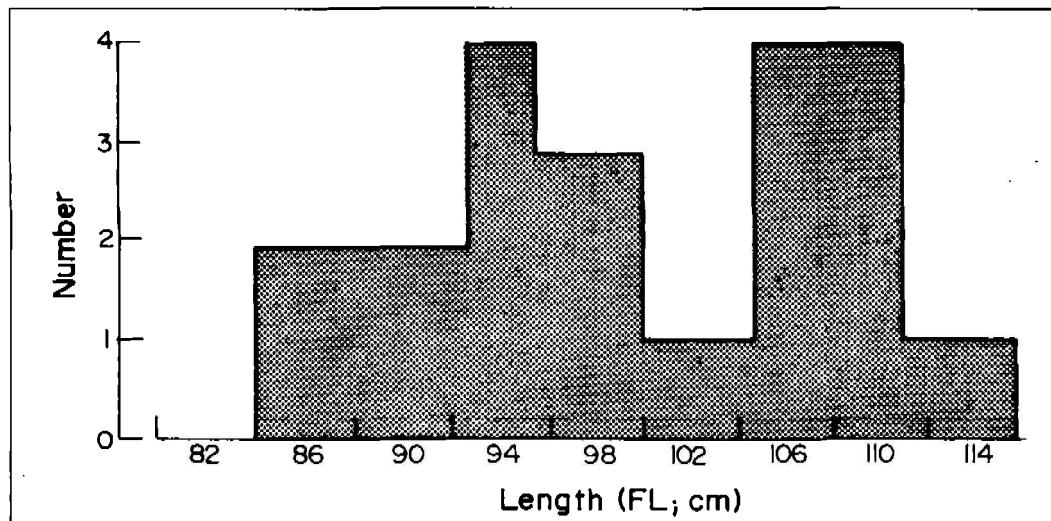


Fig. 2. Length-frequency distribution for a sample of red snapper (*Lutjanus agennes*) landed by the tuna purse seiner Bougainville. [Distribución de frecuencia de longitudes para una muestra de pargo colorado africano (*Lutjanus agennes*) descargados por el barco atunero de cerco Bougainville.]

stomach and gonad examinations (Table 1). Two were males in reproductive state and one was female with gonads in an advanced stage of maturation. The stomachs were empty.

During the 1970-1980 period, other records of catches of red snappers forming surface schools were found in tuna purse seiner logbooks.

On 11 March 1975, the purse seiners *Cap St. Paul* and *Kernevad* caught large red snappers in the south of Cape Three Points (Fig. 1, location 2) in fine weather. The *Cap St. Paul* fishing took place on a surface school visible by the naked eye and catch of 12.8 t was composed of lutjanids weighing 10-20 kg each. The location was south of Cape Three Points, near the continental shelf, above 1 500-2 000 m depth. The species was not exactly determined, but considering their lengths, these were probably *Lutjanus agennes*, *L. goreensis* (Valenciennes 1830) or *L. dentatus* (Duméril 1858). The haul of the *Kernevad* was composed of 10 t of red snapper, of 10-30 kg each, and of 25 t yellowfin (*Thunnus albacares*), and skipjack tuna (*Katsuwonus pelamis*), all of 4-5 kg each.

The tuna purse seiner *Jacques Coeur* also caught red snappers at the end of 1970,

west of Luanda (Angola) by 8°30'-8°40'S (Fig. 1, location 3). The purse seiner *Ille Boulay* also caught Lutjanidae in front of the Cape Palmas above 400-500 m depths (Fig. 1, location 4), mixed with skipjacks and small yellowfins.

More recently, on 12 March 1980, 60 nautical miles south of the coast of Côte d'Ivoire, at 4°07'N and 3°31'W (Fig. 1, location 5), the Spanish tuna purse seiner *Almadabra Uno* caught red snapper (without information on the quantity) mixed with 18 t of yellowfin, of 2-10 kg each, and skipjack, of 1-2 kg each. The sea surface temperature was 28°C.

It is possible to draw general considerations on the observations mentioned above (and in Caverivière 1981) and which concern four different years over the period from 1970 to 1980 (the more recent period is not documented): 1) the sea surface schools of red snapper were fished in the warm season, near the continental shelf; 2) all lutjanids caught were large; and 3) the association with tunas is common.

Knowledge of lutjanid biology is very poor for the East tropical Atlantic but better in the West tropical Atlantic, where there are several fisheries targeting red snappers. This is noteworthy in that if the East

Table 1. Biological observations on three *Lutjanus agennes* fished by the tuna purse seiner *Bougainville* (all stomachs were empty). [Observaciones biológicas de tres ejemplares de *Lutjanus agennes* obtenidos por el barco atunero de cerco *Bougainville*.]

Length (FL; cm)	Weight (kg)	Sex	Gonad weight (g)	Gonad state
97	17.5	male	855	flowing
108	23.0	male	860	mature
109	25.0	female	520	maturing

Atlantic red snappers are littoral species on rocky bottoms, most of the West Atlantic red snappers prefer deeper waters.

One hypothesis to explain such concentrations in surface schools of fishes living usually near the bottom and nearer the coasts in more scattered groups is that these concentrations are related to reproductive behavior. This hypothesis is supported by the fact that the schools fished were only composed of adults and were only seen in the warm season, which is the reproductive period for the West Atlantic Lutjanidae (the only ones for which a reproductive schedule is available). Further support for this hypothesis is the high maturation state of the gonads and the emptiness of the stomachs (Table 1). The phenomenon could denote a particular reproductive strategy, although the survival rates for larvae and juveniles (which usually develop near the coast) would be low so far from the coasts. Also, we can assume that the old red snappers forming these surface schools die quickly.

References

- Allen, G.R. 1981. Lutjanidae. In W. Fischer, G. Bianchi and W.B. Scott (eds). *Fiches FAO d'identification des espèces pour les besoins de la pêche. Atlantique centre est; zones de pêche 34, 47 (en partie). Vol II. Canada Fonds de Dépôt*, Ottawa, Ministère des Pêcheries et Océans, Canada, pag. var.
- Blache, J., J. Cadenat and A. Stauch. 1970. Clés de détermination des poissons de mer signalés dans l'Atlantique oriental (entre le 20° parallèle N. et le 15° parallèle S.). *Faune Tropicale*, XVIII. ORSTOM, Paris. 480 p.
- Caverivière, A. 1981. Note sur des pêches de bancs de lutjanidés par des thoniers senneurs au large des côtes de l'Afrique de l'ouest. *Centre Rech. Océanogr. Abidjan (Côte d'Ivoire)*, Doc. Sci., XII(1):91-94.
- Séret, B. and P. Opic. 1981. Poissons de mer de l'ouest africain tropical. ORSTOM (Paris) Init. Doc. Tec. 49, 450 p.

ENTERED IN LIBRARY

APR 14 1998

Uncommon Mortality of Groupers at the End of the Warm Season in the Coastal Area of Sénegal (West Africa)

A. CAVERIVIÈRE

*Institut Francais de Recherche Scientifique Pour
le Developpement en Cooperation (ORSTOM) B.P. 1386
Dakar, Sénégal*

D. TOURÉ

*Centre de Recherches Océanographiques de Dakar-Thiaroye
B.P. 2241 Dakar, Sénégal*

CAVERIVIÈRE, A. and D. TOURÉ. 1996. Uncommon mortality of groupers at the end of the warm season in the coastal area of Sénegal (West Africa) [Mortalidad poco común de meros al final de la temporada de calor en el área de las costas de Senegal (África Occidental)], p. 96-105. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

A large number of serranids, *Epinephelus guaza*, *E. aeneus* and *Mycteroperca rubra* were found, dead or alive, on the sea surface above the Sénégalese continental shelf, at the end of the warm season (October-November) in 1987 and, to a lesser extent, in 1988. Their abdomens were drastically distended. These events are probably related to exceptional hydrological conditions.

Resumen

Un gran número de peces serránidos fueron encontrados, muertos y vivos, en la superficie del mar sobre la plataforma continental de Sénegal, al finalizar la temporada de calor (Octubre-Noviembre) en 1987; y en 1988 con una menor magnitud. El abdomen estaba drásticamente distendido. Las especies observadas fueron *Epinephelus guaza*, *E. aeneus* y *Mycteroperca rubra*. Estos eventos podrían estar relacionados con condiciones hidrológicas excepcionales.

Introduction

In the beginning of October 1987, many very large demersal groupers (Serranidae) were found, dead and alive, above the Sénégalese continental shelf between Dakar and Cape Roxo (Fig. 1). Their abdomens were drastically distended. The concerned species were the dusky grouper (*Epinephelus guaza*), the white grouper (*Epinephelus aeneus*) and the comb grouper (*Mycteroperca rubra*). Later, it appeared that the Grande Côte of Sénégal and the southern shelf of Mauritania were also affected by this phenomenon. According to trawler captains, it also extended southwards, to the shelves of the Republics of Guinea Bissau and Guinea Conakry. The mortality induced by the phenomenon was extensive and in October 1987 many artisanal canoes went to the sea only to collect groupers on the surface. This mortality can be termed as "natural" because it was not induced by fishing gears. The fish caught still alive by the fishers were eaten without causing any health problems. The phenomenon appeared to diminish in November and the last information is dated 10 December, when a canoe landed 10 dusky groupers weighing about 100 kg, in Dakar. They had been collected alive, with their abdomens distended, near Joal.

At the end of the 1988 warm season, between September and the middle of November, new manifestations of this type of mortality were observed. They were a great deal less than those of the year 1987. According to old fishers, the phenomenon had been seen on occasions before 1987, always at the end of the warm season.

Scientific Observations of Groupers on the Sea Surface

During the two last weeks of October 1987, a trawl survey carried out on the entire Sénégalese continental shelf on the

R/V Louis Sauger permitted the observation of several groupers on the sea surface (Fig. 1).

The first grouper was located on 15 October in the North Gambia area ($13^{\circ}42'N$) above 32 m depth (Fig. 1, spot 1). It was a dead dusky grouper (*E. guaza*) weighing about 10 kg. The decomposed body prevented other observations. A bottom trawl tow carried out minutes before the discovery of the grouper caught a very small quantity of fish mainly composed of semipelagic species. The few specimens of demersal species were small in size.

On 18 October, three dusky groupers (*E. guaza*) and a white grouper (*E. aeneus*), apparently dead, were observed on the sea surface in front of the Sangomar peninsula ($13^{\circ}50'-13^{\circ}57'N$), above 8-12 m depth (Fig. 1, spot 2). The trawl tow underway prevented capturing them. According to the benthic habitat and the composition of the catch, these groupers had certainly drifted in from deeper waters.

On 22 October, a live white grouper was caught on the sea surface in front of the mouth of the Casamance river ($12^{\circ}37'N$) above 35 m depth (Fig. 1, spot 3). This grouper was still robust and only the drastically distended abdomen impeded its escape. Despite numerous attempts it was not able to dive below 2 m. It was 61 cm in total length and weighed 2.9 kg. The gills were apparently in excellent condition, as was the abdominal cavity. No parasite was seen by the naked eyes on and inside the fish. The stomach was empty. Only 16 kg of other fish were caught in the bottom trawl, mainly composed of semipelagic species. The few specimens of demersal species were very small in size. The water was very clear.

The last grouper observed on the sea surface was a white grouper, 57.5 cm in length and 2.1 kg in weight, caught alive to the north of Casamance ($12^{\circ}51'N$) above 50 m depth (Fig. 1, spot 4). Like the former, it was still very robust although its abdomen

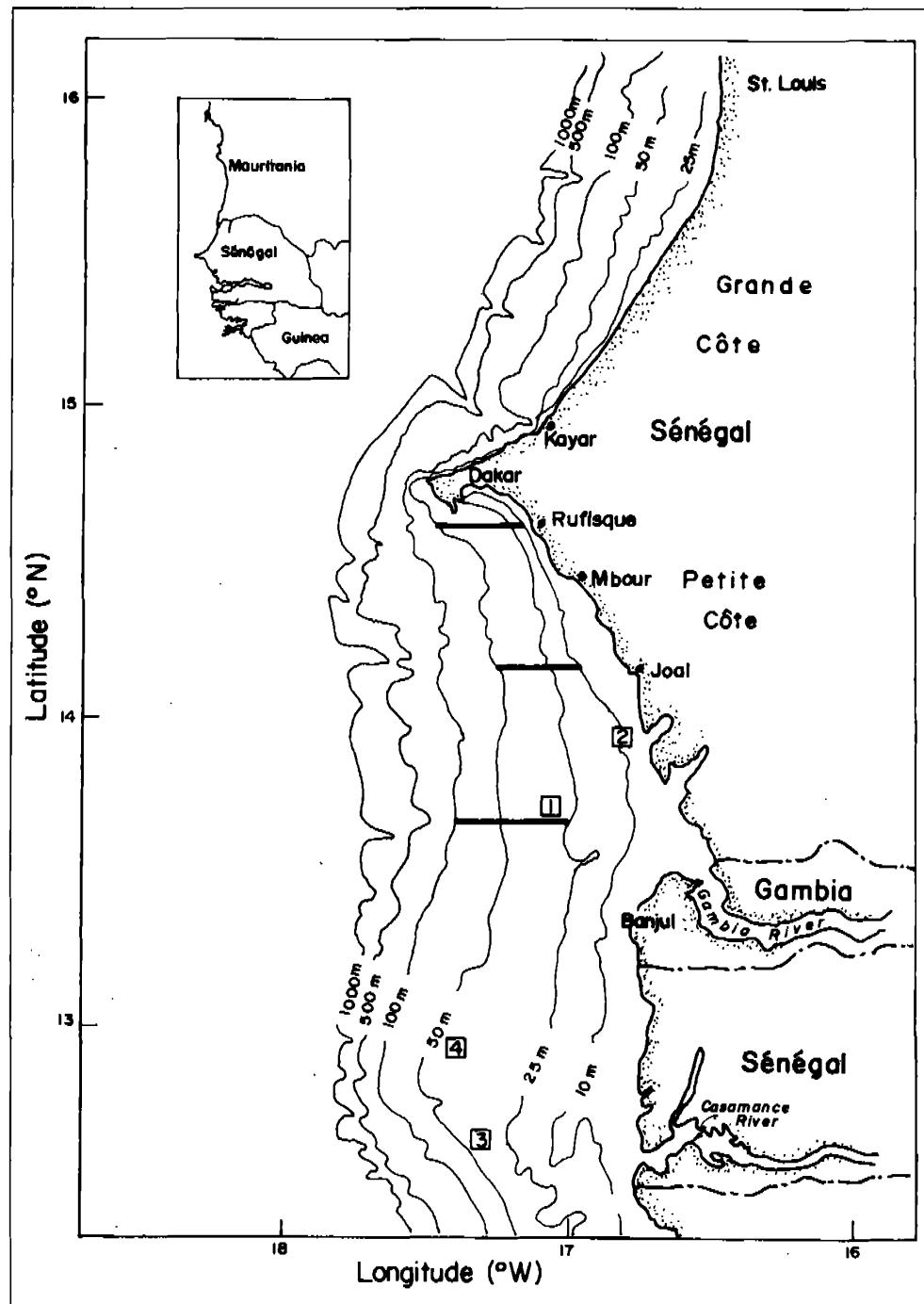


Fig. 1. Locations of the groupers (squares 1-4) observed on the sea surface by the R/V Louis Sauger and locations of the hydrological transects (—). [Localización de los meros (cuadrantes 1 a 4) observados en la superficie por el R/V Louis Sauger y localización de los transectos hidrológicos (—).]

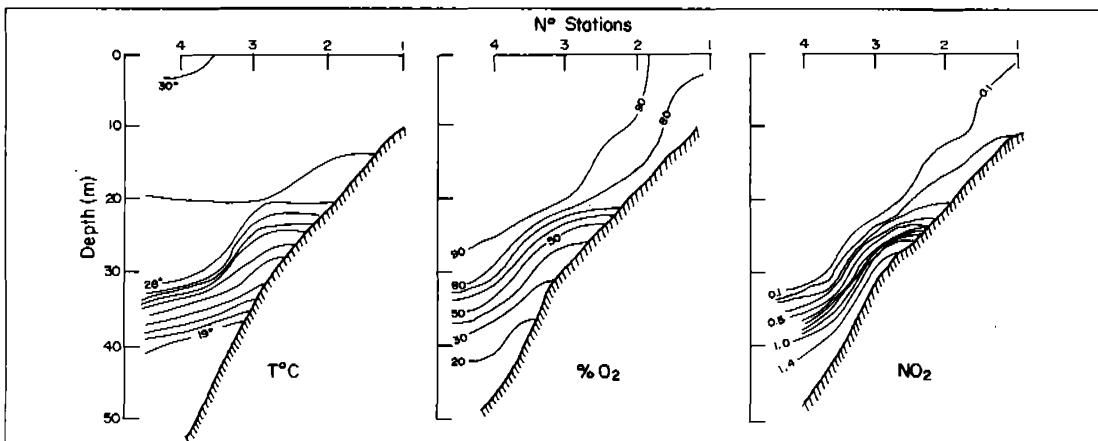


Fig. 2. Temperatures, saturation rates of dissolved oxygen and nitrite concentrations in the North-Gambia transect, October 1987. [Transecto al Norte de Gambia en Octubre de 1987. Temperaturas, tasa de saturación de oxígeno disuelto, y tasa de nitratos.]

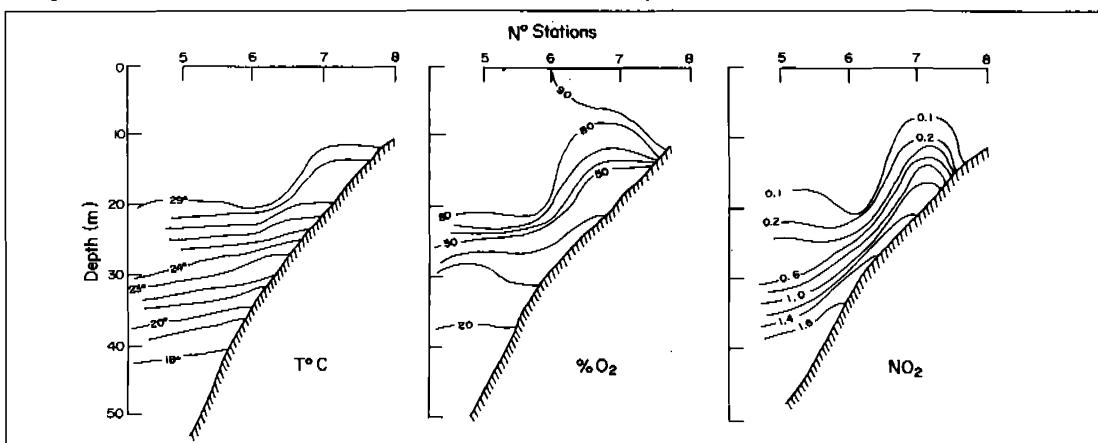


Fig. 3. Temperatures, saturation rates of dissolved oxygen and nitrite concentrations in the Joal transect, October 1987. [Transecto de Joal en Octubre de 1987. Temperatura, tasa de saturación de oxígeno disuelto y tasa de nitratos.]

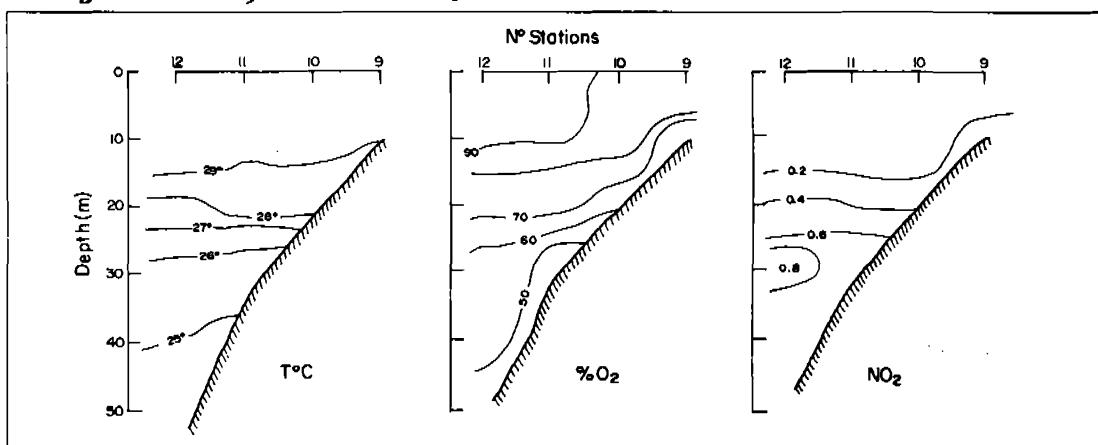


Fig. 4. Temperatures, saturation rates of dissolved oxygen and nitrite concentrations in the Rufisque transect, October 1987. [Transecto de Rufisque en Octubre de 1987. Temperaturas, tasa de saturación de oxígeno disuelto y tasas de nitratos.]

was very distended. A rough examination showed that a gill arch was broken. Two trawl hauls near to this point in 38 m and 52 m depths yielded 36 kg and 72 kg, respectively, mainly composed of semi-pelagic species with a few small-sized demersal specimens.

Between 27 and 31 October, the trawl survey along the Grande Côte (Dakar to Saint-Louis) showed no groupers on the sea surface. The observations may have been impeded by the state of the sea which was rough, but probably the phenomenon had stopped in this area, at least temporarily.

The Environmental Conditions

The two first days of the survey were used to determine the sea water conditions along three transects located in front of the Petite-Côte (Rufisque, Joal and North-Gambia transects) between the depths of 10 and 50 m (Fig. 1). The object was to compare the results with those obtained

during the sea water surveys carried out in the same area in the previous years (Caverivière and Touré 1990).

The temperature, salinity, dissolved oxygen and two salts (nitrates and nitrites) were the main physical and chemical parameters analyzed. Phytoplankton and zooplankton were also sampled.

Temperature

During the transects, an important warming of the sea surface was observed and sometimes the temperature went beyond 30°C, reading 30.5°C at the 40 m station of the North-Gambia transect. With the lack of wind, this warming resulted in the formation of a strong thermocline separating a stratum of homogeneous warm water from the deep cold waters. The longitudinal sections drawn in Figs. 2-4 clearly show the existence of a strong thermal gradient between 30 and 40 m. This thermocline is more marked in the southern and intermediate transects (North-Gambia and Joal) than in

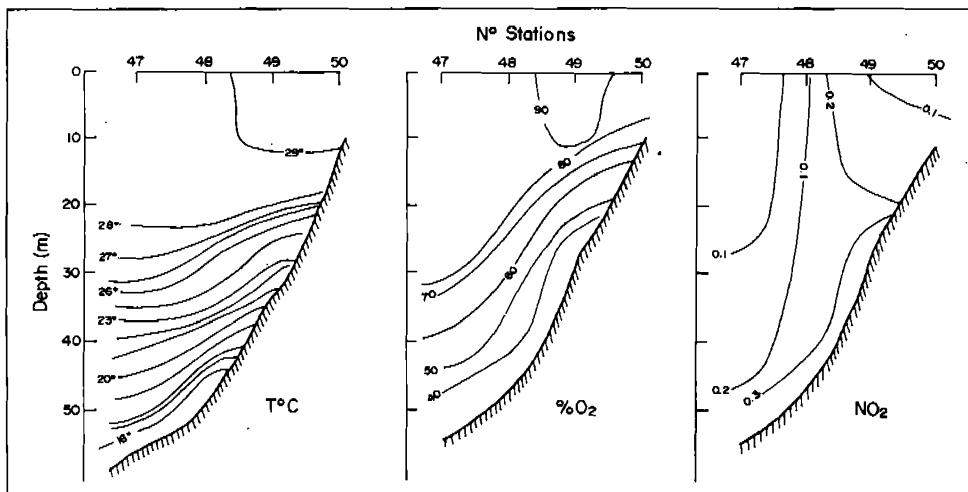


Fig. 5. Temperatures, saturation rates of dissolved oxygen and nitrite concentrations in the North-Gambia transect, October 1986. [Transecto al Norte de Gambia en Octubre de 1986. Temperatura, tasa de saturación de oxígeno disuelto y tasas de nitratos.]

the Rufisque transect. In the North-Gambia transect the thermal gradient reached values of up to 1°C per meter. The intermediate sea water layer with a strong thermal gradient also had a strong density gradient (pycnocline) which can form a barrier and reduce or impede exchanges between the homogeneous surface layer and the deep waters.

The standard situation in the warm season was shown by the North-Gambia transect in September 1986 (Fig. 5). The thermocline

is less marked with more separated isotherms. Exchanges by diffusion (molecular and turbulent) can occur more easily between the deep and shallower waters.

A study of the sea surface temperatures collected daily at two beaches, Mbour (Petite Côte) and Yoff (suburbs north of Dakar), showed that the entire summer of 1987 was particularly warm. Tables 1 and 2 show the monthly mean temperatures from July to October, since 1952 for Mbour and since 1974 for Yoff.

Table 1. Sea surface temperatures (°C). Monthly means (July to October) and warm season means in the Mbour coastal station (1952 to 1988). Values equal to or above 1987 values are in bold type. [Temperaturas de la superficie del mar (°C). Medias mensuales (Julio a Octubre) y medias de la época calurosa en la estación costera Mbour (1952-1988). Valores iguales o mayores a los presentados en 1987 se muestran en negritas.]

Month Year	July	August	September	October	MEAN
1952	28.4	28.1	28.4	27.8	28.2
1953	27.7	28.6	28.6	28.2	28.3
1954	27.7	28.3	28.9	29.3	28.6
1955	(28.7)	(28.7)	(29.2)	(29.0)	(28.9)
1956	28.0	28.4	28.0	28.8	28.3
1957	27.3	28.3	28.5	26.1	27.6
1958	28.3	27.7	29.1	28.7	28.5
1959	28.2	27.7	28.8	28.5	28.3
1960	27.4	28.5	28.4	28.6	28.2
1961	27.8	27.9	28.4	27.8	28.0
1962	27.9	28.1	27.9	28.9	28.2
1963	28.2	28.6	28.8	27.8	28.4
1964	27.5	27.8	27.6	28.1	27.8
1965	27.3	27.2	27.7	27.9	27.5
1966	27.5	28.0	28.4	28.6	28.1
1967	(28.8)	(28.8)	(28.4)	(27.8)	28.5
1968	26.9	28.2	28.7	28.3	28.0
1969	28.6	28.8	28.8	28.8	28.8
1970	27.6	28.1	28.7	28.7	28.3
1971	27.7	28.2	28.8	28.5	28.3
1972	27.1	28.4	28.9	28.9	28.3
1973	27.9	28.9	28.7	28.4	28.5
1974	27.4	28.4	29.0	27.5	28.1
1975	28.2	29.0	28.2	28.9	28.6
1976	27.6	28.7	29.1	28.6	28.5
1977	28.4	28.6	29.0	28.7	28.7
1978	27.9	28.6	28.6	28.5	28.4
1979	28.1	28.7	28.8	28.6	28.6
1980	27.4	28.5	29.3	28.0	28.2
1981		28.5	29.3	28.5	(28.8)
1982	27.8	28.4	29.0	28.4	28.4
1983	28.2	28.4	29.1	29.1	28.7
1984	27.9	29.0	28.5	28.1	28.4
1985	27.8	28.6	28.4	29.0	28.5
1986	27.4	28.5	28.7	28.7	28.3
1987	28.6	29.2	29.1	29.1	29.0
1988	27.9	28.4	28.6	28.2	28.3

Table 2. Sea surface temperatures (°C). Monthly means (July to October) and warm season means in the Yoff coastal station (1974 to 1988). Values equal to or above 1987 values are in bold type. [Temperatura de la superficie del mar (°C). Medias mensuales (Julio a Octubre) y medias de la época calurosa en la estación costera de Yoff (1974 a 1988). Valores iguales o mayores a los de 1987 se muestran en negritas.]

Month Year	July	August	September	October	MEAN
1974	26.8	27.3	27.8	25.9	27.0
1975	26.8	27.7	27.4	27.0	27.2
1976	26.9	27.6	27.9	26.9	27.3
1977	27.0	27.0	27.0	25.9	26.7
1978	26.9	27.7	27.7	27.1	27.4
1979	26.8	27.6	27.9	27.1	27.4
1980	27.0	27.1	27.3	25.8	26.8
1981	27.3	28.0	28.5	28.2	28.0
1982	27.8	27.7	28.7	27.4	27.9
1983	28.1	28.2	28.3	28.5	28.3
1984	26.9	27.2	27.5	26.0	26.9
1985	26.2	27.7	27.5	26.3	26.9
1986	27.0	27.6	27.7	26.8	27.3
<u>1987</u>	27.9	28.2	28.2	27.7	28.0
1988	26.9	27.9	27.6	25.9	27.1

Dissolved oxygen

In October 1987 the saturation rates in dissolved oxygen for the homogeneous surface layer were similar to the rates observed in September 1986. In contrast, the rates were abnormally low on the grounds deeper than 30 m on the Joal and North-Gambia transects. In 1987 the absolute values (1.5 ml/l and sometimes 1.1 ml/l at 40 m) were much lower than those observed during the standard period.

This strong oxygen deficit could be explained by the existence of an intermediate sea water layer with a strong density gradient. This density barrier impedes all exchanges between the homogeneous surface layer rich in oxygen and the deeper layer. In this case the dissolved oxygen contained in the deep layer cannot be renewed. It would be slowly consumed by the organisms living in these waters and on the bottom, as well as by the decomposition of organic matter.

Nitrites

At first, the degradation of the nitrogenous organic products (ammonia eliminated by gills, excrement, plants, dead organisms) forms ammoniated compounds. These compounds are then transformed into nitrites (NO_2^-) by bacteria, after which other bacteria transform the nitrites into nitrates (NO_3^-). All these microorganisms are oxygen consumers and a strong oxygen deficit could slow the last step, the nitrate production by specialized bacteria, and consequently increase nitrite concentrations. Nitrite toxicity in fish is a great deal higher than nitrate toxicity (Terver 1985).

In October 1987 (Figs. 2-4) the nitrite concentrations in the homogeneous surface layer were normal. In contrast, the deeper waters showed concentrations of up to $1.73 \mu\text{g.l}^{-1}$. In the standard situation (September 1986) the maximum reaches only $0.3 \mu\text{g.l}^{-1}$ (Fig. 5).

Phytoplankton and zooplankton

The biomasses of phytoplankton and zooplankton sampled during the transects were low but showed the usual species composition. It is possible that the last windy periods at the end of the rainy season enabled the release and/or an increase of inorganic salts into the euphotic area and consequently a phytoplankton bloom. Once a high water stability occurred, this phytoplankton could have been subject to a high mortality and formed a deposit on the bottom. Then, the aerobic bacteria could have proliferated, leading to an increase in nitrite. In a new fish tank, the concentration of toxic nitrites reaches a maximum 17 days after the tank has been put into service (Terver 1985); prior to that the bacteria transforming nitrites into nitrates are not sufficiently abundant. This lack may be of the same magnitude in the open sea, where the bacterial counts are low under normal conditions.

Discussion

Two factors may be related to the presence of groupers occurring on the surface with abdomens distended by a gas which cannot be evacuated, and consequently impede diving and finally cause death. The first can be an exogenous factor related to the environmental conditions, and the second an endogenous factor, e.g., a disease.

The exogenous factor could be related to the strong oxygen deficits and the strong nitrite concentrations observed on the 30-40 m grounds, where groupers prefer to live. Respiratory difficulties could have forced the fish to rise too quickly. In this case, the gas contained in the swim bladder expands and if the fish cannot evacuate a part of this gas quickly and/or slow down

its ascent, then it will necessarily be carried away to the surface. It is dangerous for fish that have no pneumatic duct connecting the swim bladder to the alimentary canal (i.e., physoclists) to make sudden upward movements (Bertin 1958). Then, the swim bladder can explode or a general hernia of viscera into the mouth can occur. This is often observed during the capture of serranids by trawl or hooks, particularly for *E. guaza* and *E. aeneus*.

Generally a decrease of dissolved oxygen in water below a certain level results in the escape of the fish, without mortality. Troadec (1971) showed that in Côte d'Ivoire, where the fish communities are similar to those in Sénégal, the yields of some species decrease when the dissolved oxygen levels are below 2.0 ml/l. This phenomenon also must be true in Sénégalese waters because, as indicated above, the trawl catches were low, and principally consisted of semipelagic species, when groupers were observed on the surface. The effect of the low oxygen concentrations on respiration could have been increased by the effect of nitrite concentrations five times higher than normal: nitrites are toxic salts acting on the oxygen fixation by haemoglobin (Terver 1985).

The bibliographic study of Person-Le Ruyet (1986) on the oxygen requirements of marine fish indicates that these requirements can be increased strongly by temperature increases. According to the adaptability of the species, a 10°C temperature variation could double, triple or even quadruple oxygen requirements.

In all instances there are few species which can maintain normal metabolic activity under a very large thermal increase. Incidentally, it is worth noting that Sénégalese groupers are subject to strong thermal variations between summer and winter, generally higher than 10°C. In 1987, the maximum amplitude of the sea surface temperatures

was 12.2°C (17.9°C to 30.1°C) in Mbour beach. Moreover, the critical threshold of respiratory dependence (oxygen concentration threshold below which there is a direct correspondence between consumption and oxygen availability) increases if the other environmental conditions are not optimal; this must be the case in the warm season and particularly at the end of the 1987 summer. In contrast, the critical threshold is reduced if there is a progressive acclimation of the fish to low oxygen pressures. The critical threshold is high; for marine species it is always above 4.5 ppm (3.2 ml/l). The lethal threshold for the entire population (LD_{100}) is a great deal lower when all other conditions are good: 0.3 to 0.6 ml/l. No data exist for LD_{10} and LD_{50} .

If the hypothesis on respiratory difficulties is correct, we can assume that the groupers will have stayed too long in unfavorable waters, which may be related to their territorial habits. It is well known that serranids, particularly the dusky grouper *Epinephelus guaza*, choose a shelter in the middle of their hunting territory and are, with age, increasingly reluctant to move away from it. According to Neill (1967), *E. guaza* generally would not venture 5 m beyond its territory. When the environmental conditions became intolerable, probably first for the big groupers whose oxygen requirements are considerable, it would have been too late to swim away following the bottom and the fishes had no choice but to swim towards the surface.

Alternatively the mortality may have been induced by an endogenous factor, e.g., a bacterial infection leading to release of gas into the visceral cavity or the swim bladder. This epidemic would, however, have to be narrowly linked to the hydrological conditions, because it occurred only in the

warm season, particularly towards the end: during the end of the *R/V Louis Sauger* survey in October 1987, groupers on the sea surface were not observed to the north of Sénégal, between Dakar and Saint-Louis. At this time, the trade winds had already induced a return to a more normal hydrological situation by breaking the stratification.

Moreover, diseases and parasites previously known among the groupers *Epinephelus guaza* and *E. aeneus* (Bruslé 1985) do not seem related to the mortality observed in Sénégalese waters.

Conclusion

It is concluded that the high unusual mortality of groupers observed in October 1987 resulted from abnormal environmental conditions. It seems likely that significant warming of the surface waters and the lack of wind had induced a strong vertical gradient (thermocline and pycnocline) separating the homogeneous warm water from the deep cold waters and that respiration and decomposition resulted in an oxygen deficit below 30-40 m. The large increase in nitrites was probably related to the oxygen deficit. It is believed that respiratory difficulties induced by low dissolved oxygen levels, aggravated by the abnormally high nitrite concentrations, led to the grouper mortality. The results of benthic trawl tows at 30-50 m showed that most of the fish species had moved, particularly the demersal fishes. However, the chain of events leading to inflation of the grouper swim bladders is not clearly understood and the occurrence of an epidemic disease, almost surely related to the environmental conditions, cannot be dismissed.

References

- Bertin, L. 1958. Vessie gazeuse, p. 1342-1362.
In P.P. Grassé (ed.) *Traité de zoologie*.
 Tome XIII. Fasc. II. Masson, Paris.
- Bruslé, J. 1985. Exposé, synoptique des données biologiques sur les mérous *Epinephelus aeneus* (Geoffroy Saint Hilaire, 1809) et *Epinephelus guaza* (Linnaeus, 1758) de l'Océan Atlantique et de la Méditerranée. FAO Synop. Pêche 129, 64 p.
- Caverivière, A. and D. Touré. 1990. Note sur les mortalités de mérou (Serranidae) observées en fin de saison chaude devant les côtes du Sénégal, particulièrement en 1987. Centre Océanogr. (Dakar-Thiaroye) Doc. Sci. 116:43-63.
- Neill, J.R. 1967. Observations on the behaviour of the grouper species *Epinephelus guaza* and *E. alexandrinus* (Serranidae). Underwat. Assoc. Rep. 1966-67: 101-106.
- Person-Le Ruyet, J. 1986. Les besoins en oxygène des poissons marins et leur comportement en conditions hypoxiques. Revue bibliographique. IFREMER (Brest, France) DRV-86-04, 24 p.
- Terver, D. 1985. Manuel d'aquariologie. L'aquarium d'eau douce - eau de mer. Réalisations Editoriales Pédagogiques, Paris. 303 p.
- Troadec, J.P. 1971. Biologie et dynamique d'un Sciaenidae ouest-africain, *Pseudotolithus senegalensis* (V.). Centre Rech. Océanogr. (Abidjan) Doc. Scient. 3, 225 p.

ENTERED IN NAGA

APR 14 1998

Groupers and Snappers of India: Biology and Exploitation^a

P.S.B.R. JAMES

V. SRIRAMACHANDRA MURTY

P. NAMMALWAR

*Central Marine Fisheries Research Institute
Cochin-14, India*

JAMES, P.S.B.R., V. SRIRAMACHANDRA MURTY and P. NAMMALWAR. 1996. Groupers and snappers of India: biology and exploitation [*Meros y pargos de la India: biología y explotación*], p. 106-136. In F. Arregui-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

The fishes of the families Serranidae (groupers) and Lutjanidae (snappers) are an important resource along the Indian coast. They are represented by 79 species in the Indian seas, reach up to 2 m and are abundant in and around rocky outgrowths and coral ridges at depths extending to about 360 m. Their exploitation presently yields an average annual landing of 8 000 t or about 3% of total Indian marine fish landings. This paper summarizes present knowledge on distribution, exploitation, culture and biology of groupers and snappers in India.

Resumen

Los peces de la familia Serranidae (meros) y Lutjanidae (pargos) representan un importante recurso a lo largo de las costas de la India. Están representados por 79 especies dentro de los mares de la India, algunos alcanzan mas de 2 m de longitud y son abundantes dentro y en los alrededores de fondos rocosos y bordes arrecifales a profundidades que se extienden a mas de 360 m. La explotación rinde actualmente un promedio anual de 8 000 t que equivalen al 3% del total de peces marinos descargados en la India. Este trabajo sintetiza el conocimiento actual sobre la distribución, explotación, cultivo y biología de meros y pargos de la India.

^a This contribution was assembled by the editors based on two submitted manuscripts: "Groupers and snappers of India: their distribution, exploitation and biology" by P.S.B.R. James and V. Sriramachandra Murty, and "Studies on the fishery, biology and cultivation of groupers and snappers along the Indian coast - exploitation and management" by P. Nammalwar, and complemented by a FishBase list of the groupers and snappers of India, also used to update the scientific names of the originals.

Introduction

Groupers belonging to *Epinephelus* and other genera (Family Serranidae) are large-sized marine food fishes reaching up to 270 cm in length and weights of up to 455 kg. Thirty-eight species of groupers have been reported from the seas around India (Appendix I). Most species of groupers inhabit coral reefs and rocky habitats but some show a preference for seagrass beds and muddy or sandy bottoms. Juveniles of some species of groupers are also found in upper reaches of estuaries. Most species are solitary and all are predators on fishes and invertebrates including crabs and lobsters. Usually, groupers are protogynous hermaphrodites, i.e., they first mature as females, then transform into males. Groupers are excellent food fishes and hence have assumed importance for commercial culture in various countries, including India.

Snappers (Family Lutjanidae) are brightly colored, predatory marine fishes reaching 170 cm and weights of up to 57 kg. Forty-one species of lutjanids have been reported from the seas around India (Appendix II). Most of them are demersal, and occur in shallow coastal waters and coral reefs; juveniles of some species of snappers are also found in estuaries. Snappers are predators of fishes and invertebrates, mainly crabs and prawns. Being excellent food fishes, snappers are gaining importance in mariculture.

Distribution

Exploratory and experimental fishing surveys by different agencies in India have generated valuable information on the distribution of groupers and snappers around the country (Gopinath 1954; Menon and Joseph 1969; Silas 1969; Menon et al. 1977; Bapat et al. 1982; Ninan et al. 1984; Somavanshi and Bhar 1984; Philip et al. 1984; Sivaprakasam 1986; Joseph et al. 1987;

Sulochanan and John 1988; and Oomen 1989). The Indian coast is divided into four regions: 1) northwest consisting of Gujarat and Maharashtra states; 2) southwest consisting of Goa, Karnataka and Kerala; 3) southeast consisting of Tamil Nadu, Pondicherry and Andhra Pradesh; and 4) northeast consisting of Orissa and West Bengal (Fig. 1).

Northwest: Bapat et al. (1982) conducted a survey in 1977 from 24°N (55-360 m depth) with a 70-m vessel using bottom and pelagic trawls. A total of six cruises were made during which 247 bottom trawl and 542 pelagic trawl hauls were taken.

The highest bottom trawl catch rate, of $88 \text{ kg} \cdot \text{hour}^{-1}$, was obtained at 17°N 126-360 m during April-May followed by $69 \text{ kg} \cdot \text{hour}^{-1}$ at 91-125 m at the same latitude, also in April-May. Among groupers, six species (*Epinephelus areolatus*, *E. fasciatus*, *E. malabaricus*, *E. lanceolatus* and *E. latifasciatus*) contributed to the catches. During the entire bottom trawl survey, the highest catch rate of groupers, of $13.3 \text{ kg hour}^{-1}$ was obtained from 91-125 m, followed by 6.1 kg hour^{-1} in 126-360 m and 1.93 kg in the 55-90 m depth zone. The highest catch rate of pelagic trawls was $43.5 \text{ kg hour}^{-1}$ in the 126-360 m depth zone, at 19°N during February-April, and next was 9.7 kg hour^{-1} at 20°N, from 55-90 m during November-December. In the pelagic trawl survey as a whole, the highest catch rate of 0.7 kg hour^{-1} was obtained at 126-360 m depth followed by 0.3 kg hour^{-1} at 55-90 m depth and zero in the 91-126 m depth range.

In this survey, the snappers also were represented by six species (*Lutjanus argentimaculatus*, *L. johnii*, *L. vitta*, *L. malabaricus*, *L. sanguineus* and *L. fulvus*). For bottom trawling, the catch rate of snappers was $4.6 \text{ kg} \cdot \text{hour}^{-1}$ in the 91-125 m depth range followed by $1.89 \text{ kg} \cdot \text{hour}^{-1}$ in the 126-360 m and $1.5 \text{ kg} \cdot \text{hour}^{-1}$ in the 55-90 m depth zones. The highest catch rate of $32.7 \text{ kg} \cdot \text{hour}^{-1}$ was obtained in April-May in the

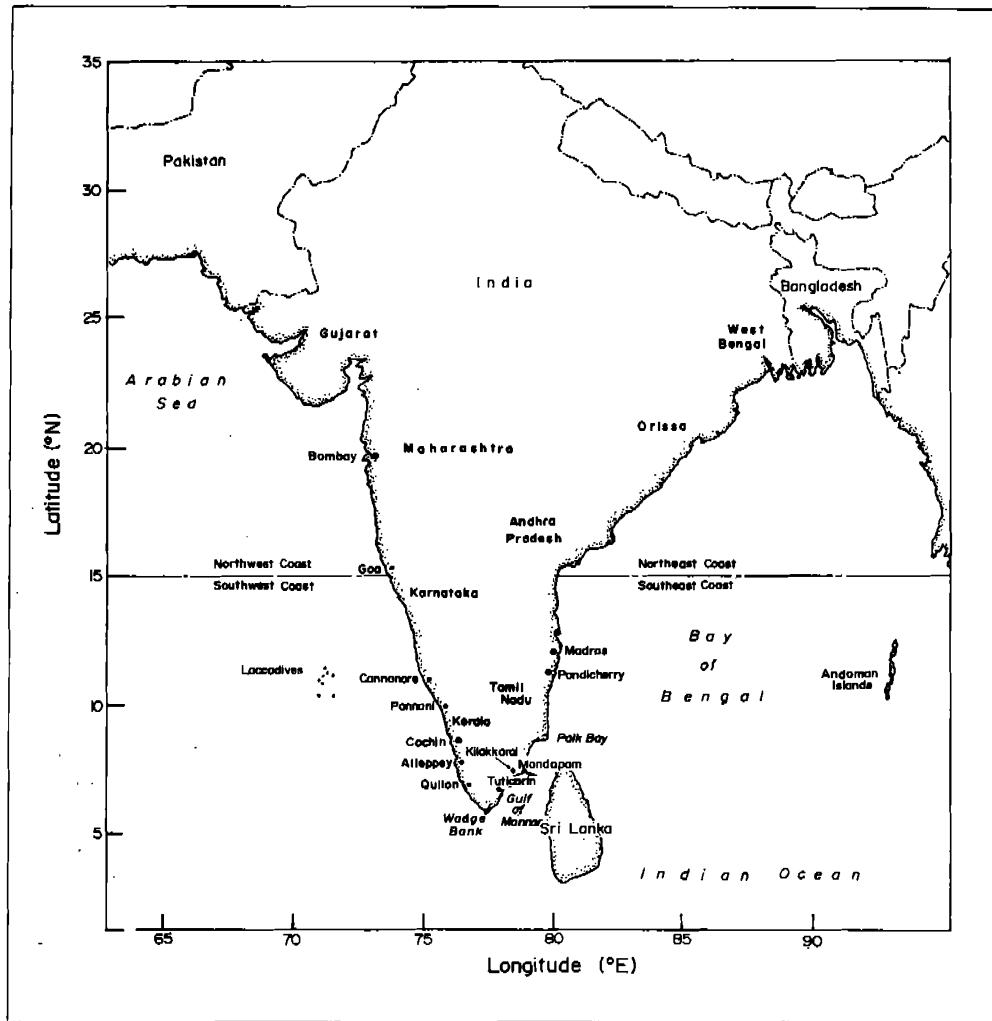


Fig. 1. Map of the Indian coast showing the four regions surveyed and the locations mentioned in the text. [Mapa de las costas de la India mostrando cuatro regiones exploradas y las áreas mencionadas en el texto.]

91-125 m depth from 16 to 17°N. Nearby, but in the 55-90 m depth range, a catch rate of 14.3 kg·hour⁻¹ was obtained.

For the pelagic trawl, only the area between 55-90 m depth yielded catches of snappers with an average catch rate of 3.3 kg·hour⁻¹; the area between 22 and 23°N yielded the highest catch rate of 16.8 kg·hour⁻¹ in April-May followed by 10.6 kg·hour⁻¹ in the area between 18 and 19°N.

The results of a survey conducted at 20-23°N and 68-70°E during 1985-88 using a trawl with a 32-m head rope (Vivekanandan et al. 1990) showed that "perches" (of which groupers and snappers are a major component) formed 4.2% of the total catch, with a period of peak abundance extending from October to February. The catch rates varied strongly between years, ranging from zero to about 3 kg·hour⁻¹, being highest between 41 and 70 m.

Southwest. The survey of Philip et al. (1984) conducted in the area between 10-15°N and 72-76°E from 50 to 500 m depth and using 47 m shrimp trawl and 27 m fish trawl showed that groupers and snappers, along with other perches, were most abundant from 14 to 15°N, with catch rates of up to 4.3 kg·hour⁻¹.

In the area between 8 and 13°N at depths of 60-150 m, the bottom is uneven, with rocky outcrops and coralline areas forming extensive ridges reaching up to 5 m from ground level (Silas 1969; Oomen 1989). These areas are rich in groupers and snappers ("kalava") and are therefore called "kalava grounds". According to Silas (1969) these grounds cover nearly 14 000 km² in the 75-100 m depth range off the southwest coast of India (8-13°N). The handline fishing trials made by Silas (1969) yielded 200-300 kg·100 hooks⁻¹·hour⁻¹ from 8 to 9°N and near 11°N, and 180-190 kg·100 hooks⁻¹·hour⁻¹ from 10 to 11°N. The species caught were *Epinephelus chlorostigma*, *E. diacanthus*, *E. areolatus*, *E. tauvina*, *E. morrhua*, *Pristipomoides typus*^b and *Lutjanus gibbus*. Of these, *E. chlorostigma* was the most common species in the catch, and *P. typus*, which was next in abundance, was predominant at 11°N.

Handline trials conducted from 8 to 13°N from 1969-81 with six vessels, yielded 78 561 kg of groupers and snappers with 1 854 hours of fishing, i.e., 42 kg·hour⁻¹ (Oomen 1989). Maximum catches and catch rates (60.2 kg hour⁻¹) were obtained during January; the species composition was similar to that obtained by Silas (1969). Another handline survey, conducted from 1967 to 1968 in the shelf extending from Cannanore to southwest of Quilon (8°30'-10°15'N) yielded 87 t of groupers and snappers in 1 280 fishing hours, i.e., 68 kg·hour⁻¹ (Menon and Joseph 1969). *E. areolatus*, *E. chlorostigma*, *E. diacanthus* and *P. typus* were the main species caught. Highest catch rates were obtained during February. The survey showed that the grounds from 11

to 12°N yielded higher catches of these species than the areas further south.

Menon et al. (1977) conducted experimental fishing using traps (186 x 86 x 86 cm) during 1975-76 using three vessels in the area off 8-11°N, 74-76°E and found the area between Alleppey and Ponnani to be richest in groupers and snappers. The number of fish caught varied from a minimum of 5 per trap in August to a maximum of 48 per trap in April, while the weight per hour of trapping was highest during April-June and October-December. Of the six species caught *E. chlorostigma* was the most abundant.

The ten-year trap survey described by Oomen (1989) was based on the same design as that of Menon et al. (1977) but was conducted from 8 to 13°N. It showed that the average catch rate of the above six species was about 80 kg·hour⁻¹; maximum catch per trap hour (166 kg) was obtained in June.

The trawl survey reported upon by Sulochanan and John (1988) yielded 62-96 kg·hour⁻¹ during October-December and 60-78 kg during March-May in the 40-50 m depth zone in an area south of 8°N. The 50-100 m depth zone yielded highest catch rate of 40 kg·hour⁻¹ during the same period, and 19 kg·hour⁻¹ during October.

Southeast. Joseph et al. (1987) reported on a trawl survey conducted from October 1981 to April 1983 using a 41-m vessel and 34-m two-seam bottom trawl in an area of 3 600 nm² of Wadge Bank between 7°00'-8°20'N and 76°30'-78°00'E at depths extending up to 223 m. The bottom was generally hard, covered with dense growth of sea fans and coral, and rich in groupers and snappers.

During the survey, groupers, snappers and pigface breams were found to contribute to 37% of total catches. The northeast part of the Wadge Bank was found to be richest for these fishes followed by the northwest part. A well-defined fishing ground for these fishes was located off 7°40'-8°00'N and 77°20'-78°00'E at depths of 36-64 m.

^b This species is not listed by Heemstra and Randall (1993) among groupers occurring in India.

The catch rates at different depths showed that the abundance of these fishes decreased with increasing depth.

Well-defined variations in seasonal abundance occurred, with July-September having the greatest catch rates (up to 153.4 kg·hour⁻¹) at depths of 18-45 m (7°N).

The species that contributed to the catches were: *E. diacanthus*, *E. areolatus*, *E. malabaricus*, *E. longispinis* and *E. tauvina* among groupers and *L. argentimaculatus*, *L. malabaricus*, *L. lutjanus*, *L. vitta* and *L. rivulatus* among snappers. The survey allowed the estimation of a standing stock of perches of 10 000 t, of which most (55%) occurred in the 18-45 m depth range.

The trawl survey by Sivaprakasam (1986) on Wadge Bank and Gulf of Mannar at depths ranging from 250 to 500 m during October-March 1985 revealed the dominant species of groupers and snappers in the area to be *Epinephelus diacanthus*, *E. tauvina*, *E. lanceolatus*, *Lutjanus argentimaculatus*, *L. malabaricus*, *L. lutjanus*, *L. rivulatus*, *Pristipomoides typus* and *Aprion virescens*. The survey also confirmed that groupers and snappers were most abundant in the 20-50 m depth zone in the Wadge Bank area, their abundance decreasing with depth, as also described by Joseph et al. (1987); there was no catch of these fishes in the 200-500 m depth zone. In the Gulf of Mannar as well, maximum catch rates were obtained at depths of 20-50 m, with very poor or no catches in deeper waters. On the Wadge Bank, the peak period of abundance of the fishes was observed to be January-February whereas the same was in May, July, October and December in the Gulf of Mannar.

Somavanshi and Bhar (1984) conducted a brief trawl survey (October 1983-March 1984) in the Gulf of Mannar (8-10°N). Perches (*E. diacanthus* and other serranids, *L. argentimaculatus* and other lutjanids,

lethrinids, acanthurids and scolopsids) formed 21% of the catches. Of these, the snappers were found to be dominant, followed by groupers and pigface breams. Depths of up to 50 m were found to be most productive for these fishes.

Northeast: Ninan et al. (1984) conducted a trawl survey during 1983-84 in the region off 14°04'-17°30'N at depths of 45-330 m. The perches (including groupers and snappers) formed 4.4% of the total catch of 176 t obtained during that survey.

Biology

Though groupers form an important component of the perch fisheries in the southwest coast of India, there is little information on the biology of commercially important species. Although many species of groupers have been reported from the seas around India (see Appendix I), only a few of them are represented in commercial catches. Among them, *Epinephelus tauvina*, *E. malabaricus* and *E. bleekeri* are commonly found. Groupers are predatory fishes feeding on crabs, prawns, polychaetes and other fishes such as *Terapon* and *Ambassis* (Devanesan and Chidambaram 1948). Most groupers are hermaphrodites, first maturing as females, then becoming males with advancing age and size.

Some ecological conditions of areas where groupers and snappers are abundant, i.e., along the east and west coasts of India, and their seasonal variations were studied in successive cruises of *R/V Sagar Sampada* (CMFRI 1985-1992). Depthwise (10-100 m), salinity ranged from 33.05 to 34.57 ppt, temperature from 26.85 to 23.15°C, and dissolved oxygen from 1.85 to 4.85 ml·l⁻¹ on the east coast and from 33.50-35.87 ppt, 26.25-29.15°C and 3.63-4.35 ml·l⁻¹ in the west coast, respectively.

Only preliminary investigations on the biology of grouper and snapper species have been published, as follows:

1. *Pristipomoides typus*^b: Oomen (1976) studied food and feeding habits based on samples taken off the Kerala Coast. Fish, cumaceans, mysids, crabs, stomatopods and cephalopods formed the important food items, but 62% of fish examined had everted stomachs. On the basis of 345 specimens of 21.5-34.9 cm, the length-weight relationship was calculated as $\log W = -5.1002 + 3.0303 \log L$. Preliminary studies of supraoccipital crest in fishes of 26.0-27.4 cm revealed three growth rings and a fourth under formation in the 27.5-28.9 cm group.

Premalatha (1989) estimated the length-weight relationship using females ranging from 35-60 cm as $\log W = -1.4959 + 2.7063 \log L$. The spawning season was determined to be February-June.

2. *E. diacanthus*: Bapat et al. (1982) observed mature and spent adults in September. Silas (1969) collected juveniles of this species from 30-60 m and 100-160 m depths. In June 1966, 10 kg of juveniles of this species were collected from trawl catches from 160 m depth. Growth and mortality parameters were estimated as $L_{\infty} = 45.5$ cm, $K=0.45$ year⁻¹, $M=0.76$ year⁻¹ and $F=0.31$ year⁻¹ (Anon. 1991). Premalatha (1989) estimated a length-weight relationship for the female of this species (females) as $\log W = -1.3056 + 2.6117 \log L$ based on specimens ranging from 20 to 55 cm. The spawning period was determined as May-June.

3. *E. areolatus*: Off Kerala State, the spawning season was determined as June-July and length-weight relationship $\log W = -1.2521 + 2.55772 \log L$ for females and $\log W = -0.8994 + 2.3287 \log L$ for males were derived based on specimens ranging from 29 to 55 cm (Premalatha 1989).

4. *E. tauvina*: Fish of 45-50 cm length mature as females while fish of more than 74 cm and weighing 11 kg become males having ripe testes. In specimens of 66-72 cm length, transitional gonads contain male and female tissues. Ameer Hamsa and Mohamad Kasim (1992) studied the growth of juveniles in cages ($5 \times 5 \times 2$ m) in the Gulf of Mannar starting with juveniles of 14-25 cm. The growth was studied for different periods ranging from about 160 to 334 days; this led to the growth parameter estimates $L_{\infty}=67.1$ cm and $K=0.462$ year⁻¹. Also, Selvaraj and Rajagopalan (1973) presented some observations on morphometric and meristic characteristics, and on fecundity and spawning habits of this species.

5. *E. chlorostigma*: length-weight relationships were estimated as $\log W = -2.7115 + 3.0425 \log L$ in females and $\log W = -1.7501 + 2.8497 \log L$ in males, using fishes of the length range 32-65 cm. The spawning period is June-July (Premalatha 1989).

6. *Lutjanus kasmira*: This species appears to spawn only once during November-March. Length at first maturity was estimated as 20 cm and fecundity as ranging from 42 100 to 332 620 (Rangarajan 1972b).

Fishery

The groupers and snappers, along with other "perches" are exploited by trawl, hook-and-line and traps. There is however, no targeted fishing for these resources except for hook-and-line fisheries along the Kerala and Tamil Nadu coasts.

During the period from 1985 to 1992, annual landings of groupers ranged from a minimum of about 2 500 t in 1982 to a maximum of about 6 300 t in 1991 (Table 1). Regionally, the highest landings occur off Tamil Nadu followed by Maharashtra, Kerala, Gujarat and Karnataka (Table 2). There were no landings of groupers along West Bengal and only negligible quantities were landed in Orissa.

In the case of snappers, annual landings ranged from about 2 200 t in 1982 to about 4 200 t in 1992 (Table 2). Maximum landings were recorded off Tamil Nadu followed by Andhra Pradesh (Table 2). There were no landings of snappers along the West Bengal coast. In Orissa, landings of lutjanids were highest in 1986 (212 t), and were followed by a collapse in subsequent years.

Table 1. Nominal catch of groupers and snappers along the coasts of India, 1982-1992 (in tons)^a. [Captura nominal de meros y pargos de las costas de la India, 1982 - 1992 (toneladas).]

Year	Groupers	Snappers
1982	2 511	2 202
1983	4 415	3 340
1984	2 635	3 793
1985	3 264	4 098
1986	2 611	2 623
1987	4 807 (4 797)	3 808 (3 783)
1988	5 104	4 136
1989	5 553	3 705
1990	4 718	2 746
1991	6 287 (6 023)	2 257
1992	5 340 (8 548)	4 150 (2 762)

^aThe figures in brackets document differences between the two manuscripts underlying this contribution.

Table 2 also shows that considerable seasonal changes in serranid and lutjanid catches occur in most states.

In Tamil Nadu there is an organized fishery for perches along the Gulf of Mannar and Wadge Bank using hook-and-line, gill nets and traps. There, annual landings of groupers varied from 970 t to 3 124 t, with peak landings usually taken during first and third quarters (Table 2). As for snappers, the yearly catches varied from about 500 t to 1 400 t during 1985-92, with peak landings occurring during the first quarter of the year.

In the Gulf of Mannar, off Tuticorin (8-9°N), the bottom is rocky and also rich in coral reefs. In this region about 250-300 country crafts with hook-and-line and gill nets operated over depths of 35-60 m, targeting perches. Serranids form 23% of that catch; the main species are *E. tauvina* (53% of the grouper catch), *E. malabaricus* (16%), *E. diacanthus* (14%), *E. chlorostigma* (11%) and *E. undulatus* (6%). Peak catches occur during July-October. Lutjanids form 14% of perch catch, and consist of *Lutjanus rivulatus* (42.5% of snappers), *L. argentimaculatus* (27%), *L. malabaricus* (21%) and *Pristipomoides typus* (10%).

In the Gulf of Mannar, off Keelakari (S.E. coast), there is a subsistence trap fishery exploiting groupers and snappers along with other coral reef fishes.

Fishers based in Tuticorin migrate to the Mandapam region during December-March to fish using plank-built boats and hook-and-line over 18-25 m depth off Dhanushkodi (Jayasankar 1990). Lutjanids ranging from 15 to 70 cm and serranids ranging from 20 to 80 cm are targeted. From December 1988 to March 1989, 2 t of serranids, 6 t of lutjanids and 15 t of other fish were caught (Jayasankar 1990).

Hand-lines for perches 30-40 km off the coast have been traditionally used along the southwest coast as well as on Wadge Bank. Hornell (1916) commented on the fishing grounds in the 25-40 fathom depths in Wadge Bank area, while John (1948)

Table 2. Regionwise and statewise average annual landings of groupers and snappers. (Values in parentheses are percentages in the total national catch of the group.) [Descargas anuales, regionales y estatales, de meros y pargos (valores entre paréntesis son porcentajes del total anual nacional de cada grupo).]

Region	State	Groupers				Total	Snappers				Total
		I	II	III	IV		% by quarter	I	II	III	
Northwest coast	Gujarat	35.3	10.0	1.6	53.1	499 (9.7)	34.1	9.7	5.4	50.8	370 (11.4)
	Maharashtra	28.8	12.8	4.9	53.5	1 416 (27.8)	17.1	9.1	15.8	58.0	658 (20.3)
Southwest coast	Goa	96.3	0	3.7	0	27 (0.5)	0	36.4	9.1	54.5	10 (0.3)
	Karnataka	46.8	9.6	3.4	40.3	293 (5.8)	4.6	2.3	74.4	18.6	45 (1.4)
	Kerala	47.6	2.5	5.9	44.0	1 079 (21.2)	68.3	2.6	1.0	28.2	506 (15.6)
Southeast coast	Tamil Nadu	36.2	18.1	33.3	12.4	1 704 (33.4)	40.4	16.4	25.8	17.4	825 (25.4)
	Pondicherry	16.7	50.0	33.3	0	6 (0.1)	55.6	11.1	33.3	0	18 (0.6)
	Andhra Pradesh	38.5	16.9	24.6	20.0	65 (1.3)	33.2	24.5	19.8	22.5	779 (24.0)
Northeast coast	Orissa	61.6	7.1	14.2	17.1	10 (0.2)	56.4	28.7	4.2	10.6	37 (1.1)
	West Bengal	-	-	-	-	-	-	-	-	-	-

indicated that the depths between 60 and 70 fathoms off Anjengo and Chavara were good for line fishing. Gopinath (1954) gave a preliminary account on perch fishery south of Alleppey and of the Wadge Bank.

Since October 1956, the Indo-Norwegian Project vessels, *M.F.V. Cochin* (Rechristened *M.O. Kristensen*) and other vessels were engaged in hand-line fishing off Cochin. The most successful vessel for this purpose was *R/V Kalava* which, in the course of about 200 fishing days (up to December 1966), landed approximately 75 t of perches, mainly from the grouper grounds between Ponnani and Alleppey. The grouper grounds off the Kerala coast are different from the perch fishing grounds on Wadge Bank, where trawling for perches is possible over large areas. Details of various species of groupers caught from 72 to 114 m during the exploratory survey by *R/V Varuna* on the southwest coast of India were reported by Silas (1969). The species caught were *Epinephelus chlorostigma*, *Pristipomoides typus*, *E. diacanthus*, *E. areolatus*, *E. morrhua*, *E. tauvina* and *Lutjanus gibbus*.

In Kerala, the estimated annual landings of serranids varied from 335 t in 1985 to 2 994 t in 1992. Peak catches were obtained during the first and last quarters. An estimated 120 t-1 200 t of lutjanids were landed in different years in Kerala during 1985-92 and the first quarter produced 60% of year's catch (Table 2).

Off Cochin, the hook-and-line fishery starts around December and continues till March (Mathew and Venugopalan 1990). Fishing is conducted by mechanized boats ranging from 7.6 to 9.4 m. Maximum effort is expended during November-March but the highest landings occur in December and January. The estimated yield from these operations was 750 t in 1987 and 530 t in 1988, with perches forming over 90% of the catch (Mathew and Venugopalan 1990).

Among perches, serranids and lutjanids were dominant, and formed over 80% of the perch catch. Groupers and snappers were represented by *E. diacanthus* (range: 19-59 cm), *E. chlorostigma* (24-62 cm), *E. tauvina* (42-85 cm), *E. bleekeri* (21-64 cm), *E. areolatus*, *E. epistictus* and *Pristipomoides typus* (19-69 cm).

Off Quilon ($8^{\circ}20'40''N$, $77^{\circ}02'05''E$) at depths ranging from 50 to 150 m, there is a regular fishery by country crafts using hook-and-line from January to April. Of an estimated 18 000 t of perches landed during 1980 and 1981, serranids formed 21% and lutjanids 73% (Madan 1983). A total of 14 species of groupers were caught, among which *E. areolatus* and *E. diacanthus* were dominant. Among snappers, seven species contributed to the fishery. Here *Aprion* sp. and *Aphareus* sp. were dominant, jointly forming 70% of perch catch.

Off the coast of Karnataka, the annual landings of groupers varied from 21 to 839 t and those of snappers from 3 to 254 t during 1985-92, with the first quarter being most productive for groupers and the third quarter for snappers. In Maharashtra, the landings from 1985 to 1992 varied from 280 to 2 450 t for groupers and from 200 to 1 100 t for snappers. In both cases, the peak period was the fourth quarter (Table 2). In 1988, an estimated 4 000 t of perches were landed at Bombay by small trawlers. *E. diacanthus* and *E. tauvina* were the dominant species (Anon. 1989).

In Lakshadweep (=Laccadives), there is no commercial fishery for groupers and snappers except on a sustenance basis. Of the several species occurring there (Jones and Kumaran 1980), *Cephalopholis argus*, *Aethaloperca roga*, *Lutjanus gibbus*, *L. kasmira*, *L. russelli* and *L. bohar* are common in the reef flats of the different islands (Kumaran et al. 1989). From 1975 to 1984 an average annual catch of 230 t of perches

were landed (Alagaraja 1987) in which groupers and snappers were dominant.

From the Andaman Islands, an estimated average of 330 t·year⁻¹ of perches were landed in 1975-1984, forming 13% of total landings (Alagaraja 1987), with *Lutjanus kasmira* as the dominant species.

Mariculture

The earliest attempts at culturing groupers (*E. tauvina* and *E. malabaricus*), along with seabass and snappers, occurred in Malaysia, Thailand, Singapore and Hongkong in the 1970s (Teng et al. 1977; Teng and Chua 1978; Chua and Teng 1978, 1979, 1980). In the Philippines, six species of groupers, *E. malabaricus*, *E. tauvina*, *E. sexfasciatus* and *E. bleekeri* are farmed (Kohno et al. 1988). *E. suillus* and *E. amblycephalus* are farmed in Taiwan, *E. akaara* in HongKong and Japan, and *E. tauvina* in Malaysia, Indonesia, Thailand, Kuwait and India (Ukawa et al. 1966; Moe 1969; Hussain et al. 1975; Lanjumin 1982; Rahim 1982; Ameer Hamsa and Mohamad Kasim 1992).

Snappers such as *Lutjanus johnii*, *L. russelli*, and *L. sebae* are farmed in floating netcages in Singapore, Malaysia, Thailand and the Philippines, (Lee 1982; Rahim 1982; Tanomkiat 1982; Anon. 1979).

In India, farming of groupers is in the initial stage of development and entirely supported by the supply of seeds collected from the natural habitat, due to the absence of technology for the mass production of seeds by induced breeding (Bensam 1993). Hence, projects on culture and seed production for these two species of groupers should be taken up on priority basis for implementation in India, as is already the case in Southeast Asia. With the growing interest in aquaculture, the need for seed is increasing. Seeds available from natural sources are usually seasonal, unreliable and not sufficient to meet the demand.

Experiments were carried out by the Central Marine Fisheries Research Institute at Mandapam (Palk Bay) to investigate the possibilities of culturing some economically important marine fishes in fixed netcages made of palmyrah leaf stalks in coastal waters (Ameer Hamsa 1982). *Epinephelus tauvina*, *E. hexagonatus* along with rabbit fishes (*Siganus canaliculatus* and *S. javus*), and sand whiting (*Sillago sihama*) were cultured in cages (James et al. 1985b). The mean monthly growth was 0.85 cm·3.1 g⁻¹ and 0.56-0.62 cm·2-3.05 g⁻¹ for *E. tauvina*. Other growth and production estimates for the grouper *E. tauvina* cultured in fixed netcages in Mandapam (Gulf of Mannar) coastal waters are reported by Ameer Hamsa and Mohamad Kasim (1992).

Discussion

The above review shows that the distribution and abundance in space and time of Indian groupers and snappers are generally understood. Rough and untrawlable grounds rich in these resources exist, particularly along the northwest coast, southwest coast (particularly off Kerala), Wadge Bank and in the Gulf of Mannar. Where trawling is possible, groupers and snappers are exploited mainly as a bycatch. Groupers and snappers are abundant, as is clear from the results of different surveys, in rocky and coralline areas beyond 50 m depth and down to 360 m depth in certain areas presently not exploited by commercial fleets. The landing figures show that about 8 000 t only are landed annually whereas on Wadge Bank alone, the standing stock of groupers and snappers along with other perches was estimated to be around 9 400 t (Joseph et al. 1987). Joseph and John (1987) and James et al. (1987) suggested that serranids and lutjanids offer a large scope for increased exploitation along both coasts of India, particularly along the southwest

coast and on Wadge Bank. Fishing by handlines (Silas 1969; Oomen 1989) could yield considerably larger catches. Also, Menon et al. (1977) and Oomen (1989) showed that the rocky and rough grounds off the southwest coast could yield considerable catches of groupers and snappers if exploited using traps. Thus, increase in production of these fishes could be achieved by introducing fish traps and intensifying fishing with hook-and-line in the 75-100 m depth zone off southwest coast, at depths of 35-65 m in the Gulf of Mannar and in the northeast region of the Wadge Bank, and at depths of 91-125 m along the northwest coast where groupers and snappers are known to be abundant.

Planned exploratory fishing programs with *FORV Sagar Sampada* in addition to the exploratory fishing vessels of FSI, INP, IFP and CIFNET, will enable further mapping of the distribution of demersal fish stocks. Moreover, there is an urgent need to utilize the present knowledge on the distribution of the various demersal fishery resources on the continental shelf for simulated commercial fishing operations on these stocks. Such operations will demonstrate the economic feasibility of fishing operations and provide enough data for private entrepreneurs to initiate fishing ventures. The immediate objective is to increase the production of perches, especially groupers and snappers, by tapping the underexploited fraction of conventional fish resources at depths of up to 100 m by adopting diversified fishing methods instead of continuing trawling in shallow inshore waters. Since most of the marine fishing gear capture a multiplicity of fish species which have different growth, mortality and recruitment schedules, management of the fisheries is difficult. Thus, to solve this problem, new approaches for modelling the dynamics of resource species in a multispecies context should be developed. This will require intensifying studies on the growth, food and feeding habits, reproduction and

other aspects of the biology of snappers and groupers. Also, in view of the existence of large numbers of species in these two groups and lack of adequate knowledge on the population differences among them, concerted efforts should be made to improve our knowledge of the taxonomy of Indian groupers and snappers.

References^c

- Alagaraja, K. 1987. An appraisal of the marine fisheries of Lakshadweep and Andaman and Nicobar islands. CMFRI Spec. Pub. 39, 18 p.
- Allen, G.R. 1984. Family Lutjanidae, var. p. In W. Fischer and G. Bianchi (eds). FAO identification sheets for fishery purposes. Western Indian Ocean. Vol. IV. Food and Agriculture Organization, Rome.
- Allen, G.R. 1985. FAO species catalogue. Vol. 6. Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date. FAO Fish. Synop. 6(125):208 p.
- Ameer Hamsa, K.M.S. 1982. Present status of pen and cage culture of finfishes in Southeast Asia. Proc. Nat'l. Sem. Cage Pen Culture: 69-79.
- Ameer Hamsa, K.M.S. and H. Mohamad Kasim. 1992. Growth and production potential of young grouper *Epinephelus tauvina* (Forsskål) reared in fixed netcages. J. Mar. Biol. Assoc. India 34 (1&2):271-277.
- Anon. 1979. International Workshop on Pen and Cage Culture of Fish, 11-12 February 1979, Tigbauan, Iloilo, Philippines.
- Anon. 1989. Annual Report 1988. Central Marine Fisheries Institute, Cochin. 97 p.
- Anon. 1991. Report of the working groups on revalidation of the potential marine fisheries of exclusive economic zone of India. Ministry of Agriculture, Government of India, New Delhi.
- Bal, D.V. and K.V. Rao. 1984. Marine fisheries. Tata McGraw-Hill Publishing Co. Ltd., New Delhi. 470 p.

^c This list includes all references originally included in the two manuscripts upon which this contribution was based, whether presently cited or not.

- Bapat, S.V., V.M. Deshmukh, B. Krishnamoorthi, C. Muthiah, P.V. Kagwade, C.P. Ramamirtham, K.J. Mathew, S. Krishnapillai and C. Mukundan. 1982. Fisheries resources of the Exclusive Economic Zone of the northwest coast of India. Bull. Cent. Mar. Fish. Res. Inst. 33, 80 p.
- Basheeruddin, S. and K.N. Nayar. 1962. A preliminary study of the juvenile fishes of the coastal waters off Madras City. Indian J. Fish. 8(1):169-188.
- Bensam, P. 1993. Prospects of farming groupers in India. Presented in the Business Session of India's First Aquaculture Show INDAQUA, 20-23 March 1993, Madras, Organized by the Marine Products Export Development Authority, Cochin, India. 16 p.
- Chacko, P.I. 1949. Food and feeding habits of the fishes of the Gulf of Mannar. Proc. World. Maricult. Soc. 10:260-271.
- Chua, T. and S. Teng. 1978. Effects of feeding frequency on the growth of young estuarine grouper *Epinephelus tauvina* (Forsskål) cultured in floating cages. Aquaculture 14:31-47.
- Chua, T. and S. Teng. 1979. Relative growth and production of the estuary grouper *Epinephelus salmoides* under different stocking densities in floating net cages. Mar. Biol. 54:363-372.
- Chua, T. and S. Teng. 1980. Economic production of estuary grouper *Epinephelus salmoides* Madwell reared in floating netcages. Aquaculture 20:187-228.
- CMFRI. 1989. Annual Report 1988. Central Marine Fisheries Research Institute, Cochin, India. 97 p.
- CMFRI. 1985-1992. FORV Sagar Sampada Cruise reports. Central Marine Fisheries Research Institute, Cochin, India.
- Devanesan, D.W. and K. Chidambaram. 1948. The common food fishes of the Madras Presidency, Madras. Government Press.
- Fischer, W. and G. Bianchi, Editors. 1984. FAO species identification sheets for fishery purposes. Western Indian Ocean. Vol. 4. Food and Agriculture Organization, Rome.
- Fischer, W. and P.J.P. Whitehead, Editors. 1974. FAO species identification sheets for fishery purposes. Eastern Indian Ocean and Western Central Pacific. Vols. II & IV. Food and Agriculture Organization, Rome.
- Gopinath, K. 1954. A note on some deep sea fishing experiments off the south western coast of India. Indian J. Fish. 1(1&2):163-216.
- Heemstra, P., J.L.B. Smith and J.E. Randall. 1984. Family Serranidae, var. p. In W. Fischer and G. Bianchi (eds). FAO species identification sheets for fishery purposes. Western Indian Ocean. Vol. IV. Food and Agriculture Organization, Rome.
- Heemstra, P.C. and J.E. Randall. 1993. FAO species catalogue. Vol. 16. Groupers of the world. (Family Serranidae, Subfamily Epinephelinae). An annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper and lyretail species known to date. FAO Fish. Synops. No. 125, Vol. 16.
- Hornell, J. 1916. Notes on two exploring cruises in search of trawl grounds off the Indian and Ceylon coasts. Madras Fish. Bull. 14:33-70.
- Huguene, J.E. and F.J. Ansuiini. 1978. A review of the technology and economics of marine fish cage systems. Aquaculture 15:151-170.
- Hussain, N., M. Saif and M. Ukawa. 1975. On the culture of *Epinephelus tauvina* (Forsskål). Kuwait Institute for Scientific Research MAB-IIIXXI, 12 p.
- James, P.S.B.R., K. Alagarswami, K.V. Narayana Rao, M.S. Muthu, M.S. Rajagopalan, K. Alagaraja and C. Mukundan. 1987. Potential marine fishery resources of India. CMFRI Spl. Pub. 30: 44-74.
- James, P.S.B.R., R. Soundararajan and J.X. Rodrigo. 1985. Preliminary studies on culture of finfishes in cages in the coastal waters of Palk Bay at Mandapam. Proc. Symp. Coastal Aquaculture, Cochin 3:910-915.
- Jayasankar, P. 1990. On the seasonal hooks and line fishery at Pamban, near Mandapam. Mar. Fish. Infor. Serv. Tech. Extn. Ser. 105:13-14.
- Job, T.J. 1940. An investigation on the nutrition of the perches of the Madras coast. Proc. Indian. Mus. 42:289-364.
- Joel, J.J. and I.P. Ebenezer. 1991. Note on giant perch caught off Kanya-kumari. Mar. Fish. Infor. Serv. Tech. Extn. Ser. 108:15.
- John, C.C. 1948. Progress Report of the Fisheries Development Schemes-Central Research Institute. Travancore University, Division of Marine Biology and Fisheries, 8 p.
- John, V., P.I. Chacko, R. Venkataraman and A.T. Sherriff. 1959. Report of fishing experiments in the offshore waters of the Madras

- State, p. 106-138. In DOF. Fish Station Rep. and Year Book, Department of Fisheries, Madras.
- Jones, S. and M. Kumaran. 1980. Fishes of the Laccadive Archipelago. Nature Conservation of Aquatic Sciences Service, Trivandrum. 760 p.
- Joseph, K.M. and M.E. John. 1987. Potential marine fishery resources. CMFRI Spl. Pub. 30:18-43.
- Joseph, K.M., P. Sulochanan, M.E. John, V.S. Somavanshi, K.N.V. Nair and A. Joseph. 1987. Demersal fishery resources of Wadge Bank. Bull. Fish. Surv. India 12:1-52.
- Kohno, H., M. Duray and J. Juario. 1988. State of grouper (Lapu-lapu) culture in the Philippines. SEAFDEC Asian Aquacult. 10(2):4-9.
- Kumaran, M., R.S. Lal Mohan and V.S. Murty 1989. Other fin fish resources, p. 65-72. In Marine living resources of the Union Territory of Lakshadweep - an indicative survey with suggestions for development. Bull. Cent. Mar. Fish. Res. Inst. 43, Cochin.
- Landless, P.J. and A. Edwards. 1976. Economical ways of assessing hydrography for fish farms. Aquaculture 8:29-43.
- Lanjumin, L. 1982. Development of cage culture of finfish in Riau Archipelago. Riau Province, Indonesia, p. 165-166. In Report of the Training Course on Small Scale Pen and Cage Culture for Finfish. South China Sea Fisheries Development and Coordinating Programme, Manila, Philippines.
- Lee, E.S. 1982. Cage culture for marine finfish in Singapore, p. 197-199. In Report of the Training Course on Small Scale Pen and Cage culture for Finfish. South China Sea Fisheries Development and Coordinating Programme, Manila, Philippines.
- Madan, M. 1983. Kalava fisheries of Pulluvila Village. Indian J. Fish. 30:135-142.
- Mathew, G. On the perch fishery of Tuticorin during 1978-80. J. Mar. Biol. Assoc. India. (In press).
- Mathew, G. and K.M. Venugopal. 1990. Hooks and line fishery for Kalava at Cochin. Indian J. Fish. 37: 347-355.
- Menon, M.D. and K.M. Joseph. 1969. Development of kalava (rock cod) fishing off south west coast of India - a prospectus. Seafood Export J. 1(2):7-28.
- Menon, M.D., C.P. Varghese and C. Haridas. 1977. Development of trap fishing for rock cod off south west coast of India. Seafood Export J. 9(1):5-14.
- Moe, M.A. 1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Prof. Pap. Ser. Fla. Dep. Nat. Resour. Mar. Res. Lab. 10, 95 p.
- Ninan, T.V., S.P. Basu and P.K. Bhargava. 1984. Observations on the demersal fishery resources along Andhra Pradesh Coast. Bull. Fish. Surv. India 13:18-22.
- Oomen, V.P. 1976. An account of the fishery and biology of Velameen *Pristipomoides argyrogrammicus* (Valenciennes). J. Mar. Biol. Assoc. India, 18:469-475.
- Oomen, V.P. 1989. A critical study on the exploitation of fishery resources by the Integrated Fisheries Project. IFP Bull. 12, 106 p.
- Philip, K.P., B. Premchand, G.K. Avadh and P.J. Joseph. 1984. A note on the deep sea demersal resources off Karnataka- north Kerala coast. Bull. Fish. Surv. India 13:23-32.
- Premalatha, P. 1989. Fishery and biology of rock cods (Order Perciformes) from the south west coast of India. Indian J. Fish. 36(4):285-291.
- Rahim, B. 1982. Cage of finfish in Peninsular Malaysia, p. 173-176. In Report of the Training Course on Small Scale Pen and Cage Culture for Finfish, South China Sea Fisheries Development and Coordinating Programme, Manila, Philippines.
- Randall, J.E., G.R. Allen and W.D. Anderson, Jr. 1987. Revision of the Indo-Pacific lutjanid genus *Pinjalo*, with description of a new species. Indo-Pac. Fish. (14):17.
- Randall, J.E. and P.C. Heemstra. 1991. Revision of Indo-Pacific groupers (Perciformes: Serranidae: Epinephelinae), with descriptions of five new species. Indo-Pac. 20, 332 p.
- Rangarajan, K. 1970. Food and feeding habits of the snapper, *Lutjanus kasmira* (Forsskål) from Andaman Sea. Indian J. Fish. 17(1&2):114-121.
- Rangarajan, K. 1972a. Food and feeding habits of the snapper, *Lutjanus kasmira* (Forsskål) from the Andaman Sea. Indian J. Fish. 17:43-52.

- Rangarajan, K. 1972b. Maturity and spawning of the snapper, *Lutjanus kasmira* (Forsskål) from the Andaman Sea. Indian J. Fish. 18:114-125.
- Rangarajan, K. 1973. Length-weight relationship in the snapper, *Lutjanus kasmira* (Forsskål). Indian J. Fish. 20(2):205-208.
- Rao, K.S. 1964. Food and feeding habits of fishes from trawl catches in the Bay of Bengal with observations on diurnal variations in the nature of food. Indian J. Fish. 11(1):277-314.
- Rao, K.V. 1969. Distribution pattern of the major exploited marine fishery resources in India. Bull. Cent. Mar. Fish. Res. Inst. 6:1-69.
- Selvaraj, G.S.D. and M. Rajagopalan. 1973. Some observations on the fecundity and spawning habits of the rock cod *Epinephelus tauvina* (Forsskål). Indian J. Fish. 20 (2):668-671.
- Silas, E.G. 1969. Exploratory fishing by R.V. *Varuna*. Bull. Cent. Mar. Fish. Res. Inst. 12:53-66.
- Sivaprakasam, T.E. 1986. A study of the demersal resources of the Wadge Bank and the Gulf of Mannar. Bull. Fish. Surv. India 15:1-37.
- Somavanshi, V.S. and P.K. Bhar. 1988. A note on demersal fishery resources survey of Gulf of Mannar. Bull. Fish. Surv. India 13:12-17.
- Sulochanan, P. and M.E. John. 1988. Offshore, deepsea and oceanic fishery resources of Kerala Coast. Bull. Fish. Surv. India 16:27-48.
- Tan, S.M. and K.S. Tan. 1974. Biology of tropical grouper *Epinephelus tauvina* (Forsskål). 1. A preliminary study on hermaphroditism in *E. tauvina*. Singapore J. Prim. Ind. 2(2):123-133.
- Tanomkiat, T. 1982. Programme on cage culture at the Phang Nga Small Scale Fisheries Assisted Project, Phong Nga Province, Thailand, p. 213. In Report of the Training Course on Small Scale Pen and Cage Culture for Finfish, South China Sea Fisheries Development and Co-ordinating Programme, Manila, Philippines.
- Teng, S. and T. Chua. 1978. Effects of stocking density on the growth of estuary grouper *Epinephelus salmoides* Maxwell cultured in net cages. Aquaculture 15:272-287.
- Teng, S.K., T.E. Chua and H.C. Lai. 1977. Construction and management of floating net cages for culturing the estuary grouper, *Epinephelus tauvina* (Forsskål) in Penang, Malaysia. SCSP/SEAFDEC. Philippines. Proc. Workshop on Aquaculture Engineering 2:359-371.
- Ukawa, M., M. Higuchi and S. Mito. 1966. Spawning habits and early life history of a serranid fish, *Epinephelus akaara* (Temminck and Schlegel). Japan. J. Ichthyol. 13(4/6):156-161.
- Venkataraman, G. 1960. Studies on the food and feeding relationships of the inshore fishes off Calicut on the Malabar coast. Indian J. Fish. 7:275-306.
- Vivekanandan, E., C. Gopal, S. Shanmugam, H.K. Dhokia and B.P. Thumber. 1990. Industrial fisheries off Saurashtra Coast based on exploratory survey during 1985-88. Mar. Fish. Infor. Serv. Tech. Extn. Ser. 103:1-5.

Appendix I

FishBase checklist of family Serranidae in India based mainly on Heemstra and Randall (1993). [Lista revisada de FishBase para la familia Serranidae de la India, basada principalmente en Heemstra y Randall (1993).]

Perciformes (perch-like)	
Serranidae	Sea basses, groupers and fairy basslets
<i>Aethaloperca rogaa</i> (Forsskål 1775)	Redmouth grouper, (Fr M) Max. 60 cm TL; SW
<i>Cephalopholls rogaa</i>	(Forsskål 1775) new combination
<i>Aethaloperca rogaa</i>	(Forsskål 1775) new combination
<i>Perca lunaris</i>	Forsskål 1775 junior synonym
<i>Perca rogaa</i>	Forsskål 1775 original combination
<i>Anyperodon leucogrammicus</i> (Valenciennes 1828)	Slender grouper, (Fr M) Max. 52 cm TL.
<i>Serranus leucogrammicus</i>	Valenciennes 1828 original combination
<i>Serranus micronotatus</i>	Ruppell 1838 junior synonym
<i>Serranus urophthalmus</i>	Bleeker 1855 junior synonym
<i>Anyperodon leucogrammicus</i>	(Valenciennes 1828) new combination
<i>Cephalopholis argus</i> Bloch & Schneider 1801	Peacock hind, Balufana, (Fr M Dan) Max. 55 cm TL. Museum: SMF 16354; SW
<i>Serranus Immunerur</i>	Thiolière 1856 questionable
<i>Serranus thyrsoites</i>	Saville-Kent 1893 other
<i>Cephalopholis argus</i>	Bloch & Schneider 1801 original combination
<i>Serranus myriaster</i>	Valencennes 1828 junior synonym
<i>Bodianus jacobevertsen</i>	Lacepède 1802 junior synonym
<i>Bodianus guttatus</i>	Bloch 1790 junior synonym
<i>Cephalopholis boenak</i> (Bloch 1790)	Chocolate hind, (Fr M), Ref. 5222 Max. 26 cm TL. Also Ref: 4787. Museum: BPBM 27657; SMF 16351 (Nicobar).
<i>Serranus stigmatopomus</i>	Richardson 1846 junior synonym
<i>Serranus boenak</i>	(Bloch 1790) new combination
<i>Serranus nigrofasciatus</i>	Hombron and Jacquinot 1853 junior synonym
<i>Cephalopholls boenacki</i>	(Bloch 1790) misspelling
<i>Serranus boelang</i>	Valencennes 1828 questionable
<i>Cephalopholis pachycentron</i>	Valencennes 1828 junior synonym
<i>Bodianus boenak</i>	Bloch 1790 original combination
<i>Cephalopholis boenak</i>	(Bloch 1790) new combination
<i>Serranus pachycentron</i>	Valencennes 1828 junior synonym
<i>Cephalopholis boenack</i>	(Bloch 1790) misspelling
<i>Cephalopholls formosa</i> (Shaw & Nodder 1812)	Bluelined hind, Bontoo, (Fr M) Max. 34 cm TL. Also Ref: 4787. Museum: ZMB 163; BMNH 1888.11.6.2.4; AMS B.8215; MNHN 7423, 7424; BPBM 27656; NMW 39881.
<i>Sciaena formosa</i>	Shaw and Nodder 1812 original combination
<i>Cephalopholls formosa</i>	(Shaw & Nodder 1812) new combination
<i>Cephalopholis leopardus</i> (Lacepède 1801)	Leopard hind, (Fr M) Max. 20 cm TL.
<i>Labrus leopardus</i>	Lacepède 1801 original combination
<i>Serranus spilurus</i>	Valencennes 1833 junior synonym
<i>Serranus homfrayi</i>	Day 1870 junior synonym
<i>Epinephelus urodelops</i>	Schultz 1943 junior synonym
<i>Cephalopholis leopardus</i>	(Lacepède 1801) new combination

(continued)

Appendix I (continued)

Perciformes (perch-like)	
Serranidae	Sea basses, groupers and fairy basslets
<i>Cephalopholis minlata</i> (Forsskål 1775)	Coral hind, (Fr M) Max. 40 cm TL. Museum: SMF 16353 (Nicobar Is.). Also Ref: 5222.
<i>Serranus cyanostigmatooides</i>	Bleeker 1849 junior synonym
<i>Cephalopholis cyanostigma</i>	(non Valenciennes 1828) misidentification
<i>Cephalopholis minlatus</i>	(Forsskål 1775) misspelling
<i>Cephalopholis boninius</i>	Jordan and Thompson 1914 junior synonym
<i>Cephalopholls formosanus</i>	Tanaka 1911 junior synonym
<i>Serranus perguttatus</i>	De Vis 1884 questionable
<i>Cephalopholis minlata</i>	(Forsskål 1775) new combination
<i>Pomacentrus burdi</i>	Lacepède 1802 junior synonym
<i>Perca minlata</i>	Forsskål 1775 original combination
<i>Cephalopholls maculatus</i>	Seale and Bean 1907 junior synonym
<i>Cephalopholis sonnerati</i> (Valenciennes 1828)	Tomato hind, Bontoo, (Fr M) Max. 57 cm TL. Museum: BPBM 20590; MNHN A.5774, A.7686 (paratypes of <i>S. sonnerati</i> Valenciennes), A.7671 (lectotype); NMW 40813; SMF 22343; SU 41923.
<i>Cephalopholls purpureus</i>	Fourmanoir 1966 junior synonym
<i>Serranus zanarella</i>	Valenciennes 1828 junior synonym
<i>Epinephelus janthinopterus</i>	Bleeker 1874 junior synonym
<i>Serranus unicolor</i>	Liénard 1875 junior synonym
<i>Cephalopholis formosanus</i>	(non Tanaka 1911) misidentification
<i>Cephalopholls sonneratl</i>	(Valenciennes 1828) new combination
<i>Serranus sonnerati</i>	Valenciennes 1828 original combination
<i>Cephalopholis aurantius</i>	(non Valenciennes 1828) misidentification
<i>Cromileptes altivelis</i> (Valenciennes 1828)	Humpback grouper, (Fr M) Max. 70 cm TL.
<i>Serranus altivelis</i>	Valenciennes 1828 original combination
<i>Chromileptes altivelis</i>	(Valenciennes 1828) misspelling
<i>Cromileptis altivelis</i>	(Valenciennes 1828) misspelling
<i>Cromileptes altivelis</i>	(Valenciennes 1828) new combination
<i>Epinephelus areolatus</i> (Forsskål 1775)	Areolate grouper, Hontu, (Fr M), Max. 50 cm SL. NW; SW; SE
<i>Epinephelus craspedurus</i>	Jordan & Richardson 1910 junior synonym
<i>Serranus waandersii</i>	Bleeker 1858 junior synonym
<i>Perca areolata</i>	Forsskål 1775 original combination
<i>Epinephelus chlorostigma</i>	(non Valenciennes 1828) misidentification
<i>Bodianus melanurus</i>	Geoffroy St. Hilaire 1809 junior synonym
<i>Serranus angularis</i>	Valenciennes 1828 junior synonym
<i>Serranus celebicus</i>	Bleeker 1851 junior synonym
<i>Serranus glaucus</i>	Day 1870 junior synonym
<i>Epinephelus areolatus</i>	(Forsskål 1775) new combination
<i>Epinephelus angularis</i>	(Valenciennes 1828) junior synonym
<i>Epinephelus bleekeri</i> (Vaillant 1877)	Duskytail grouper, (Fr M) Max. 76 cm TL. Museum: BMNH 1888.12.30.4; NMW 39248; BPBM 23749, 27479; RUSI 16297; SW (non Valenciennes 1828) misidentification
<i>Serranus variolosus</i>	

(continued)

Appendix I (continued)

Perciformes (perch-like) Serranidae	Sea basses, groupers and fairy basslets
<i>Serranus bleekeri</i>	Vaillant 1877 original combination
<i>Serranus coromandelicus</i>	Day 1878 junior synonym
<i>Epinephelus albimaculatus</i>	Seale 1909 junior synonym
<i>Epinephelus bleekeri</i>	(Vaillant 1877) new combination
<i>Epinephelus dayi</i>	(non Bleeker 1873) misidentification
<i>Epinephelus caeruleopunctatus</i> (Bloch 1790)	Whitespotted grouper, (Fr M) Max. 76 cm TL. Museum: SMF uncat. (Nicobar Islands); MNHN 7650 (Holotype of <i>S. dermochirius</i> , Valenciennes); FMNH 98053.
<i>Holocentrus caeruleo-punctatus</i>	Bloch 1790 original combination
<i>Serranus alboguttatus</i>	Valenciennes 1828 junior synonym
<i>Serranus flavoguttatus</i>	Peters 1855 junior synonym
<i>Serranus dermochirius</i>	Valenciennes 1830 junior synonym
<i>Serranus hoevenii</i>	Bleeker 1849 junior synonym
<i>Epinephelus hoevenii</i>	(Bleeker 1849) junior synonym
<i>Serranus kunhardtii</i>	Bleeker 1851 junior synonym
<i>Epinephelus caeruleopunctatus</i>	(Bloch 1790) new combination
<i>Epinephelus chabaudi</i> (Castelnau 1861)	Moustache grouper, (Fr M) Max. 137 cm TL.
<i>Epinephelus chabaudi</i>	(Castelnau 1861) new combination
<i>Serranus chabaudi</i>	Castelnau 1861 original combination
<i>Epinephelus modestus</i>	Gilchrist & Thompson 1909 junior synonym
<i>Epinephelus clarkei</i>	Smith 1958 junior synonym
<i>Epinephelus chlorostigma</i> (Valenciennes 1828)	Brownspotted grouper, (Fr M) Max. 75 cm TL. Lakshadweep Islands and Nicobar Islands; SW; SE
<i>Epinephelus chlorostigma</i>	(Valenciennes 1828) new combination
<i>Serranus assabensis</i>	Giglioli 1888 junior synonym
<i>Serranus chlorostigma</i>	Valenciennes 1828 original combination
<i>Serranus tauvina</i>	(non Forsskål 1775) misidentification
<i>Serranus areolatus japonicus</i>	Temminck and Schlegel 1842 junior synonym
<i>Serranus reevesii</i>	Richardson 1846 junior synonym
<i>Serranus geoffroyi</i>	Klunzinger 1870 junior synonym
<i>Serranus celebicus</i>	Kossman and Räuber 1877 questionable
var. <i>multipunctatus</i>	
<i>Serranus geoffroyi</i>	(Klunzinger 1870) junior synonym
<i>Epinephelus coioides</i> (Hamilton 1822)	Orange-spotted grouper, (Fr Br M) Max. 100 cm SL. Museum: MNHN 7289, 7288, A.7710; NMW 40924, 39457, 40923; RUSI 11413, 11407-8, 11410, 11379, 26040; BPBM 27509, 30596, 20591; SU 41928; ZMB 191. Nicobar Islands, SMF 16349.
<i>Homalogrystes guntheri</i>	Alleyne & Macleay 1877 junior synonym
<i>Serranus suillus</i>	Valenciennes 1828 junior synonym
<i>Bola coioides</i>	Hamilton 1822 original combination
<i>Epinephelus tauvina</i>	(non Forsskål 1775) misidentification
<i>Epinephelus malabaricus</i>	(non Bloch & Schneider 1801) misidentification
<i>Epinephelus suillus</i>	(Valenciennes 1828) junior synonym
<i>Epinephelus coioides</i>	(Hamilton 1822) new combination
<i>Serranus nebulosus</i>	Valenciennes 1828 junior synonym
<i>Serranus waandersi</i>	(non Bleeker 1858) misidentification

(continued)

Appendix I (continued)

Perciformes (perch-like) Serranidae	Sea basses, groupers and fairy basslets
<i>Epinephelus diacanthus</i> (Valenciennes 1828)	Spinycheek grouper, Hekaru, (Fr M) Max. 52 cm TL. Museum: SMF 605; CAS 29595; RUSI 11414, 11406; ANSP 145517, 145522, 145544; MNHN 7157, 7158, 1989-1018, 1981-1118; BPBM 27494, 27537; CMFR uncat; SW; SE (Valenciennes 1828) new combination Bleeker 1873 misidentification Valenciennes 1828 original combination (non Valenciennes 1828) misidentification
<i>Epinephelus diacanthus</i> <i>Epinephelus dayi</i> <i>Serranus diacanthus</i> <i>Serranus sexfasciatus</i>	
<i>Epinephelus epistictus</i> (Temminck & Schlegel 1842)	Dotted grouper, (Fr M) Max. 80 cm TL. Museum: Kerala, Cochin, BPBM 27483; SW (non Fowler 1904) misidentification Cheng & Yang 1983 junior synonym (Temminck & Schlegel 1842) new combination (Boulenger 1887) junior synonym (not applicable) misidentification Boulenger 1887 junior synonym Temminck & Schlegel 1842 original combination (non Postel, Fourmanoir & Guézé 1963) misidentification
<i>Epinephelus heniachus</i> <i>Epinephelus stigmogrammacus</i> <i>Epinephelus epistictus</i> <i>Epinephelus praepercularis</i> <i>Epinephelus</i> sp. <i>Serranus praepercularis</i> <i>Serranus epistictus</i> <i>Epinephelus magniscutellus</i>	
<i>Epinephelus erythrurus</i> (Valenciennes 1828)	Cloudy grouper, (Fr Br M) Max. 43 cm TL. Museum: Gulf of Kutch, N side of Okha Pt., ANSP 159277. Dwarka, BMNH 1912.5.2.11. Bombay, BPBM 31301. Malabar, MNHN 7545 (Holotype of <i>S. erythrurus</i>). Travancore, BMNH 1912.7.20.14. Valenciennes 1828 original combination Boulenger 1898 junior synonym (Valenciennes 1828) new combination
<i>Serranus erythrurus</i> <i>Epinephelus townsendi</i> <i>Epinephelus erythrurus</i>	
<i>Epinephelus fasciatus</i> (Forsskål 1775)	Blacktip grouper, Teda, (Fr M) Max. 40 cm TL. Museum: Tuticorin, BPBM 20669. Also occurs in Lakshadweep Islands; NW De Vis 1885 junior synonym De Vis 1884 junior synonym (Valenciennes 1828) misspelling (Valenciennes 1828) junior synonym (Forsskål 1775) new combination Whitley 1945 junior synonym Seale 1906 junior synonym De Vis 1885 junior synonym Forsskål 1775 original combination (Valenciennes 1828) junior synonym Lacepède 1802 other Bloch 1793 junior synonym (non Valenciennes 1830) misidentification (Forsskål 1775) new combination Forster 1844 junior synonym Poll 1949 junior synonym Lacepède 1802 other
<i>Serranus geometricus</i> <i>Serranus cruentus</i> <i>Epinephelus alexandrinus</i> <i>Epinephelus alexandrinus</i> <i>Epinephelus fasciatus</i> <i>Epinephelus spiramen</i> <i>Epinephelus zapyrus</i> <i>Serranus subfasciatus</i> <i>Perca fasciata</i> <i>Cerna alexandrina</i> <i>Holocentrus marginatus</i> <i>Epinephelus marginalis</i> <i>Epinephelus goreensis</i> <i>Plectropoma fasciata</i> <i>Perca maculata</i> <i>Epinephelus zaslavskii</i> <i>Holocentrus forskael</i>	

(continued)

Appendix I (continued)

Perciformes (perch-like) Serranidae	Sea basses, groupers and fairy basslets
<i>Cerna chrysotaenia</i> <i>Holocentrus rosmarus</i> <i>Holocentrus oceanicus</i> <i>Serranus alexandrinus</i> <i>Epinephelus emoryi</i> <i>Serranus variolosus</i> <i>Serranus tsirilmen-ara</i> <i>Holocentrus erythraeus</i>	(non Doderlein 1882) misidentification Lacepède 1802 junior synonym Lacepède 1802 junior synonym Valenciennes 1828 junior synonym Schultz 1953 junior synonym Valenciennes 1828 junior synonym Temminck and Schlegel 1842 junior synonym Bloch and Schneider 1801 junior synonym
<i>Epinephelus faveatus</i> (Valenciennes 1828)	Barred-chest grouper. (Fr M) Max. 32 cm TL. Museum: Kerala, Trivandrum, Travancore, BMNH 1912.7.20.11-13. Kovalam, BPBM 27633, 30641; MNHN 1981-1185. Vizhinjam CMFRI uncat. Tuticorin, BPBM 20593; RUSI 11381. Mandapam, RUSI 11383. Madras, BMNH 1888.11.6.1. Valenciennes 1828 original combination Valenciennes 1828 junior synonym (non Valenciennes 1830) misidentification (Valenciennes 1828) new combination
<i>Serranus faveatus</i> <i>Serranus bontoo</i> <i>Epinephelus quoyanus</i> <i>Epinephelus faveatus</i>	
<i>Epinephelus flavocaeruleus</i> (Lacepède 1802)	Blue and yellow grouper. (Fr M) Max. 80 cm TL. Lakshadweep Islands and the Andaman Islands. Museum: Madras?, BMNH 1803.11.26.14.
<i>Holocentrus gymnosus</i> <i>Bodianus macrocephalus</i> <i>Serranus borbonicus</i> <i>Perca flava-purpurea</i> <i>Cynlichthys flava-purpuratus</i> <i>Epinephelus flavocoeruleus</i> <i>Epinephelus flavocaeruleus</i> <i>Holocentrus flavo-caeruleus</i>	Lacepède 1802 junior synonym Lacepède 1802 junior synonym Quoy and Gaimard 1824 junior synonym Bennett 1830 junior synonym Swainson 1839 other (Lacepède 1803) misspelling (Lacepède 1802) new combination Lacepède 1802 original combination
<i>Epinephelus fuscoguttatus</i> (Forsskål 1775) <i>Epinephelus fuscoguttatus</i> <i>Serranus taeniocheirus</i> <i>Perca summana</i> var. <i>fusco-guttata</i> <i>Serranus horridus</i> <i>Serranus lutra</i>	Brown-marbled grouper. (Fr M Dan) Max. 120 cm. Lakshadweep (Laccadive Islands). (Forsskål 1775) new combination Valenciennes 1830 junior synonym Forsskål 1775 original combination Valenciennes 1828 junior synonym Valenciennes 1831 junior synonym
<i>Epinephelus lanceolatus</i> (Bloch 1790)	Giant grouper. (Fr Br M Dan) Max. 270 cm Museum: Vishakhapatnam, SU 41935; NW; SE
<i>Holocentrus lanceolatus</i> <i>Serranus geographicus</i> <i>Serranus phaeostigmaeus</i> <i>Promicrops lanceolatus</i> <i>Stereolepoides thompsoni</i> <i>Batrachus gigas</i> <i>Oligorus terrae-reginae</i> <i>Oligorus goliath</i>	Bloch 1790 original combination Valenciennes 1828 junior synonym Fowler 1907 junior synonym (Bloch 1790) new combination Fowler 1923 junior synonym Gunther 1869 junior synonym Ramsay 1880 junior synonym De Vis 1883 junior synonym

(continued)

Appendix I (continued)

Perciformes (perch-like) Serranidae	Sea basses, groupers and fairy basslets
<i>Serranus abdominalis</i>	Peters 1855 junior synonym
<i>Epinephelus lanceolatus</i>	(Bloch 1790) new combination
<i>Epinephelus latifasciatus</i> (Temminck & Schlegel 1842)	Striped grouper, (Fr M) Max. 137 cm SL. Museum: NW of Bombay, CMFRI uncat. Quilon, CMFRI uncat. Cochin, BPBM 27566, 27585; RUSI 11380. SW of Cochin, RUSI 11411. Madras, ANSP 100153; BPBM 20515; NW Day 1868 junior synonym (Temminck & Schlegel 1842) new combination
<i>Priacanthichthys maderaspensis</i>	Day 1867 junior synonym
<i>Epinephelus latifasciatus</i>	Temminck and Schlegel 1842 original combination
<i>Serranus grammicus</i>	
<i>Serranus latifasciatus</i>	
<i>Epinephelus longispinis</i> (Kner 1864)	Longspine grouper, (Fr M) Max. 55 cm. Museum: Kerala, Kovalam, BPBM 27682. Tuticorin, BPBM 20569. In Lakshadweep Islands and Nicobars: SE
<i>Epinephelus galmaryi</i>	(non Valenciennes 1830) misidentification
<i>Epinephelus fario</i>	(Thunberg 1793) other
<i>Epinephelus maculatus</i>	(non Bloch 1790) misidentification
<i>Epinephelus longispinus</i>	(Kner 1864) new combination
<i>Serranus longispinis</i>	Kner 1864 original combination
<i>Epinephelus macrospilos</i> (Bleeker 1855)	Snubnose grouper, (Fr M) Max. 51 cm TL. Museum: Nicobar Is., SMF 20433.
<i>Serranus cylindricus</i>	Günther 1859 junior synonym
<i>Epinephelus macrospilos</i>	(Bleeker 1855) new combination
<i>Epinephelus quoyanus</i>	(non Valenciennes 1830) misidentification
<i>Epinephelus faveatus</i>	(non Valenciennes 1828) misidentification
<i>Epinephelus macrospilus</i>	(Bleeker 1855) misspelling
<i>Serranus macrospilos</i>	Bleeker 1855 original combination
<i>Epinephelus megachir</i>	(non Richardson 1846) misidentification
<i>Epinephelus malabaricus</i> (Bloch & Schneider 1801)	Malabar grouper, (Fr Br M) Max. 234 cm. Museum: BPBM 27497, 27993, 20592; CMFRI 143, 173; RUSI 11382; MNHN 743 (Holotype of <i>S. semipunctatus</i>); NW; SE
<i>Serranus salmonoides</i>	Valenciennes 1828 other
<i>Serranus crapao</i>	Cuvier 1829 junior synonym
<i>Epinephelus salmonoides</i>	(Lacepède 1802) junior synonym
<i>Epinephelus malabaricus</i>	(Bloch & Schneider 1801) new combination
<i>Epinephelus tauvina</i>	(non Forsskål 1775) misidentification
<i>Holocentrus salmonoides</i>	Lacepède 1802 junior synonym
<i>Serranus polypodophilus</i>	Bleeker 1849 junior synonym
<i>Serranus semi-punctatus</i>	Valenciennes 1828 junior synonym
<i>Holocentrus malabaricus</i>	Schneider 1801 original combination
<i>Epinephelus abdominalis</i>	(non Peters 1855) misidentification
<i>Epinephelus salmoides</i>	(Lacepède 1802) junior synonym
<i>Epinephelus cylindricus</i>	Postel 1965 junior synonym
<i>Serranus estuarius</i>	Macleay 1884 questionable
<i>Epinephelus salmonoides</i>	(Lacepède 1802) junior synonym

(continued)

Appendix I (continued)

Perciformes (perch-like) Serranidae	Sea basses, groupers and fairy basslets
<i>Epinephelus morrhua</i> (Valenciennes 1833)	Comet grouper, (Fr M Dan) Max. 90 cm TL. In Lakshadweep Islands. (Valenciennes 1833) new combination; SW (non Temminck & Schlegel 1842) misidentification Valenciennes 1833 original combination Tanaka 1927 junior synonym
<i>Epinephelus morrhua</i> <i>Epinephelus poecilonotus</i> <i>Serranus morrhua</i> <i>Epinephelus cometae</i>	
<i>Epinephelus octofasciatus</i> Griffin 1926	Eightbar grouper, (Fr. M), Max. 130 cm TL. Lakshadweep (Laccadive) Is. Postel, Fourmanoir, & Guézé 1963 junior synonym Griffin 1926 original combination (non Poey 1852) misidentification (non Thunberg 1793) misidentification
<i>Epinephelus compressus</i> <i>Epinephelus octofasciatus</i> <i>Epinephelus mystacinus</i> <i>Epinephelus septemfasciatus</i>	
<i>Epinephelus poecilonotus</i> (Temminck & Schlegel 1842)	Dot-dash grouper, (Fr M), Max. 65 cm . Museum: Madras, AMS B.5342. Also found in Lakshadweep Islands. Temminck & Schlegel 1842 original combination (non Valenciennes 1833) misidentification (Temminck & Schlegel 1842) new combination
<i>Serranus poëcilonotus</i> <i>Epinephelus morrhua</i> <i>Epinephelus poecilonotus</i>	
<i>Epinephelus polylepis</i> Randall & Heemstra 1991	Smallscaled grouper, (Fr M)
<i>Epinephelus chlorostigma</i> <i>Epinephelus</i> sp. <i>Epinephelus polylepis</i>	(non Valenciennes 1895) misidentification Not applicable misidentification Randall & Heemstra 1991 original combination
<i>Epinephelus polyphekadion</i> (Bleeker 1849)	Camouflage grouper, (Fr M Dan) Max. 90 cm SL. Museum: Mandapam, Kulak Karai, RUSI 16296.
<i>Serranus polyphekadion</i> <i>Epinephelus polyphekadion</i> <i>Epinephelus microdon</i> <i>Epinephelus goldmani</i> <i>Serranus dispar</i> var. b <i>Serranus microdon</i> <i>Serranus goldmanni</i>	Bleeker 1849 original combination (Bleeker 1849) new combination (Bleeker 1856) junior synonym (Bleeker 1855) junior synonym Playfair 1867 junior synonym Bleeker 1856 junior synonym Bleeker 1855 junior synonym
<i>Epinephelus radiatus</i> (Day 1867)	Oblique-banded grouper, (Fr M) Max. 70 cm SL. Museum: Vishakhapatnam, USNM 272429.
<i>Epinephelus radiatus</i> <i>Serranus radiatus</i> <i>Serranus morrhua</i> <i>Serranus brunneus</i> <i>Epinephelus doderleinii</i> <i>Epinephelus morrhua</i>	(Day 1867) new combination Day 1867 original combination (non Valenciennes 1833) misidentification (non Bloch 1793) misidentification Franz 1910 junior synonym (non Valenciennes 1833) misidentification
<i>Epinephelus spilotoceps</i> Schultz 1953	Foursaddle grouper, (Fr M) Max. 25 cm SL. Found in Lakshadweep (Laccadive) Islands.
<i>Epinephelus spilotoceps</i> <i>Epinephelus salonotus</i>	Schultz 1953 original combination Smith and Smith 1963 junior synonym

(continued)

Appendix I (continued)

Perciformes (perch-like) Serranidae	Sea basses, groupers and fairy basslets
<i>Epinephelus tauvina</i> (Forsskål 1775)	Greasy grouper, (Fr M) Max. 75 cm TL. Museum: Lakshadweep (Laccadive Is.), Minicoy and Kulta, CMFRI-LA-F 115/117; SW; SE Macleay 1883 junior synonym Bleeker 1857 questionable Lacepède 1801 junior synonym Forsskål 1775 original combination Schultz 1953 junior synonym Morgans 1966 junior synonym (Forsskål 1775) new combination (non Lacepède 1802) misidentification
<i>Serranus goldiei</i> <i>Serranus jansenii</i> <i>Holocentrus pantherinus</i> <i>Perca tauvina</i> <i>Epinephelus elongatus</i> <i>Epinephelus chewa</i> <i>Epinephelus tauvina</i> <i>Epinephelus salmoides</i>	
<i>Epinephelus tukula</i> Morgans 1959	Potato grouper, (Fr Br M) Max. 200 cm . Museum: Kerala, Kovalam, BPBM 27634. Morgans 1959 original combination (non Forsskål 1775) misidentification (non Forsskål 1775) misidentification Playfair & Gunther 1867 junior synonym
<i>Epinephelus tukula</i> <i>Epinephelus fuscoguttatus</i> <i>Serranus fuscoguttatus</i> <i>Serranus dispar</i> var. A	
<i>Epinephelus undulosus</i> (Quoy & Gaimard 1824)	Wavy-lined grouper, Heraku, (Fr M Fi) Max. 73 cm TL. Museum: Vizhinjam, BPBM 27702. Tuticorin, BPBM 20570. CMFRI 97; RUSI 11412. Pondicherry, MNHN 7544 (Syntype of <i>S. lineatus</i>). Madras, BMNH 1889.2.1.4226 (Paratype of <i>S. coromandelicus</i>); NMW 40392; SE Quoy and Gaimard 1824 original combination Valenciennes 1828 junior synonym Bleeker 1852 junior synonym (Quoy & Gaimard 1824) new combination
<i>Bodianus undulosus</i> <i>Serranus lineatus</i> <i>Serranus amboinensis</i> <i>Epinephelus undulosus</i>	
<i>Variola louti</i> (Forsskål 1775)	Yellow-edged lyretail, (Fr M Dan) Max. 81 cm TL.
<i>Serranus luti</i> <i>Variola longipinna</i> <i>Serranus longipinna</i> <i>Variola louti</i> <i>Variola melanotaenia</i> <i>Serranus roseus</i> <i>Serranus flavimarginatus</i> <i>Labrus punctulatus</i> <i>Perca louti</i> <i>Serranus phaeostomus</i> <i>Serranus cernipedis</i>	Valenciennes 1828 other Swainson 1839 junior synonym Swainson 1839 junior synonym (Forsskål 1775) new combination Bleeker 1857 junior synonym Valenciennes 1828 junior synonym Rüppell 1830 junior synonym Lacepède 1801 junior synonym Forsskål 1775 original combination Swainson 1839 junior synonym Miranda-Ribeiro 1915 questionable

M = marine; Br = brackish; Fr = freshwater; Fi = fishery; Aq = aquaculture; Or = ornamental; Sp = sport; Bait = used as bait; Dan = dangerous to human; Thr = threatened; En = endemic; In = introduced and still present; Ex = extirpated; Mi = misidentified; Pr = protected; Rest = restricted; NW = occurring on northwest coast of India; SW = occurring on Southwest coast of India (including Laccadives); SE = occurring on southeast coast of India. M, Br, Fr, Dan, and Thr refer to the species in general.

Museum: refers to museum specimens collected in this country.

Note: This list of species was assembled from country records for species entered in FishBase as of 18 June 1996. The scientific name is followed by the international FishBase name and, if available, a common name used in the country. Not all extant species of fishes are included in this version of FishBase, nor have all species been assigned to the countries in which they occur. Thus, this list is likely to be incomplete. Conversely, this list may include fish that are very rare or extinct, or reported only once from a given country. Please check FishBase 96 or subsequent versions under the name of the species in question for additional information.

Appendix II

FishBase checklist of family Lutjanidae in India based mainly on Allen (1985). [Lista revisada de FishBase para la familia Lutjanidae de la India, basada principalmente en Allen (1985).]

Perciformes (perch-like)	Snappers
Lutjanidae	
<i>Aphareus furca</i> (Lacepède 1801)	Small toothed jobfish, (Fr M) Max. 40 cm SL.
<i>Aphareus flavivultus</i>	Jenkins 1901 junior synonym
<i>Caranxomorus sacrestinus</i>	Lacepède 1803 junior synonym
<i>Labrus furca</i>	Lacepède 1801 original combination
<i>Aphareus furcatus</i>	(Lacepède 1801) misspelling
<i>Aphareus furca</i>	(Lacepède 1801) new combination
<i>Aphareus caerulescens</i>	Cuvier 1830 junior synonym
<i>Aphareus rutilans</i> Cuvier 1830	Rusty jobfish, (Fr M) Max. 80 cm SL.
<i>Aphareus thompsoni</i>	Fowler 1923 junior synonym
<i>Aphareus rutilans</i>	Cuvier 1830 original combination
<i>Aprion virescens</i> Valenciennes 1830	Green jobfish, (Fr M Dan) Max. 80 cm SL; SE
<i>Aprion konekonis</i>	Tanaka 1914 junior synonym
<i>Mesopriion microchir</i>	Bleeker 1853 junior synonym
<i>Sparopsis elongatus</i>	Kner 1868 junior synonym
<i>Sparopsis latifrons</i>	Kner 1868 junior synonym
<i>Aprion virescens</i>	Valenciennes 1830 original combination
<i>Etelis carbunculus</i> Cuvier 1828	Ruby snapper, (Fr M) Max. 127 cm FL.
<i>Etelis coruscans</i>	(non Valenciennes 1862) misidentification
<i>Etelis carbunculus</i>	Cuvier 1828 original combination
<i>Eteliscus marshi</i>	Jenkins 1903 junior synonym
<i>Etelis evurus</i>	(non Jordan & Evermann 1903) misidentification
<i>Etelis coruscans</i> Valenciennes 1862	Flame snapper, (Fr M) Max. 85 cm SL.
<i>Etelis carbunculus</i>	(non Cuvier 1828) misidentification
<i>Etelis coruscans</i>	Valenciennes 1862 original combination
<i>Etelis evurus</i>	Jordan & Evermann 1903 junior synonym
<i>Etelis radiosus</i> Anderson 1981	Scarlet snapper, (Fr M) Max. 80 cm SL.
<i>Etelis radiosus</i>	Anderson 1981 original combination
<i>Lipocheilus carnolabrum</i> (Chan 1970)	Tang's snapper, (Fr M) Max. 50 cm SL.
<i>Tangia carnolabrum</i>	Chan 1970 original combination
<i>Lipocheilus carnolabrum</i>	(Chan 1970) new combination
<i>Lutjanus argentimaculatus</i> (Forsskål 1775)	Mangrove red snapper, Banda, (Fr Br M) Max. 150 cm TL; NW; SE
<i>Mesopriion roseigaster</i>	Macleay 1881 junior synonym
<i>Mesopriion sexfasciatus</i>	Macleay 1883 junior synonym
<i>Mesopriion taenlops</i>	Valenciennes 1830 junior synonym
<i>Sciaena argentata</i>	Gmelin 1789 junior synonym

(continued)

Appendix II (continued)

Perciformes (perch-like) Lutjanidae	Snappers
<i>Lutjanus argentimaculatus</i>	(Forsskål 1775) new combination
<i>Lutjanus johngarah</i>	Day 1875 junior synonym
<i>Mesopriion olivaceus</i>	Cuvier 1828 junior synonym
<i>Sciaena argentimaculata</i>	Forsskål 1775 original combination
<i>Mesopriion griseoides</i>	Gülichot 1862 junior synonym
<i>Mesopriion garretti</i>	Günther 1873 junior synonym
<i>Alphestes gembra</i>	Schneider 1801 junior synonym
<i>Lutjanus salmonoides</i>	Gilchrist & Thompson 1908 junior synonym
<i>Mesopriion flavipinnis</i>	Cuvier 1828 junior synonym
<i>Diacope superbus</i>	Castelnau 1878 junior synonym
<i>Mesopriion obscurus</i>	Macleay 1881 junior synonym
<i>Lutjanus bengalensis</i> (Bloch 1790)	Bengal snapper. (Fr M) Max. 30 cm TL.
<i>Holocentrus bengalensis</i>	Bloch 1790 original combination
<i>Lutjanus bengalensis</i>	(Bloch 1790) new combination
<i>Mesopriion pomacanthus</i>	Bleeker 1855 junior synonym
<i>Diacope octovittata</i>	Valenciennes 1830 junior synonym
<i>Diacope octolineata</i>	Cuvier 1828 junior synonym
<i>Lutjanus biguttatus</i> (Valenciennes 1830)	Two-spot banded snapper. (Fr M) Max. 20 cm TL.
<i>Mesopriion elongatus</i>	Hombron & Jacquinot 1853 junior synonym
<i>Serranus biguttatus</i>	Valenciennes 1830 original combination
<i>Lutjanus biguttatus</i>	(Valenciennes 1830) new combination
<i>Mesopriion bleekeri</i>	Günther 1859 junior synonym
<i>Lutjanus bohar</i> (Forsskål 1775)	Two-spot red snapper. (Fr M Dan) Max. 75 cm TL; SW
<i>Sparus lepisurus</i>	Lacepède 1802 junior synonym
<i>Mesopriion rubens</i>	Macleay 1882 junior synonym
<i>Lutjanus bohar</i>	(Forsskål 1775) new combination
<i>Sciaena bohar</i>	Forsskål 1775 original combination
<i>Lutjanus coatesi</i>	Whitley 1934 junior synonym
<i>Diacope labuan</i>	Thiollière 1856 junior synonym
<i>Lutjanus nukuhivae</i>	Seale 1906 junior synonym
<i>Mesopriion rangus</i>	Cuvier 1828 junior synonym
<i>Diacope quadriguttata</i>	Cuvier 1828 junior synonym
<i>Lutjanus rangus</i>	(Cuvier 1828) junior synonym
<i>Lutjanus carponotatus</i> (Richardson 1842)	Spanish flag snapper. (Fr M) Max. 40 cm TL.
<i>Lutjanus chrysotaenia</i>	(Bleeker 1851) junior synonym
<i>Mesopriion carponotatus</i>	Richardson 1842 original combination
<i>Mesopriion naborer</i>	Thiollière 1856 junior synonym
<i>Mesopriion chrysotaenia</i>	Bleeker 1851 junior synonym
<i>Lutjanus carponotatus</i>	(Richardson 1842) new combination
<i>Lutjanus decussatus</i> (Cuvier 1828)	Checkered snapper. (Fr M) Max. 30 cm TL.
<i>Mesopriion therapon</i>	Day 1869 junior synonym
<i>Mesopriion decussatus</i>	Cuvier 1828 original combination
<i>Lutjanus decussatus</i>	(Cuvier 1828) new combination

(continued)

Appendix II (continued)

Perciformes (perch-like) Lutjanidae	Snappers
<i>Lutjanus ehrenbergii</i> (Peters 1869)	Blackspot snapper, (Fr M) Max. 35 cm TL.
<i>Lutjanus ehrenbergii</i>	Peters 1869 original combination
<i>Lutjanus ehrenbergii</i>	(Peters 1869) new combination
<i>Lutjanus oligolepis</i>	Bleeker 1873 junior synonym
<i>Lutjanus erythropterus</i> Bloch 1790	Crimson snapper, (Fr M) Max. 60 cm TL.
<i>Lutjanus altifrontalis</i>	Chan 1970 junior synonym
<i>Lutjanus longmani</i>	Whitley 1937 junior synonym
<i>Mesopriion annularis</i>	Cuvier 1828 junior synonym
<i>Mesopriion chirtah</i>	Cuvier 1828 junior synonym
<i>Mesopriion rubellus</i>	Cuvier 1828 junior synonym
<i>Lutjanus malabaricus</i>	(non Schneider) misidentification
<i>Lutjanus annularis</i>	(Cuvier 1828) junior synonym
<i>Lutjanus erythropterus</i>	Bloch 1790 original combination
<i>Genyoroge macleayana</i>	Ramsay 1883 junior synonym
<i>Lutjanus fulviflamma</i> (Forsskål 1775)	Blackspot snapper, (Fr M) Max. 35 cm TL.
<i>Mesopriion aureovittatus</i>	Macleay 1879 junior synonym
<i>Lutjanus fulviflampus</i>	(Forsskål 1775) misspelling
<i>Sclaena fulviflamma</i>	Forsskål 1775 original combination
<i>Lutjanus fulviflamma</i>	(Forsskål 1775) new combination
<i>Lutjanus unimaculatus</i>	Quoy & Gaimard 1824 junior synonym
<i>Centropomus hofer</i>	Lacepède 1802 junior synonym
<i>Mesopriion terubuan</i>	Thiolière 1856 junior synonym
<i>Mesopriion aurolineatus</i>	Cuvier 1830 junior synonym
<i>Lutjanus fulvus</i> (Schneider 1801)	Blacktail snapper, (Fr M Dan) Max. 40 cm TL; NW
<i>Mesopriion argenteus</i>	Hombron & Jacquinot 1853 junior synonym
<i>Lutjanus fulvus</i>	(Schneider 1801) new combination
<i>Lutjanus marginatus</i>	(Cuvier 1828) junior synonym
<i>Mesopriion marginiplinnis</i>	Macleay 1883 junior synonym
<i>Lutjanus vaigiensis</i>	(Quoy & Gaimard 1824) junior synonym
<i>Holocentrus fulvus</i>	Schneider 1801 original combination
<i>Mesopriion maus</i>	Thiolière 1856 junior synonym
<i>Mesopriion gaimardi</i>	Bleeker 1859 junior synonym
<i>Lutjanus marginatooides</i>	Kendall & Goldsborough 1911 junior synonym
<i>Genyoroge nigricauda</i>	De Vis 1885 junior synonym
<i>Diacope xanthopus</i>	Cuvier 1829 junior synonym
<i>Diacope vaigiensis</i>	Quoy & Gaimard 1824 junior synonym
<i>Diacope marginata</i>	Cuvier 1828 junior synonym
<i>Diacope immaculata</i>	Cuvier 1828 junior synonym
<i>Diacope flavipes</i>	Valenciennes 1830 junior synonym
<i>Diacope aurantiaca</i>	Valenciennes 1830 junior synonym
<i>Diacope analis</i>	Valenciennes 1830 junior synonym
<i>Mesopriion kagoshimna</i>	Steindachner & Doederlein 1883 junior synonym

(continued)

Appendix II (continued)

Perciformes (perch-like) Lutjanidae	Snappers
<i>Lutjanus gibbus</i> (Forsskål 1775)	Humpback snapper, (Fr M Dan) Max. 50 cm TL; SW
<i>Diacope lineata</i>	Quoy & Gaimard 1824 junior synonym
<i>Diacope axillaris</i>	Valenciennes 1830 junior synonym
<i>Diacope borensis</i>	Cuvier 1828 junior synonym
<i>Diacope melanura</i>	Ruppell 1838 junior synonym
<i>Diacope coccinea</i>	Cuvier 1828 junior synonym
<i>Diacope striata</i>	Cuvier 1828 junior synonym
<i>Diacope tiea</i>	Lesson 1830 junior synonym
<i>Genyoroge bidens</i>	Macleay 1883 junior synonym
<i>Lutjanus tahitiensis</i>	Seale 1906 junior synonym
<i>Lutjanus comoriensis</i>	Fourmanoir 1957 junior synonym
<i>Mesopriion janthinurus</i>	Bleeker 1854 junior synonym
<i>Sclaena gibba</i>	Forsskål 1775 original combination
<i>Lutjanus gibbus</i>	(Forsskål 1775) new combination
<i>Diacope rosea</i>	Valenciennes 1830 junior synonym
<i>Lutjanus guilcheri</i> Fourmanoir 1959	Yellowfin red snapper, (Fr M) Max. 60 cm TL.
<i>Lutjanus guilcheri</i>	Fourmanoir 1959 original combination
<i>Lutjanus johnii</i> (Bloch 1792)	John's snapper, (Fr M) Max. 70 cm TL; NW
<i>Mesopriion yapilli</i>	Cuvier 1828 junior synonym
<i>Lutjanus johnii</i>	(Bloch 1792) new combination
<i>Lutjanus Johni</i>	(Bloch 1792) misspelling
<i>Anthias johnii</i>	Bloch 1792 original combination
<i>Serranus pavoninus</i>	Valenciennes 1831 junior synonym
<i>Diacope xanthozona</i>	Bleeker 1845 other
<i>Colus catius</i>	Buchanan 1822 junior synonym
<i>Sparus tranquebaricus</i>	Shaw 1803 junior synonym
<i>Lutjanus kasmira</i> (Forsskål 1775)	Common bluestripe snapper, (Fr M) Max. 40 cm TL; SW
<i>Diacope octolineata</i>	(non Cuvier 1828) misidentification
<i>Mesopriion etaape</i>	Lesson 1830 junior synonym
<i>Mesopriion pomacanthus</i>	(non Bleeker 1855) misidentification
<i>Sciaena kasmira</i>	Forsskål 1775 original combination
<i>Lutjanus kasmira</i>	(Forsskål 1775) new combination
<i>Lutjanus lemniscatus</i> (Valenciennes 1828)	Yellowstreaked snapper, (Fr M) Max. 65 cm TL.
<i>Lutjanus rangus</i>	(non Cuvier 1828) misidentification
<i>Lutjanus janthinuropterus</i>	(Bleeker 1852) junior synonym
<i>Lutjanus lemniscatus</i>	(Valenciennes 1828) new combination
<i>Mesopriion janthinuropterus</i>	Bleeker 1852 junior synonym
<i>Lutjanus furvicaudatus</i>	Fowler 1904 junior synonym
<i>Mesopriion immaculatus</i>	Cuvier 1828 junior synonym
<i>Serranus lemniscatus</i>	Valenciennes 1828 original combination

(continued)

Appendix II (continued)

Perciformes (perch-like)	Snappers
Lutjanidae	
<i>Lutjanus lunulatus</i> (Park 1797)	Lunartail snapper, Chemara, (Fr M) Max. 35 cm TL.
<i>Mesopriion caudalis</i>	Valenciennes 1830 junior synonym
<i>Perca lunulata</i>	Park 1797 original combination
<i>Lutjanus lunulatus</i>	(Park 1797) new combination
<i>Lutjanus madras</i> (Valenciennes 1831)	Indian snapper, (Fr M) Max. 30 cm TL.
<i>Lutjanus madras</i>	(Valenciennes 1831) new combination
<i>Mesopriion madras</i>	Valenciennes 1831 original combination
<i>Lutjanus malabaricus</i> (Bloch & Schneider 1801)	Malabar blood snapper, (Fr M) Max. 100 cm TL; NW; SE
<i>Lutjanus dodecacanthus</i>	(Bleeker 1853) junior synonym
<i>Lutjanus malabaricus</i>	(Bloch & Schneider 1801) new combination (non Cuvier 1828) misidentification
<i>Lutjanus sanguineus</i>	Bleeker 1853 junior synonym
<i>Mesopriion dodecacanthus</i>	Bloch & Schneider 1801 original combination
<i>Sparus malabaricus</i>	
<i>Lutjanus monostigma</i> (Cuvier 1828)	One-spot snapper, (Fr M Dan) Max. 60 cm TL.
<i>Lutlanus monostigma</i>	(Cuvier 1828) misspelling
<i>Lutjanus monostigmus</i>	(Cuvier 1828) misspelling
<i>Lutjanus lioglossus</i>	(Bleeker 1873) junior synonym
<i>Lutjanus monostigma</i>	(Cuvier 1828) new combination
<i>Mesopriion monostigma</i>	Cuvier 1828 original combination
<i>Lutjanus quinquelineatus</i> (Bloch 1790)	Five-lined snapper, (Fr M) Max. 38 cm TL.
<i>Holocentrus quinquelinearis</i>	Bloch 1790 junior synonym
<i>Lutjanus quinquelineatus</i>	(Bloch 1790) new combination
<i>Lutjanus spilurus</i>	(Bennett 1832) junior synonym
<i>Genyoroge notata</i> var. <i>sublineata</i>	De Vis 1885 junior synonym
<i>Genyoroge notata</i> var. <i>sexlineata</i>	Kent 1893 junior synonym
<i>Genyoroge grammica</i>	Day 1870 junior synonym
<i>Diacope spirula</i>	Bennett 1832 junior synonym
<i>Diacope decemlineata</i>	Valenciennes 1830 junior synonym
<i>Holocentrus quinquelineatus</i>	Bloch 1790 original combination
<i>Lutjanus rivulatus</i> (Cuvier 1828)	Blubberlip snapper, (Fr M) Max. 65 cm TL; SE
<i>Mesopriion parvidens</i>	Macleay 1883 junior synonym
<i>Diacope rivulata</i>	Cuvier 1828 original combination
<i>Lutjanus rlvulatus</i>	(Cuvier 1828) new combination
<i>Mesopriion quadripunctatus</i>	Günther 1859 junior synonym
<i>Diacope sinal</i>	Thiolière 1857 junior synonym
<i>Diacope revulina</i>	Cuvier 1828 misspelling
<i>Diacope alboguttata</i>	Valenciennes 1831 junior synonym
<i>Diacope coeruleo-punctata</i>	Cuvier 1828 junior synonym
<i>Mesopriion myrlaster</i>	Liénard 1839 junior synonym

(continued)

Appendix II (continued)

Perciformes (perch-like)		
Lutjanidae	Snappers	
<i>Lutjanus russelli</i> (Bleeker 1849)	Russell's snapper, (Fr M) Max. 50 cm TL; SW	
<i>Lutjanus nishikawai</i>	Smith & Pope 1906 junior synonym	
<i>Lutjanus orientalis</i>	Séale 1909 junior synonym	
<i>Mesopriion russelli</i>	Bleeker 1849 original combination	
<i>Lutjanus russelli</i>	(Bleeker 1849) new combination	
<i>Lutjanus russelli</i>	(Bleeker 1849) misspelling	
<i>Lutjanus sanguineus</i> (Cuvier 1828)	Humphead snapper, (Fr M) Max. 90 cm FL; NW (non Cuvier 1828) misidentification	
<i>Lutjanus coccineus</i>	Cuvier 1828 original combination	
<i>Diacope sanguinea</i>	Ruppell 1838 junior synonym	
<i>Diacope erythrina</i>	(Cuvier 1828) new combination	
<i>Lutjanus sanguineus</i>		
<i>Lutjanus sebae</i> (Cuvier 1816)	Emperor red snapper, (Fr M) Max. 100 cm TL.	
<i>Diacope civis</i>	Valenciennes 1831 junior synonym	
<i>Diacope siamensis</i>	Valenciennes 1830 junior synonym	
<i>Genyoroge regia</i>	De Vis 1885 junior synonym	
<i>Diacope sebae</i>	Cuvier 1816 original combination	
<i>Lutjanus sebae</i>	(Cuvier 1816) new combination	
<i>Lutjanus vitta</i> (Quoy & Gaimard 1824)	Brownstripe red snapper, (Fr M) Max. 40 cm TL.; NW; SE	
<i>Lutjanus lita</i>	(Quoy & Gaimard 1824) misspelling	
<i>Serranus vitta</i>	Quoy & Gaimard 1824 original combination	
<i>Lutjanus vitta</i>	(Quoy & Gaimard 1824) new combination	
<i>Lutjanus lutjanus</i>	(non Bloch 1790) misidentification	
<i>Mesopriion phaiotaeniatus</i>	Bleeker 1849 junior synonym	
<i>Mesopriion ophuysenii</i>	(non Bleeker 1860) misidentification	
<i>Mesopriion enneacanthus</i>	Bleeker 1849 junior synonym	
<i>Lutjanus vittus</i>	(Quoy & Gaimard 1824) misspelling	
<i>Macolor niger</i> (Forsskål 1775)	Black and white snapper, (Fr M) Max. 48 cm SL.	
<i>Diacope macolor</i>	Lesson 1827 junior synonym	
<i>Macolor typus</i>	Bleeker 1867 junior synonym	
<i>Sciaena nigra</i>	Forsskål 1775 original combination	
<i>Macolor niger</i>	(Forsskål 1775) new combination	
<i>Macolor macolor</i>	(Lesson 1827) junior synonym	
<i>Macolor macularis</i>	(non Fowler 1931) misidentification	
<i>Paracaelio sordida</i> Abe & Shinohara 1962	Dirty ordure snapper, (Fr M) Max. 40 cm SL.	
<i>Paracaelio solididus</i>	Abe & Shinohara 1962 misspelling	
<i>Paracaelio sordida</i>	Abe & Shinohara 1962 original combination	
<i>Paracaelio xanthura</i> (Bleeker 1869)	Yellowtail blue snapper, (Fr M) Max. 40 cm SL.	
<i>Paracaelio pedleyi</i>	McCulloch & Waite 1916 questionable	
<i>Paracaelio xanthura</i>	(Bleeker 1869) new combination	

(continued)

Appendix II (continued)

Perciformes (perch-like) Lutjanidae	Snappers
<i>Paracaesio xanthurus</i>	(Bleeker 1869) misspelling
<i>Vegetichthys tumidus</i>	Tanaka 1917 junior synonym
<i>Aetiasia cantharoides</i>	Barnard 1937 junior synonym
<i>Caesio xanthurus</i>	Bleeker 1869 original combination
<i>Pinjalo lewisi</i>	Slender pinjalo, (Fr M)
Randall, Allen, & Anderson 1987	Max. 36 cm SL.
<i>Pinjalo microphthalmus</i>	Lee 1987 questionable
<i>Pinjalo lewisi</i>	Randall, Allen, & Anderson 1987 original combination
<i>Pinjalo</i> sp.	N.A. questionable N.A. misidentification
<i>Macolor</i> sp.	Not applicable misidentification
<i>Paracaesio</i> sp.	Not applicable misidentification
<i>Pinjalo typus</i>	(non Bleeker) misidentification
<i>Pinjalo pinjalo</i>	(non Bleeker 1850) misidentification
<i>Pinjalo pinjalo</i> (Bleeker 1850)	Pinjalo, (Fr M)
<i>Mesopriion mitchelli</i>	Max. 46 cm SL.
<i>Caesio pinjalo</i>	Günther 1867 junior synonym
<i>Pinjalo typus</i>	Bleeker 1850 original combination
<i>Odontonectes pinjalo</i>	Bleeker 1873 junior synonym
<i>Odontonectes erythrogaster</i>	(Bleeker 1850) new combination
<i>Pinjalo pinjalo</i>	(non Cuvier 1830) misidentification
<i>Pinjalo</i> sp.	(Bleeker 1850) new combination
<i>Pinjalo microphthalmus</i>	Not applicable misidentification
<i>Pinjalo</i> sp. (Lee 1987)	Lee 1987 questionable
<i>Pristipomoides filamentosus</i> (Valenciennes 1830)	Crimson jobfish, (Fr M)
<i>Aphareus roseus</i>	Max. 80 cm SL.
<i>Chaetopterus microlepis</i>	Castelnau 1879 junior synonym
<i>Aprion kanekonis</i>	Bleeker 1869 junior synonym
<i>Pristipomoides filamentosus</i>	Tanaka 1935 junior synonym
<i>Pristipomoides microlepis</i>	(Valenciennes 1830) new combination
<i>Etelis brevirostris</i>	(Bleeker 1868) junior synonym
<i>Bowersia violescens</i>	Vaillant 1873 junior synonym
<i>Aprion microdon</i>	Jordan & Evermann 1903 junior synonym
<i>Serranus filamentosus</i>	Steindachner 1876 junior synonym
<i>Pristipomoides multidens</i> (Day 1870)	Valenciennes 1830 original combination
<i>Pristipomoides multidens</i>	Goldbanded jobfish, (Fr M)
<i>Diacope sparus</i>	Max. 70 cm SL.
<i>Mesopriion multidens</i>	(Day 1870) new combination
<i>Pristipomoides sieboldii</i> (Bleeker 1857)	Temminck & Schlegel 1842 junior synonym
<i>Pristipomoides microdon</i>	Day 1870 original combination
<i>Bowersia ulaula</i>	Lavender jobfish, (Fr M)
<i>Chaetopterus dubius</i>	Max. 50 cm SL.
<i>Pristipomoides sieboldii</i>	(Steindachner 1876) questionable
<i>Chaetopterus sieboldii</i>	Jordan & Evermann 1903 junior synonym

(continued)

Appendix II (continued)

Perciformes (perch-like) Lutjanidae	Snappers
<i>Pristipomoides zonatus</i> (Valenciennes 1830)	Oblique-banded snapper. (Fr M), Ref. 55 Max. 40 cm SL.
<i>Serranus argyrogrammicus</i>	Valenciennes 1831 questionable
<i>Rooseveltia aloha</i>	Jordan & Snyder 1907 junior synonym
<i>Serranus brighami</i>	Seale 1901 junior synonym
<i>Serranus telfairi</i>	Bennett 1831 junior synonym
<i>Rooseveltia brighami</i>	(Seale 1901) junior synonym
<i>Tropidinhus zonatus</i>	(Valenciennes 1830) new combination
<i>Serranus zonatus</i>	Valenciennes 1830 original combination
<i>Pristipomoides zonatus</i>	(Valenciennes 1830) new combination

M = marine; Br = brackish; Fr = freshwater; Fi = fishery; Aq = aquaculture; Or = ornamental; Sp = sport; Bait = used as bait; Dan = dangerous to human; Thr = threatened; En = endemic; In = introduced and still present; Ex = extirpated; Mi = misidentified; Pr = protected; Rest = restricted; NW = occurring on Northwest coast of India; SW = occurring on Southwest coast of India (including Laccadives); SE = occurring on Southeast of India. M, Br, Fr, Dan, and Thr refer to the species in general.

Museum: refers to museum specimens collected in this country.

Note: This list of species was assembled from country records for species entered in FishBase as of 18 June 1996. The scientific name is followed by the international FishBase name and, if available, a common name used in the country. Not all extant species of fishes are included in this version of FishBase, nor have all species been assigned to the countries in which they occur. Thus, this list is likely to be incomplete. Conversely, this list may include fish that are very rare or extinct, or reported only once from a given country. Please check FishBase 96 or subsequent version under the name of the species in question for additional information.

ENTERED IN NAGA

APR 14 1998

PART III: AGE, GROWTH AND REPRODUCTION IN THE WILD

Reproduction, Age and Growth of the Caribbean Red Snapper (*Lutjanus purpureus*) in Waters off Trinidad and Tobago

S.C. MANICKCHAND-HEILEMAN*

D.A.T. PHILLIP

Institute of Marine Affairs

P.O. Box 3160

Carenage P.O., Carenage

Trinidad, West Indies

MANICKCHAND-HEILEMAN, S.C. and D.A.T. PHILLIP. 1996. Reproduction, age and growth of the Caribbean red snapper (*Lutjanus purpureus*) in waters off Trinidad and Tobago [Reproducción, edad y crecimiento del pargo colorado (*Lutjanus purpureus*) en aguas de Trinidad y Tobago], p. 137-149. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Size at maturity, time of spawning, growth and mortality parameters were estimated for the Caribbean red snapper (*Lutjanus purpureus*) in Trinidad and Tobago. Size at maturity was 27 cm TL for males and 39 cm for females. Spawning occurred year-round with peak activity from September to February. The length-weight relationship was $W = 0.0141 \cdot TL^{2.99}$ where W is weight in g and TL is total length in cm. Age was determined from cross-sections of sagittae and opaque rings were deposited annually from December to April. Twenty age groups were found and the von Bertalanffy growth equation was: $L_t = 85 [1 - \exp(-0.13(t+0.86))]$, where L_t is length (cm) at time t (years). Total mortality was 0.57, natural mortality 0.28 and fishing mortality 0.29·year $^{-1}$. Yield-per-recruit analysis showed the snapper to be overfished at the present level of fishing mortality and age at first capture of 1.4 years (21.7 cm TL).

Resumen

La talla de madurez, época de desove, crecimiento y mortalidad fueron determinados para el pargo colorado (*Lutjanus purpureus*) en Trinidad y Tobago. La talla de madurez fue de 27 cm de longitud total para machos y de 39 cm LT para hembras. El desove se presenta durante todo el año con una época de máxima actividad de septiembre a febrero. La relación peso-longitud fué $W = 0.0141 \cdot TL^{2.99}$ donde W , es el peso en gramos y LT la longitud total en centímetros. La edad fué determinada de secciones transversales de la sagita donde los anillos opacos fueron depositados anualmente de diciembre a abril. Veinte grupos de edad fueron encontrados, y la ecuación de crecimiento de von Bertalanffy fué: $L_t = 85 [1 - \exp(-0.13(t+0.86))]$, donde L_t es la longitud total (cm) al tiempo t (años). La mortalidad total fué 0.57, la mortalidad natural de 0.28 y la mortalidad por pesca de 0.29·año $^{-1}$. El análisis de rendimiento por recluta mostró que el pargo colorado está sobrepeñándose al nivel actual de mortalidad por pesca y edad de primera captura de 1.4 años (21.7 cm LT).

* Present address: Instituto de Ciencias del Mar y Limnología, Lab. Ecología del Benthos Universidad Nacional Autónoma de México, Apartado Postal 70-305, México 04510 D.F. México; e-mail: sherry@mar.icm.unam.mx

Introduction

The Caribbean or southern red snapper (*Lutjanus purpureus*) is a large lutjanid, distributed along the southern coast of Cuba, the Yucatan Peninsula, and the shelves of Central and South America, down to northeast Brazil (Fischer 1978). This species is most abundant in depths between 30 and 160 m on the continental shelf off Honduras and the Guyanas. The Caribbean red snapper closely resembles the northern red snapper (*Lutjanus campechanus*), found in the Gulf of Mexico and the southern Atlantic coast of the United States (see Collins et al., this vol.).

L. purpureus is of significant commercial value in this region, especially in northeastern Brazil (Ivo and Hanson 1982) and in Venezuela (Gonzalez and Ceiaya 1986). This species is also one of the most important

species of finfish in Trinidad and Tobago, supporting a lucrative export market (Manickchand-Heileman and Phillip 1996). It comprises about 76% of trap-caught fish, which consist mainly of other species of snappers, groupers and grunts (see Marcano et al., this vol.). Historically, this species has been fished by artisanal vessels, mainly using traps on the continental shelf and shelf edge northwest of Tobago and along the north and northeastern coasts of Trinidad (Fig. 1).

Due to declining catches in the traditional fishing areas, the trap fishery has shifted south to the offshore continental shelf and shelf edge to the east of Trinidad. Several larger, mechanized vessels have recently entered the fishery (Manickchand-Heileman and Phillip 1996), posing a serious threat of overfishing. There is urgent need for management of the trap fishery, but lack

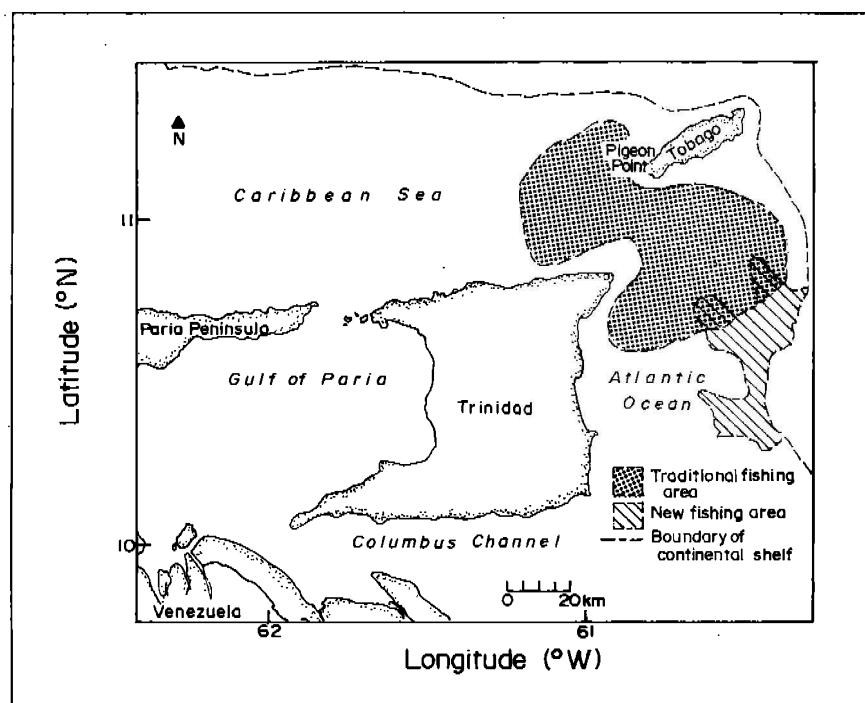


Fig. 1. Fishing areas and location of sampling area for *Lutjanus purpureus* in Trinidad and Tobago. [Areas de pesca y localidades de muestreo para *Lutjanus purpureus* en Trinidad y Tobago.]

of the necessary data is an impediment to the development of a management plan for this fishery in Trinidad and Tobago.

Because of its commercial significance, the biology and population dynamics of the snapper have been widely studied in north and northeastern Brazil. The reproductive biology has been investigated by several authors, for example, DeMoraes and Dos Santos (1969), DeMoraes (1970), Fonteles-Filho (1970, 1972b), Alves (1971), Gesteira and Ivo (1973) and Ivo (1973a, 1973b, 1975, 1976). Age and growth studies have been conducted by Lima (1965), Menezes and Gesteira (1974), Ivo and Hanson (1982) and Ximenes and Fonteles-Filho (1988). Biology and population dynamics have been investigated by Ivo and Gesteira (1974) and Ivo and Hanson (1982). Geographical distribution of this species with respect to oceanographic conditions has been reported by Fonteles-Filho and Kurisaka (1970). A synopsis of the biology of the southern red snapper has been prepared by Ivo and de Sousa (1988).

Such studies have not been conducted in any detail for this species in Trinidad and Tobago, although preliminary studies on reproduction, age and growth were carried out by Manickchand-Heileman and Phillip (1992). The main objectives of this study were to determine age, growth, spawning season, age at sexual maturity and yield per recruit for this species in Trinidad and Tobago. This study formed part of a larger stock assessment project for snappers and groupers caught in the trap fishery in Trinidad and Tobago.

The Study Area

Trinidad and Tobago are the southernmost of the Caribbean chain of islands, lying between $10^{\circ}35'$ and $11^{\circ}15'$ north latitude and $61^{\circ}15'$ and $60^{\circ}20'$ west longitude on the South American continental shelf (Fig. 1). Topographically, the shelf in this area is relatively featureless with a substratum

of fine mud interspersed with occasional patches of shell debris and fine sand (Kenny and Bacon 1981). The shelf edge lies along the 90-100 m contour (Gade 1989) which ranges from a distance of approximately 12 km from the coast of northwest Tobago to approximately 50 km from the coast of north Trinidad.

The islands experience a dry season from December to June and a wet season from July to November. During the wet season the area is influenced by freshwater runoff from local rivers and those from the mainland, especially the Orinoco and Amazon. This results in marked seasonal changes in salinity which have been found to vary from 35.5 ppt in the dry season to less than 27 ppt in the wet season (Gade 1989). Bottom temperatures at depths of about 100 m vary from a maximum of 25°C in the dry season to a minimum of 22°C in the rainy season (Gade 1989).

Samples were obtained from the traditional fishing area on the continental shelf and slope to the northeast of Trinidad and northwest of Tobago (Fig. 1).

Methods

Field sampling

From January 1990 to December 1991, monthly samples of snappers were obtained from commercial fish landings at a wet fish processing plant in Tobago. These fish were caught by Z-shaped Antillean fishtraps in the traditional fishing area in depths of 54-150 m (Fig. 1). The number of boats supplying fish to the plant varied between one to seven on any given day, and some of them landed fish that had been gutted at sea. Random samples of small- and medium-sized fish were obtained, whereas all available fish above 600 mm total length were taken due to their scarcity in the catch. A total of 988 snappers were obtained during the study period.

The following were recorded for each fish: total length (TL) in centimeters, body weight and gonad weight in grams, sex and maturity stage based on macroscopic examination of the gonads. Five maturity stages were used: immature, active, ripe, spawning and spent. For most fish the left sagittal otolith was removed unless broken or lost, in which case the right was obtained. Otoliths were stored dry in labelled envelopes for use in age determination.

Size at maturity and spawning seasonality

Size at maturity was defined as the length at which 50% of the fish were sexually mature. The frequency of snapper in all maturity stages excluding immature was determined for each 4-cm length class and used to determine size at maturity. Time of spawning was determined from monthly variations in the frequency of fish in each maturity stage and in the mean gonosomatic index (GSI) which was gonad weight expressed as a percentage of total body weight. Time of spawning was determined using only females, as was done in the Brazilian study of Gesteira and Ivo (1973).

Age and growth

Otoliths were embedded in polyester resin which was then allowed to harden overnight. Two cross sections of each otolith were taken through the focus along a dorsoventral plane using a high speed circular saw. Sections were ground and polished using several grades of silicon carbide paper until they were thin enough to transmit light (~0.2 mm). Sections were placed in glycerol and viewed against a black background using reflected light under a dissecting microscope at a magnification of $\times 20$. Alternating opaque and translucent

bands were visible and the former were counted as annuli.

In order to validate that rings were formed annually, the frequency of occurrence of otoliths with an opaque edge was determined for each month. Otolith radius and the distance from the core to the edge of each opaque ring were measured using an ocular micrometer (1 micrometer unit = 0.125 mm). All measurements were taken along the ventral surface of the sulcus acousticus. Least squares linear regression of otolith radius (OR) on total length was carried out and the relationship used to backcalculate lengths of fish at earlier ages.

The von Bertalanffy growth function (Ricker 1975) was used to describe growth of the snapper:

$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

where L_t is total length (cm) at time t (years), L_∞ is the asymptotic length, K is the growth coefficient and t_0 is theoretical age at zero length. This was fitted to observed and backcalculated lengths at age using the FISHPARM program (Prager et al. 1987). The resultant growth curve was compared with those from the literature using phi-prime (ϕ'), where $\phi' = \log K + 2\log L_\infty$ (Pauly and Munro 1984).

The length-weight relationship, $W = aL^b$ where W is body weight in g, L is total length (cm) and a and b are constants, was determined by least squares linear regression using log transformed data. W_∞ was obtained by substituting L_∞ into the above equation.

Mortality

Natural mortality (M) was determined using the empirical equation of Pauly (1980):

$$M = \exp(-0.0152 - 0.279\ln L_\infty + 0.6543\ln K + 0.463\ln T),$$

where L_∞ and K are the growth parameters and T is the mean environmental

temperature in °C. T was taken as 23.5°C in this study area (Gade 1989).

A second estimate of M was obtained from the equation of Alagaraja (1984):

$$M_{1\%} = -\ln(0.01)/t_{\max}$$

where $M_{1\%}$ is natural mortality corresponding to 1 ppt survival, and t_{\max} represents longevity, which was taken as the oldest age found in the catch.

Total mortality (Z) was estimated from length-frequency distributions using the Wetherall plot (Wetherall 1986) as modified by Pauly (1986) in the ELEFAN suite of programs (Gayaniilo et al. 1989). Fishing mortality (F) was determined as the difference between Z and M.

Yield per recruit

Equilibrium yield-per-recruit analyses following Beverton and Holt (1957) were carried out using the LFSA computer program (Sparre 1987). The input parameters were L_{∞} , K, t_0 ; a and b from the length-

weight relationship (for the Beverton and Holt model, b is assumed to be 3); M; age at first capture (t_c); length at first capture L_c ; W_{∞} and age at recruitment (t_r) which was assumed to be one year. Length at first capture was determined using the ELEFAN suite of programs (Gayaniilo et al. 1989), and was converted to age by inverting the growth equation.

Results

Size at maturity and spawning seasonality

A total of 381 male and 408 female snappers, ranging in size from 24.7 to 84.9 cm TL were used to determine size at maturity. Males matured at a smaller size than females. The size at which 50% of the individuals were mature was 27 cm TL for males and 39 cm TL for females (Table 1).

Monthly frequency of females in each development stage showed the presence

Table 1. Frequency of mature male and female *Lutjanus purpureus* by size class. N= number in size class. [Frecuencia, en porcentaje, de hembras y machos maduros de *Lutjanus purpureus* por grupo de talla.]

Size class (TL;cm)	Females		Males	
	N	% mature	N	% mature
21-24	12	0	1	0
25-28	10	0	7	57
29-32	14	0	15	80
33-36	37	30	38	79
37-40	73	59	55	89
41-44	68	91	58	95
45-48	52	90	46	100
49-52	43	93	37	97
53-56	27	100	39	100
57-60	21	96	21	100
61-64	18	94	16	100
65-68	13	100	20	100
69-72	6	100	13	100
73-76	6	100	10	100
77-80	6	100	3	100
81-84	2	100	2	100
Total	408	-	381	-

of all stages throughout the year (Fig. 2). The highest frequency of spawning females occurred from September to February. This is indicative of a protracted spawning habit with peak spawning occurring from September to February. Monthly variation in mean gonosomatic index showed elevated values in January and from June to October (Fig. 3).

Age and growth

Monthly variation in the frequency of otoliths with an opaque edge showed elevated values from December to April (Fig. 4), indicating the formation of opaque rings during this time. In order to use otoliths for age determination,

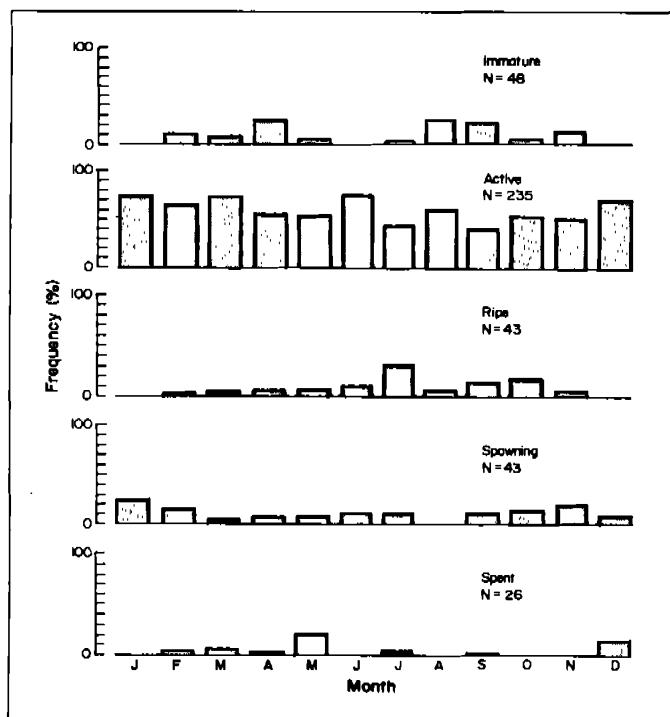


Fig. 2. Monthly frequency of female *Lutjanus purpureus* in various stages of maturity. [Frecuencia mensual de hembras de *Lutjanus purpureus* en varios estados de madurez.]

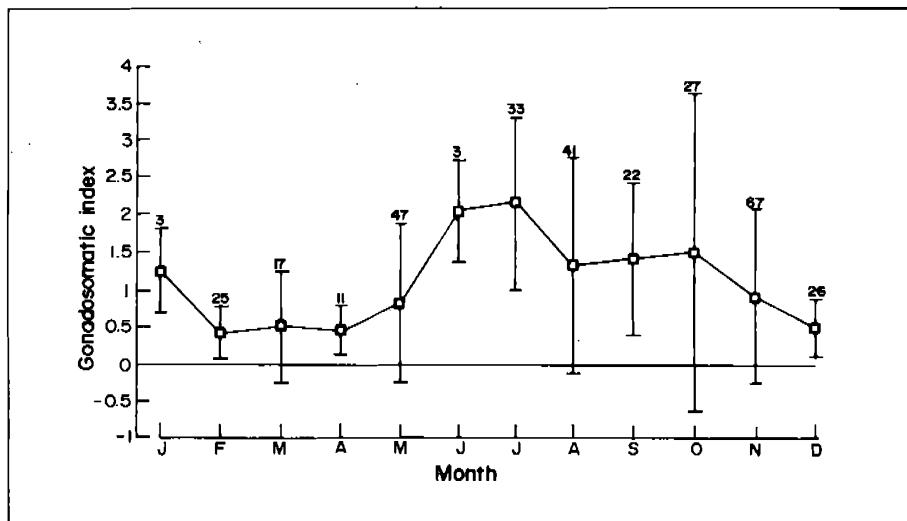


Fig. 3. Mean monthly gonosomatic Index and standard deviation of female *Lutjanus purpureus*. Sample sizes are given above data points. [Media mensual del índice gonadosomático de hembras de *Lutjanus purpureus*. Los tamaños de las muestras se indican en la parte superior de los datos.]

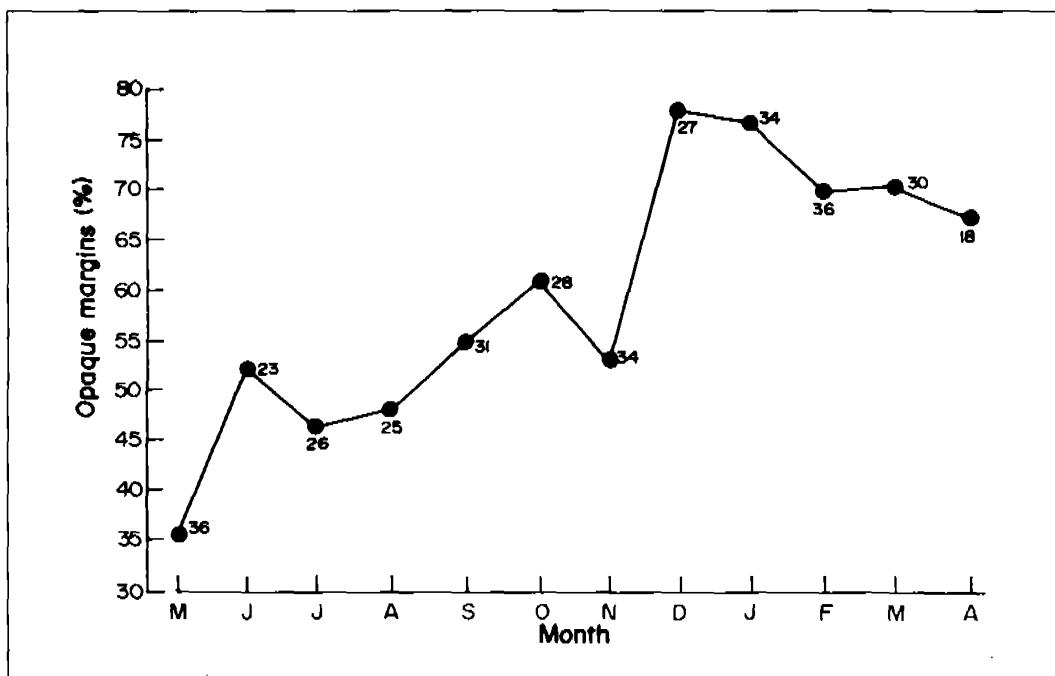


Fig. 4. Monthly frequency of occurrence of otoliths with opaque margin for *Lutjanus purpureus*. Sample sizes are given next to data points. [Frecuencia mensual de la presencia de otolitos con margen opaco para *Lutjanus purpureus*. Los tamaños de las muestras están dados por los números asociados a los puntos.]

growth of the otolith must be proportional to growth in length of the fish and number of rings must increase with body size (Van Oosten 1929). Analysis of covariance of otolith radius on total length (in mm) showed no significant difference between sexes ($p>0.05$) and data were pooled to give a single equation:

$$TL = 111.4OR - 105.2 \quad (n=330, r^2=0.93).$$

Number of rings increased with fish length, with 1-20 age groups found in snappers between the lengths of 25-84 cm.

The relationship between total length and otolith radius was used to backcalculate lengths of fish at earlier ages. Due to overlapping of rings in older individuals and resulting difficulty in making accurate measurements, ring radii were measured

only in snappers with 1-12 rings. Mean backcalculated lengths at ages 1-12 years are given in Table 2. Close agreement was found between the observed and backcalculated growth curves (Fig. 5).

The von Bertalanffy growth equation fitted to observed lengths was:

$$L_t = 85.1 (1-e^{-0.13(t+0.86)}).$$

The ϕ' value for the snapper was 2.97 which lies within the range found for Brazilian snapper (Table 3).

The relationship between body weight (W_t) and total length (TL) of the snapper was:

$$W_t = 0.0141 \cdot TL^{2.99} \quad (n=652, r^2=0.95)$$

Asymptotic weight W_∞ was 8 690 g.

Table 2. Mean backcalculated length (mm) at ages 1-12 years for *Lutjanus purpureus*. [Longitudes medias retro-calculadas a las edades 1 a 12 años para *Lutjanus purpureus*.]

Age	N	Annulus number											
		1	2	3	4	5	6	7	8	9	10	11	12
1	21	200.9	-	-	-	-	-	-	-	-	-	-	-
2	9	168.3	243.9	-	-	-	-	-	-	-	-	-	-
3	30	154.7	240.1	295.3	-	-	-	-	-	-	-	-	-
4	39	177.0	271.3	354.4	394.8	-	-	-	-	-	-	-	-
5	59	165.6	264.3	349.8	406.7	438.2	-	-	-	-	-	-	-
6	18	167.1	259.9	352.8	415.9	455.5	483.4	-	-	-	-	-	-
7	11	157.1	250.3	322.2	388.0	437.6	480.2	504.5	-	-	-	-	-
8	6	156.6	266.1	347.8	420.2	468.5	511.2	546.5	576.2	-	-	-	-
9	3	162.2	251.3	333.0	407.2	455.5	492.6	518.6	548.3	568.8	-	-	-
10	2	145.5	251.3	318.1	429.5	485.2	518.6	557.6	591.1	624.5	652.3	-	-
11	4	134.3	273.3	365.5	446.2	507.5	560.4	593.8	630.0	657.9	691.3	709.4	-
12	5	162.2	262.4	353.8	402.8	465.2	503.0	538.7	567.7	594.4	623.4	652.3	678.8
Number	207	207	186	177	147	108	49	31	20	14	10	9	5
Mean length	-	168.3	259.6	339.8	405.1	447.9	496.4	534.5	582.1	611.3	653.4	677.7	678.8
Increment	-	168.3	91.3	80.3	65.2	42.8	48.5	38.1	47.6	29.2	42.1	24.3	1.1

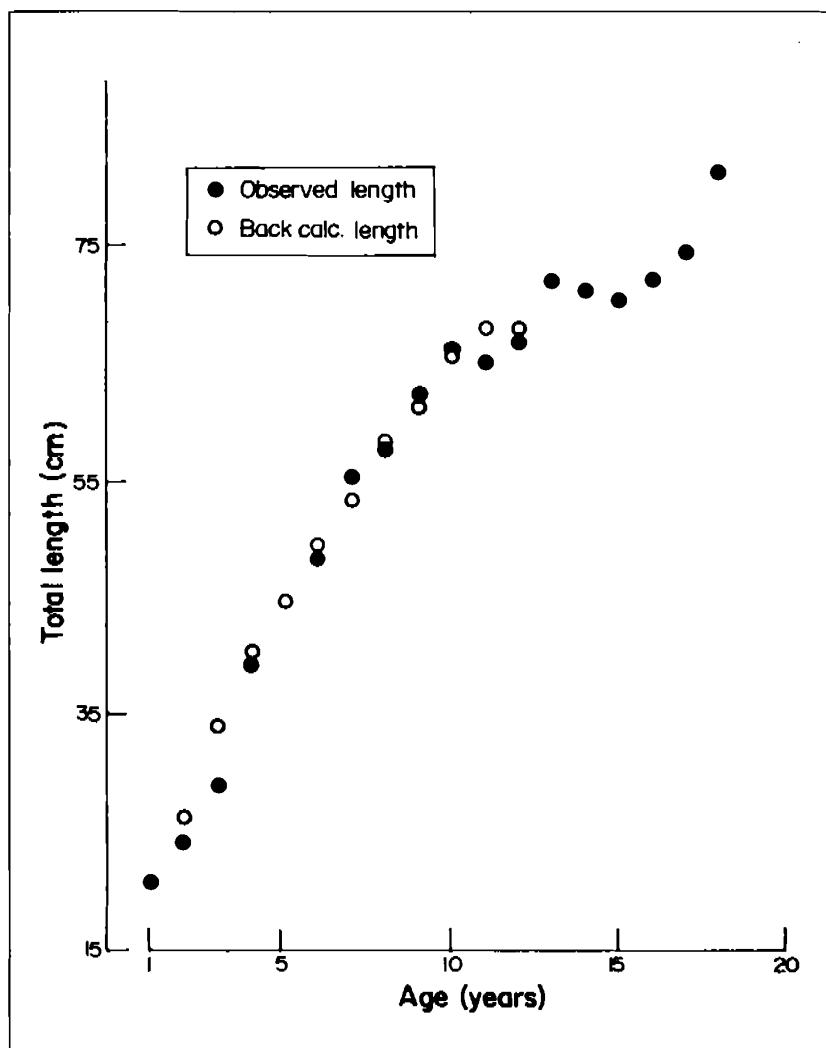


Fig. 5. Observed and backcalculated length at age for *Lutjanus purpureus*. [Longitudes observadas y retrocalculadas por edad, para *Lutjanus purpureus*.]

Table 3. von Bertalanffy growth parameters and ϕ' values for *Lutjanus purpureus*. [Parámetros de crecimiento de la ecuación de von Bertalanffy y los valores de ϕ' para *Lutjanus purpureus*.]

Method	L_{∞} (TL; cm)	K (year ⁻¹)	ϕ'^a	Location	Source
Otoliths	97.7	0.117	3.05	Brazil	Lima (1965)
Scales	98.9	0.090	2.94	Brazil	Menezes and Gesteira (1974)
Scales	92.9	0.103	2.95	Brazil	Ximenes and Fonteles-Filho (1988)
Otoliths	85.1	0.130	2.97	Trinidad and Tobago	This study

^a $\phi' = \log K + 2\log L_{\infty}$

Mortality

Natural mortality determined by Pauly's and Alagaraja's equation was 0.32 and 0.23 year⁻¹, respectively. The average of these estimates was 0.28 year⁻¹ and was used in subsequent analyses. Total mortality was 0.57 resulting in an estimate of fishing mortality of 0.29 year⁻¹.

Yield per recruit

Variations of Y/R and B/R with F for ages at first capture of 1.4, 3 and 4 years are shown in Fig. 6. Maximum yield per recruit (Y_{\max}/R) is obtained at low levels of F at all values of t_c . The current level of F (0.29) exceeds F_{\max} (0.26), indicating that the snapper is overexploited at present. A higher t_c is required to produce Y_{\max}/R at the present level of F. Increasing t_c to 3 and 4 years results in an increase in yield by 21% and 24%, respectively. $F_{0.1}$ levels are 0.15 and 0.21 for t_c of 1.4 and 3 years, respectively. Y/R at these levels of $F_{0.1}$ is not much lower than Y_{\max}/R .

B/R decreases sharply with increasing F at all values of t_c and appears to be very low even at current F_{\max} . This is shown in Fig. 6 for t_c of 1.4 years. At $F_{0.1}$, B/R is not as severely reduced (Fig. 6). Maintaining F at $F_{0.1}$ is therefore desirable since it ensures a higher B/R than F_{\max} .

Discussion

Reproduction in *L. purpureus* in Trinidad and Tobago is consistent with what has been reported for snappers in general. Grimes (1987) indicated that among snappers, males usually mature at smaller sizes than females, as was observed in this study and in a Brazilian study by Alves (1971). In the latter study, which was based on histological data from 95 specimens, the size at maturity was 40 cm FL for males and 42 cm FL for females. Gesteira and Ivo (1973), using gonosomatic indices, obtained a size at maturity of 42 cm TL for female snapper in Brazil. The size at maturity observed in this study was 27 and 39 cm TL for males and

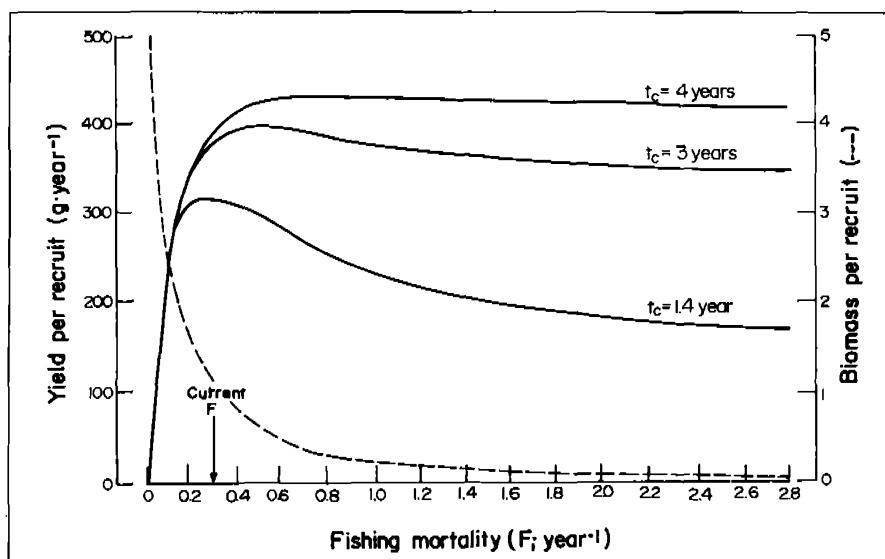


Fig. 6. Variations in yield per recruit (Y/R) and biomass per recruit (B/R) with fishing mortality (F) and age at first capture (t_c) for *Lutjanus purpureus*. [Variaciones en el rendimiento por recluta (Y/R) y biomasa por recluta (B/R) con la mortalidad por pesca (F) y edad de primera captura (t_c) para *Lutjanus purpureus*.]

and females respectively, indicating earlier maturity than in Brazil.

In this study *L. purpureus* was found to spawn year-round, with a peak from September to February. This is consistent with the general year-round pattern of spawning for lutjanids in the Caribbean (Munro et al. 1973; Grimes 1987). In Brazil, spawning is restricted to two periods from January to May and September to December (De Moraes and Dos Santos 1969; Fonteles-Filho 1970, 1972; Gesteira and Ivo 1973; Ivo 1973a).

In reviewing the spawning seasonality of lutjanids, Grimes (1987) found that spawning in continental populations is more restricted than in their insular counterparts in which spawning is year-round. In the present study the snapper demonstrates a spawning pattern that is a combination of the two, showing year-round spawning with a six-month spawning peak beginning in the wet season. Grimes (1987) also reported that spawning in continental lutjanid populations along the east coast of North America, Venezuela and Campeche Bank coincides with high summer rainfall and perhaps local production cycles.

The formation of annual marks in hard parts has already been reported for this species in Brazil (Lima 1965; Ximenes and Fonteles-Filho 1988) and for other species of snappers in the region (Claro and Reshetnikov 1981; Manickchand-Dass 1986; Palazon and Gonzalez 1986). The time of formation of opaque rings in otoliths of snapper in Trinidad and Tobago is slightly out of phase with peak spawning, indicating that the former may be related to other factors such as climatic or environmental factors. Ximenes and Fonteles-Filho (1988) found that ring formation in scales of this species in Brazil is influenced by seasonal changes in food availability. Further validation was obtained by the close agreement of observed and backcalculated lengths at age, as well as similarity of ϕ' value with those calculated for this species in Brazil.

Previous estimates of L_{∞} and K for snapper in Trinidad and Tobago were 90 cm

and 0.13 year⁻¹, respectively, and were based on a preliminary study using only 90 otoliths and without validation (Manickchand-Heileman and Phillip 1992). The growth pattern of this species is similar to that reported for snappers in general (Manooch 1987), in that it is long-lived (maximum observed age 20 years), has a high L_{∞} (85.1 cm) and low K (0.13 year⁻¹). This is also similar to the growth pattern of this species in Brazil where Menezes and Gesteira (1974) observed 2-15 age groups and reported L_{∞} of 99 cm and K of 0.09 year⁻¹, and Ximenes and Fonteles-Filho (1988) found 23 age groups and reported L_{∞} of 93 cm and K of 0.103 year⁻¹.

Estimates of L_{∞} and K for the closely related northern red snapper *Lutjanus campechanus* are slightly higher than those obtained in this study. Nelson and Manooch (1982) found L_{∞} of 94.1 cm and K of 0.17 year⁻¹ for northern red snapper in the Gulf of Mexico and L_{∞} of 97.5 cm and K of 0.16 year⁻¹ for this species in the southeastern United States. Nelson (1988) estimated L_{∞} to be 92.5 cm and K to be 0.14 year⁻¹ in the Gulf of Mexico.

At the present age at first capture and fishing mortality, the stock is being overfished. Increasing t_c results in an increase in yield per recruit and is also desirable since the current t_c is lower than the age at first maturity for females. It is recommended that t_c be increased to at least 3 years (33.6 cm TL) in order to protect immature fish. Increasing t_c can be obtained by increasing the mesh size in traps.

Fishing effort should be kept low since long-lived fish with low K may be overexploited by a large intensive fishery (Mason and Manooch 1985). As results of yield per recruit analyses have shown, the maximum yield per recruit of the snapper is obtained at low levels of F . Increasing F results in a rapid decline in biomass per recruit which may reduce recruitment to the stock. It may be desirable to maintain F at $F_{0.1}$ since B/R is not as severely reduced and Y/R is not significantly lower than Y_{max}/R .

Acknowledgements

The authors thank the Institute of Marine Affairs, the Ministry of Agriculture, Land and Marine Resources, FAO and UNDP for support in carrying out this project; Maxwell Sturm for reviewing the manuscript; and the following fishers in Tobago for facilitating field sampling: Lincoln, Garnet, Raoul, Robert (now deceased) and Clarence Yeates.

References

- Alagaraja, K. 1984. Simple methods for estimation of parameters for assessing exploited fish stocks. Indian J. Fish. 31:177-208.
- Alves, M.I.M. 1971. Sobre a maturação sexual do pargo, *Lutjanus purpureus* Poey, do nordeste brasileiro. Arq. Cienc. Mar 11:153-158.
- Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. U.K. Min. Agric. Fish. Invest. Ser. (2) 19, 533 p.
- Claro, R. and Reshetnikov, Y.S. 1981. Ecología y ciclo de vida de la biajaiba, *Lutjanus synagris* (Linnaeus), en la plataforma Cubana. Ser. Oceanol. Acad. Cienc. Cuba 174:1-28.
- De Moraes, N.U.A. 1970. Sobre a desova e a fecundidade do pargo, *Lutjanus purpureus* Poey no nordeste Brasileiro. Bol. Estud. Pesca 10(1):7-20.
- De Moraes, N.U.A. and E.P. Dos Santos. 1969. Sobre a curva de maturação do pargo, *Lutjanus purpureus* Poey. Bol. Estud. Pesca 9(3):50-57.
- Fischer, W., Editor. 1978. FAO species identification sheets for fishery purposes. Western Central Atlantic (fishing area 31). Food and Agriculture Organization, Rome.
- Fonteles-Filho, A.A. 1970. Estudo preliminar sobre a pesca do pargo, *Lutjanus purpureus* Poey, no nordeste brasileiro. Arq. Cienc. Mar 9(1):83-88.
- Fonteles-Filho, A.A. 1972. Estudo sobre a biología da pescado pargo, *Lutjanus purpureus* Poey, no nordeste brasileiro - dados de 1970 e 1971. Arq. Cienc. Mar 12(1):21-26.
- Fonteles-Filho, A.A. and S. Kurisaka. 1970. Some oceanographic conditions related to the Caribbean red snapper fishery, off the northeast Brazil. Arq. Cienc. Mar 10(2):177-180.
- Gade, H. 1989. The environmental-ecological regimes, p. 8-41. In Report on surveys of the fish resources in the shelf areas between Suriname and Columbia with the R/V Dr. Fridtjof Nansen. Institute of Marine Research, Bergen.
- Gayanilo, F.C., Jr., M. Soriano and D. Pauly. 1989. A draft guide to the Compleat ELEFAN. ICLARM Software 2, 70 p.
- Gesteira, T.C.V. and C.T.C. Ivo. 1973. Estudo da reprodução e fecundidade do pargo, *Lutjanus purpureus* Poey, do norte e nordeste do Brasil. Arq. Cienc. Mar 13(2):109-112.
- Gonzalez, L.W. and J. Celaya. 1986. Diagnóstico socio-económico de la pesquería de media altura pargo-mero del estado Nueva Esparta. Centro de Investigaciones Científicas, Univ. Oriente, Venezuela, Contrib. Científicas 8.
- Grimes, C.B. 1987. Reproductive biology of the Lutjanidae: a review, p. 239-294. In J.J. Polovina and S. Ralston (eds.). Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Ivo, C.T.C. 1973a. Estudo sobre a biología da pesca do pargo, *Lutjanus purpureus* Poey, no nordeste Brasileiro-dados de 1972. Arq. Cienc. Mar 13(1): 39-43.
- Ivo, C.T.C. 1973b. Estudo sobre a biología da pesca do pargo, *Lutjanus purpureus* Poey, no nordeste Brasileiro-dados de 1973. Arq. Cienc. Mar 13(2): 113-116.
- Ivo, C.T.C. 1975. Estudo sobre a biología da pesca do pargo, *Lutjanus purpureus* Poey, no nordeste Brasileiro-dados de 1974. Arq. Cienc. Mar 15(2): 119-123.
- Ivo, C.T.C. 1976. Estudo sobre a biología da pesca do pargo, *Lutjanus purpureus* Poey, no nordeste Brasileiro-dados de 1975. Arq. Cienc. Mar 16(2): 87-91.
- Ivo, C.T.C. and de Sousa, M.J.B. 1988. Sinopse de informações sobre o pargo, *Lutjanus purpureus* Poey (Pisces: Lutjanidae), no norte e nordeste do Brasil. Arq. Cienc. Mar 27:57-67.
- Ivo, C.T.C. and T.C.V. Gesteira. 1974. Estimacão preliminar das médias de mortalidade do pargo, *Lutjanus purpureus* Poey, no norte e nordeste Brasileiros. Arq. Cienc. Mar 14(2):123-127.

- Ivo, C.T.C. and A.J. Hanson. 1982. Aspectos da biología e dinâmica populacional do pargo, *Lutjanus purpureus* Poey, no Norte e Nordeste do Brasil. Arq. Cienc. Mar 22(1/2): 1-41.
- Kenny, J.S. and P.R. Bacon. 1981. Aquatic resources, p. 112-144. In S.G.C. Cooper and P.R. Bacon (eds). The natural resources of Trinidad and Tobago. Edward Arnold, London.
- Lima, F.R. 1965. Crescimento do "pargo" (*Lutjanus aya*, Bloch, 1795): aspectos quantitativos. Bol. Estud. Pesca 5: 33-42.
- Manickchand-Dass, S. 1986. Reproduction, age and growth of the lane snapper, *Lutjanus synagris* (Linnaeus) in Trinidad, West Indies. Bull. Mar. Sci. 40(1):22-28.
- Manickchand-Heileman, S. and D.A.T. Phillip. 1992. Preliminary stock assessment for the fishpot fishery of Tobago. Technical Report of the Project for the Establishment of Data Collection Systems and Assessment of the Fisheries Resources. FAO/UNDP: TRI/91/001/TR12.
- Manickchand-Heileman, S. and D.A.T. Phillip. 1996. Description and status of the snapper-grouper fishery of Trinidad and Tobago. Proc. Gulf and Carib. Fish. Inst. 45 (Section A): 189-204.
- Manooch, C.S. III. 1987. Age and growth of snappers and groupers, p. 329-373. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Mason, D.L. and C.S. Manooch III. 1985. Age and growth of mutton snapper along the east coast of Florida. Fish. Res. 3: 93-104.
- Menezes, M.F. de and T.C.V. Gesteira. 1974. Age and growth of the Caribbean red snapper *Lutjanus purpureus* Poey, from north and northeastern Brazil. Arq. Cienc. Mar 14(2):81-85.
- Munro, J.L., V.C. Gaut, R. Thompson and P.H. Reeson. 1973. The spawning seasons of Caribbean reef fishes. J. Fish Biol. 5: 69-84.
- Nelson, R.S. 1988. A study of the life history, ecology, and population dynamics of four sympatric reef predators (*Rhomboplites aurorubens*, *Lutjanus campechanus*, Lutjanidae; *Haemulon melanurum*, Haemulidae; and *Pagrus pagrus*, Sparidae) on the east and west Flower Garden Banks, Northwestern Gulf of Mexico. North Carolina State University, Raleigh, North Carolina. 197 p. Ph.D. thesis.
- Nelson, R.S. and C.S. Manooch III. 1982. Growth and mortality of red snappers, *Lutjanus campechanus*, in the West Central Atlantic Ocean and northern Gulf of Mexico. Trans. Am. Fish. Soc. 111: 465-475.
- Palazon, J.L. and L.W. Gonzalez. 1986. Edad y crecimiento del pargo cebal, *Lutjanus analis* (Cuvier, 1828) (Teleostei: Lutjanidae) en la isla de Margarita y alrededores, Venezuela. Inv. Pesq. 50(2): 151-165.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. CIEM 39(2): 175-192.
- Pauly, D. 1986. On improving operation and use of the ELEFAN programs. Part II. Improving the estimation of L_{∞} . Fishbyte 4(1): 18-20.
- Pauly, D. and J.L. Munro. 1984. Once more on the comparison of growth in fish and invertebrates. Fishbyte 2(1): 21.
- Prager, M.H., S.B. Saila and C.W. Recksiek. 1987. FISHPARM: a microcomputer program for parameter estimation of nonlinear models in Fishery Science. Ocean. Tech. Rep., 18 p. Old Dominion University, Norfolk, Virginia.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fish. Res. Board Can. Bull. 191, 382 p.
- Sparre, P. 1987. Computer programs for fish stock assessment. Length-based Fish Stock Assessment for Apple II Computers. FAO Fish. Tech. Pap. (101) Suppl. 2, 218 p.
- Van Oosten, J. 1929. Life history of the lake herring (*Leucichthys artedii* Le Sueur) of Lake Huron as revealed by its scales with a critique of the scale method. U.S. Dep. Comm., Bull. U.S. Bur. Fish. 44: 265-428.
- Wetherall, J.A. 1986. A new method for estimating growth and mortality parameters from length-frequency data. Fishbyte 4(1): 12-15.
- Ximenes, M.O.C. and A.A. Fontelles-Filho. 1988. Estudo da idade e crescimento do pargo, *Lutjanus purpureus* Poey (Pisces: Lutjanidae), no norte e nordeste do Brasil. Arq. Cienc. Mar 27: 69-81.

ENTERED IN NAGA

APR 14 1996

Validation of Ageing Technique for Nassau Grouper (*Epinephelus striatus*) in the Cayman Islands

P.G. BUSH*

G.C. EBANKS*

E.D. LANE†

*Department of the Environment, P.O. Box 486 GT
Grand Cayman, Cayman Islands, BWI

†Aquaculture and Fisheries, Malaspina College
900 Fifth Street, Nanaimo
B.C. V9R 5S5 Canada

BUSH, P.G., G.C. EBANKS and E.D. LANE. 1996. Validation of the ageing technique for the Nassau grouper (*Epinephelus striatus*) in the Cayman Islands [Validación de la técnica para determinación de edad de la cherna criolla (*E. striatus*) de Islas Caimán], p. 150-158. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

During its ongoing study of the local Nassau grouper spawning population, the Cayman Islands Natural Resources Unit analyzed thin sections of sagittal otoliths to determine ages of fish in the spawning population. To validate this method of ageing, fish injected with oxytetracycline-HCL (OTC) were held in submerged cages for approximately 21 months after which the fish were sacrificed and their otoliths examined. Fish were injected either intramuscularly or intraperitoneally at 100 mg OTC/kg body weight. Post-capture mortality was 36% and seemed related to various levels of trauma during capture and individual resilience. A total of 14 fish (size range 34-76 cm TL) were held captive and fed on squid and small fish. Sagittal otoliths were taken from six fish and examined. Examination of otolith sections under ultraviolet light showed a distinct fluorescent band marking the time of injection with OTC. Further analysis of banding revealed that the rings were indeed annuli. Time of annuli formation appears to be after spawning during the months of February through July.

Resumen

Durante el desarrollo del estudio sobre la población local de desovadores de la cherna criolla, la Unidad de Recursos Naturales de las Islas Caimán analizaron cortes del otolito (sagita) para determinar las edades de los peces en la población de desovadores. Para validar el método para determinación de edad, los peces fueron inyectados con oxitetraciclina-HCL (OTC) y sumergidos en jaulas por aproximadamente 21 meses, después de los cuales los peces fueron sacrificados y sus otolitos examinados. Inyecciones intramusculares e intraperitoneales fueron colocadas a cada pez en una proporción de 100 mg de OTC por cada kg de peso corporal. La mortalidad post-captura fué de 36% y se observó que estuvo relacionada con diferentes niveles de daño y resistencia individual durante la captura. Un total de 14 peces (en un intervalo de talla de 34 cm a 76 cm LT) fueron mantenidos en cautividad y alimentados con calamares y pequeños peces. Las sagitas fueron tomadas de seis peces (los ocho restantes escaparon durante una tormenta) para su análisis. El examen de las secciones de los otolitos bajo luz ultravioleta mostró una banda fluorescente distinta formada al momento de la inyección con OTC. Posterior análisis de las bandas revelaron que los anillos fueron anuli reales. El tiempo de formación de los anuli parece ocurrir después del desove, durante los meses de febrero a julio.

Introduction

The Nassau grouper (*Epinephelus striatus*) aggregates en masse to spawn each winter at various sites around the Cayman Islands (see Tucker and Woodward, this vol.). There are five main aggregations which are regularly fished by the local people (Tucker et al. 1993) and these form the basis of a seasonal subsistence level fishery. In 1987, the Cayman Islands Natural Resources Laboratory initiated a study to investigate the population structure of the spawning aggregations. Data such as catch/effort, total catch, size, sex and age of fish were taken. The need to accurately determine the age composition of the aggregations and the validation of the ageing technique employed were critical to this study and it is these two topics on which this paper will focus.

Manooch (1987) states that stable biological and environmental conditions, especially temperature, contribute to making age and growth determination in tropical fish difficult. Pannella (1974) suggested that age determination of tropical fish was difficult due to the lack of clear annual rings. However, later research of bony structures revealed an abundance of markings, though interpreting their meaning is challenging (Pannella 1980). The analysis of regularly formed marks in bony structures such as otoliths is nevertheless the preferred method of age determination of tropical fish with the only disadvantage to this technique being that great care and extensive study are required to establish a true indication of elapsed time between consecutive marks (Manooch 1987). Scientists previously unable to explain the occurrence of periodic markings, based on seasonally changing water temperatures, have now turned their efforts to studying less obvious genetic, physiological and environmental phenomena that may influence patterns of growth in tropical species (Manooch 1987).

For this study, age determination was done by examination of growth ring structure in sagittal otoliths, these typically being the preferred of the three pairs of otoliths used for age analysis. As Beamish and Chilton (1982) observe, failure by fisheries biologists to accurately validate age determination often leads to wasting and mismanagement of fisheries resources. Validation of the ageing technique in this study was carried out by injecting a number of fish with the marker antibiotic oxytetracycline (OTC), and holding them in captivity after which they were sacrificed and their otoliths taken for analysis (see Collin et al., this vol.).

Materials and Methods

Sagittal otoliths were taken from wild caught fish by medially splitting the cranium to expose the inner ear cavities. They were then individually stored in a 1:1 solution of water and glycerol with a small amount of thymol added (Beamish and Chilton 1982), for later analysis of growth ring formation. The typical break and burn technique used for many temperate fish (Beamish and Chilton 1982) was found to be unsuitable for *E. striatus* otoliths which are characteristically thick, dense, highly crystalline and irregularly shaped. Thus, these otoliths were embedded in epoxy and serially sectioned with a high speed microtome to 0.5-mm thicknesses. The sections were mounted and analyzed independently by three persons using transmitted light microscopy. Each reader aged the fish twice.

For the validation of the technique, three cages were constructed on land and deployed in a 9-m deep trench within the Marine Park on the lee side of Grand Cayman. One large oblong cage (24.57 m³), and two smaller, circular cages (7.84 m³ each) were constructed of 2.54-cm diameter stainless steel tubing for framing, and 5.1-cm

and 2.54-cm Vexar polypropylene meshing for enclosure. The cages were tethered down with stainless steel cable attached to pins embedded in the substrate to prevent movement by wave action. In each cage, artificial shelter was provided by lashing together a number of 45.7-cm and 20.3-cm diameter clay sewer pipes.

A total of 22 fish ranging in length from 36.5 cm to 76 cm were caught using large, baited, antillean fish traps. Soak time varied from 12 to 72 hours and trapping depths varied from 9 to 24 m. Each Nassau grouper was anesthetized in a 5-ppm metomidate-HCL (Marinil) seawater solution, after which they were weighed, measured, tagged with numbered plastic disc tags (secured by pins inserted through the dorsal pterygiophores) and injected with oxytetracycline HCL antibiotic (Terra-Vet 100 mg/ml) at dosages of 100 mg OTC/kg bodyweight (Sadovy, pers. comm.). Individuals were either injected intramuscularly or intraperitoneally, using 25 ga and 20 ga hypodermic needles for small and large fish, respectively. The fish were then allowed to recover from the anesthetic before being transferred to their allocated cages. The captive fish were fed on a diet predominantly of squid and occasionally small reef fish. Dates of capture extended from 9 May to 8 August 1990 and the fish were sacrificed on 10 February 1992.

The sagittal otoliths from these fish were extracted and prepared (as described previously) and then microscopically analyzed using transmitted light in combination with an ultraviolet light source.

Results and Discussion

Mortality

Total post-processing mortality was 36% (8 fish died) and varied individually within 12-120 hours. Mortality was attributed to

trauma during capture and processing. Physical damage during trapping varied greatly and was related to length of residence time in traps. Barotrauma was also an added complication in fish caught at depths of 18 m or more. Fish with distended air bladders were vented of gas by insertion of a 20 ga hypodermic needle into the air bladder.

Although employed to minimize physical trauma to fish during processing, the anesthetic itself may also possibly cause some degree of trauma. The recommended dosage for the product used resulted in an average "roll-over" (complete anesthesia) time of 1 minute with "righting" (recovery) time of 2-5 minutes. There was no appreciable difference in these times between larger and smaller fish. Upon being introduced to the anesthetic bath, many of the fish exhibited drastic color loss (an estimated 90% in some cases). Some color loss was still evident even after apparent recovery. Given the relatively rapid knockout times observed, it may be possible that the recommended dosage of this muscle relaxant may be too high, possibly resulting in some level of physiological shock especially if combined with other trauma. At the time, Marinil was being offered as a new experimental drug for the sedation of fish. Another source of trauma was the actual tagging of fish. This was especially so in large fish as it was often difficult to insert the pin through the dorsal pterygiophores even with the aid of a pliers. This process often triggered a violent muscular reaction in fish although they were anesthetized.

Injection of high concentrations of OTC is known to cause tissue necrosis (Beamish et al. 1983). A major factor in the mortality of three larger fish was that the injection of proportionally high volumes of 100 mg/ml OTC solution into the dorsal musculature produced subsequent tissue necrosis. Dissection of tissue surrounding the injection sites of these fish revealed conspicuously hard, yellow, dry and flaky tissue. This was

subsequently avoided by injecting the prescribed dosage for large individuals into a number of sites rather than a single one.

An initial dosage of 50 mg OTC/kg body weight was increased to 100 mg/kg body weight after preliminary microscopic inspection of otoliths from these fish showed weak fluorescence under ultraviolet light. Otoliths from dead fish which had been injected with the higher dosage showed stronger fluorescence.

The Nassau grouper seems to exhibit a high individual variability of resilience to trauma. Some fish showing high levels of physical and behavioral stress from trapping and processing survived, while others showing considerably lower levels of stress did not. Indeed one fish survived after being badly damaged in the trap, having its stomach everted in order to surgically remove a hook which had pierced the posterior end of the stomach wall, and having the same pushed back in with a broomstick.

Adaptation to captivity

The 14 surviving fish constituted the stable captive population within the cages for the duration of the experiment. Total lengths of these fish ranged within 36.5-57.5 cm (Table 1). The fish adapted well to captivity, utilizing the pipes for shelter, feeding on provided squid and small reef fish within

the cages, and conducting spawning activity during the weeks of the two January full moons following capture.

The disc tags did not prove to be compatible with the cryptic and demersal life style of the captive fish. The retaining pins tended to bend and break with time after being caught or rubbed against the meshing or pipes. As each fish in a cage lost its tag, it was caught and a designated dorsal spine clipped half way down in order to ensure later identification. On 8-9 February 1992, a heavy storm destroyed the large cage and one small one. The eight fish in these cages (4 very large and 4 smaller individuals) escaped and were not recovered despite trapping attempts in the area during the following weeks.

The six remaining fish of intermediate sizes (Table 1) were sacrificed and their otoliths taken on 10 February 1992. The fish had grown considerably and even though there was a feeding hierarchy dominated by the largest fish, percentage increase in length was greatest for the smaller fish.

Analysis of otoliths

Appearance of Sections

We have examined hundreds of sectioned *E. striatus* otoliths taken from fish ranging in length from 34 to 84 cm, and there was

Table 1. Project data for captive fish (IM=intramuscular; IP=intraperitoneal injections). [Datos del proyecto de peces cautivos (Inyecciones: IM=Intramuscular, IP=Intrapericoneal).]

Date injected (1990)	IM/IP	Length at injection (cm)	Final length (cm)	Increase (%)	Sex	Age (years)
9 May	IM	57.5	70.0	21.74	Male	6+
8 August	IP	51.5	61.0	18.45	Female	6+
8 August	IP	42.5	59.0	38.82	Female	5+
3 August	IP	42.5	56.5	32.94	Female	5+
7 July	IM	41.0	56.0	36.58	Female	5+
5 May	IM	36.5	50.25	37.67	Female	4+

95% agreement between readings and readers, indicating a high level of precision. Most sections revealed a distinct banding pattern of alternating light and dark bands lying perpendicular to the axis of the otolith's aragonitic crystalline structure. Usually, otoliths which were not readable were those of smaller fish. In these cases cracks and fractures caused optical refractive anomalies in the banding pattern too frequently to allow a reliable reading. The cracks were probably caused by vibratory shattering during sectioning, as smaller otoliths are generally thinner and more brittle than those of larger fish.

In this paper we define a growth zone as one pair of constituent light (hyaline) and dark (opaque) bands representing periods of slow and rapid somatic growth, respectively (Pannella 1974; Beamish and Chilton 1982). For convenience, we define the assumed annuli to be opaque zones. These zones have a higher optical density (due to an organic-rich matrix) and are more visually and structurally distinct than the amorphous hyaline zones.

The spatial distribution and progressive width of growth zones observed in *E. striatus* otoliths are consistent with those described for other tropical fish. The position of the first annulus can be difficult to locate as the central area, or nucleus, often appears similar to the organic matrix of individual annuli. However, thinner sections, and therefore increased transparency, allowed observation of an obvious band of crowded rings within this area. Many otoliths sectioned at the usual 0.5-mm thickness showed a more distinct band in this same location. We therefore conclude that this is the first annulus. The organic appearance of the nucleus area may be attributed to the likelihood that young fish experience continuous and rapid growth in the first year. The observed distance between the center of the nucleus and the first annulus is also the widest growth zone. In all otoliths there are many opaque striations distributed

between the first four annuli that are generally lacking between later ones. This also suggests continuous and rapid growth prior to sexual maturity.

Band thickness and spacing of the first three or four growth zones are much greater than in subsequent zones, which become more evenly spaced and progressively narrower towards the edge of the otolith (Table 2). This indicates fast growth which tapers off after the early years, and reflects what is known of the growth of tropical fish (Scholander 1953; Edwards et al. 1971; Pannella 1974). As tropical fish tend to grow faster than temperate ones until they reach sexual maturity (Pannella 1974), the pattern seen in *E. striatus* otoliths may suggest that sexual maturity occurs after the third or fourth year (J.W. Tucker, pers. comm.). However, more detailed study of otoliths from fish of known age is necessary to verify this.

The vast majority of otoliths analyzed in this study were taken in the spawning season in January. Otoliths of the captive fish were taken in early February. Presumed ages of fish from the spawning aggregation before validation ranged from 4+ years to 26+ years. Ages of captive fish ranged from 4+ years to 6+ years (Table 1).

Examination of the edges of otoliths taken from the January spawning individuals revealed an almost complete hyaline band

Table 2. Distances between distal edges of annuli of 6+ year old fish. [Distancias entre bordes distales de los anillos de peces de edad 6+ años.]

Annuli	Interannuli distance (μm)
1 & 2	34.5
2 & 3	32.2
3 & 4	18.4
4 & 5	11.5
5 & 6	11.5
6 & Edge	9.2

following the last visible annulus. Similar examination in otoliths from the captive fish showed what appears to be a complete hyaline band followed by visible striations reminiscent of those found in material laid down at the beginning of annulus formation. It is important to remember these observations of otolith formation in both wild and captive fish when discussing the validation itself.

Position of the OTC Marker

Analyses of sectioned otoliths from the captive fish showed a distinct fluorescent band marking the exact time of injection with OTC (Fig. 1 and Table 1). OTC marks of the two fish injected in early May lay nearly half way in from the distal edge of an opaque band (Fig. 2). This indicates that approximately half of the annulus was laid down during the months immediately prior to injection. Otoliths of fish injected in the subsequent months of July and August, respectively, displayed marks slightly within, and a short distance outwards from, the distal edge of the opaque band.

In each otolith, following the OTC mark, there occurred one complete growth zone

(hyaline/opaque), then a second full hyaline band, and finally the first striations of opaque material at the otolith's periphery. This opaque material would represent the beginning of the second annulus after the time of injection. The fact that the second annulus is just beginning to form at the time of harvest in early February indicates that it is not laid down during the period prior to spawning or during spawning itself. Thus the annulus must be laid down after spawning, during the months of February through July.

Pre- and post-injection growth zones (in the largest captive fish) were approximately equal in width. When the above is considered in combination with the knowledge that almost two years (21 months 10 days, and 18 months 10 days) had elapsed between injection and harvesting, it is obvious that almost two complete growth zones were formed within this period of time. This signifies the formation of one growth zone per year. The growth in otoliths of wild fish mentioned earlier further supports this. As wild fish were taken during spawning (no active growth), no annulus formation would have been occurring. This growth of hyaline material would therefore represent a period of approximately six months.

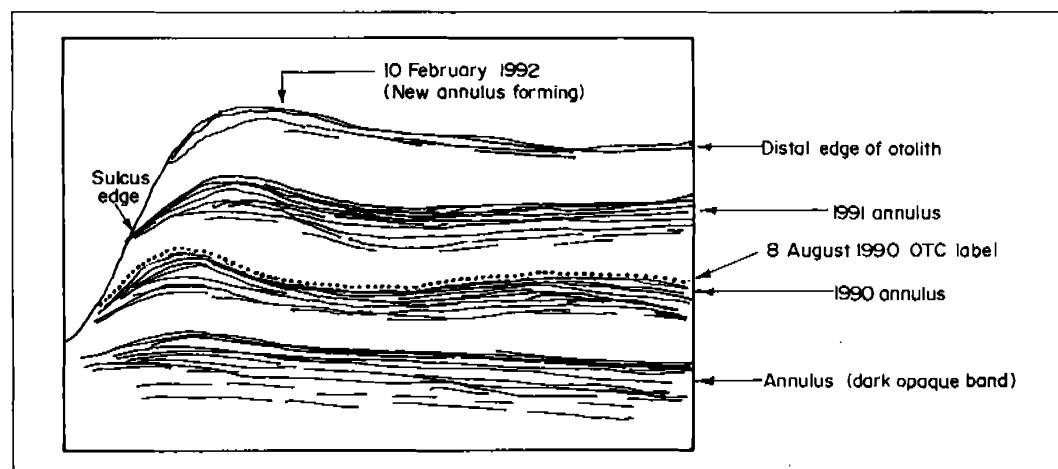


Fig. 1. Detail of otolith section showing oxytetracycline-HCl (OTC) label (drawing adapted from actual photo). [Detalle de la sección de un otolito mostrando la marca dejada por la OTC (dibujo tomado de una fotografía actual).]

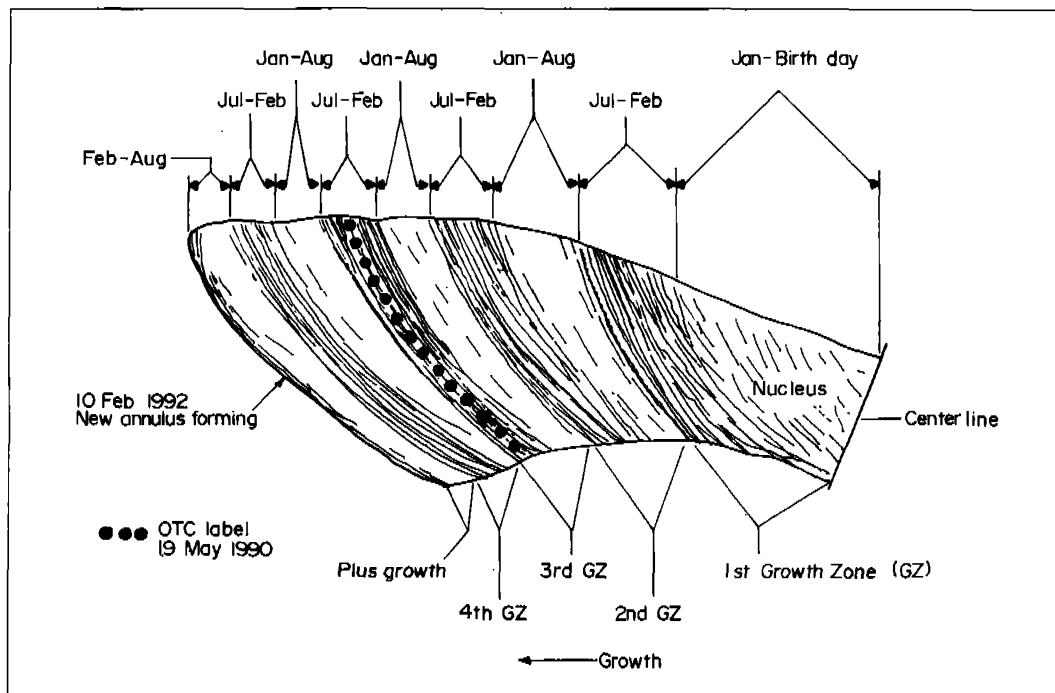


Fig. 2 Drawing of conventionalized otolith section showing sequence of growth. [Esquema de una sección convencional del otolito mostrando la secuencia del crecimiento.]

OTC labels applied in August are logically only a short distance from the previously established annulus. One would expect this as the hyaline band representing reduced somatic growth spans a period of six months from August to January.

The measured bands of the clearest sections from the 6+ year old fish show hyaline and opaque bands to be almost equal in width (average width of hyaline = 6.9 μm ; average width of opaque = 4.8 μm) - a difference of only 2.1 μm . When compared to the amount of time allocated for each type of band to be formed (6 months each) this difference is negligible.

Spacing and incremental widths in the other otoliths from fish of similar age show a similar pattern. In younger fish the comparative widths of hyaline and opaque bands are more equal, while in apparently older fish, they are more disproportionate.

As two almost complete growth zones were laid down after OTC labeling, this would mean that the smallest fish, aged at 4+ years, would have actually been 2+ years of age when injected. This is because each hyaline/opaque growth zone is completed during August through July (Fig. 2). Similarly, sacrificed fish aged at 5+ years and 6+ years would have, respectively, been 3+ years and 4+ years old at injection.

Conclusions

The number of hyaline and opaque bands beyond the OTC label in the otoliths of captive *E. striatus* was consistent with the amount of time spent in captivity. We therefore conclude that the opaque (dark) organic bands which represent peak periods of active (somatic) growth, are indeed annuli, and

that these depositions are laid down during the months of February through July. Though time of annulus formation is not related to spawning (obviously not for sexually immature fish) it does appear as if it is a regularly scheduled occurrence with unknown causal factors (but possibly related to somatic growth). No obvious spawning checks were observed in any otoliths of fish expected to be sexually mature. Incidentally, timing of injection was somewhat fortuitous in that it made the process of extrapolatory deduction simple with respect to the time and frequency of growth ring formation.

We can now say with considerable confidence that the ageing technique used here for the Nassau grouper study is valid and accurate for fish in the 3-7 year age classes. Examination of otoliths from the larger (and presumably older) fish which escaped would have revealed any difference in annual growth zone frequency past the age of 7. However this was not possible for obvious reasons. We can say with some degree of certainty that growth zone frequency does not change in the older fish as we see no real change in otolith banding and growth pattern after age 7+.

As minimal growth rate variation is expected of sexually mature fish (given the seasonality of the tropics), the only expected difference in the growth zones of otoliths in older fish would be a decreasing width of their constituent bands. This is consistent with the fact that as fish age, somatic growth decreases asymptotically - a phenomenon which we expect to be correspondingly reflected in deposition of material in the otoliths. Both decreasing widths of serial growth zones, as well as proportionally narrower annuli in the otoliths of older Nassau grouper, are obvious.

The above reasonably suggests that there is little reason for, or probability of, change in the annual life history of older *E. striatus*. Obviously, proof of this would lie in the actual validation of these age groups.

Acknowledgements

We thank Mr. Gene Parsons for his help and advice in preparing this paper, as well as Mr. S. Slaybaugh, Mr. M. Grundy, Mr. I. Young, and Mr. M. Guderian for their assistance at various points in the project.

References

- Beamish, R.J. and D.E. Chilton. 1982. Age determination methods for fishes studied by the Ground Fish Program at the Pacific Biological Station. Can. Spec. Publ. of Fish. & Aquat. Sci. 60, 107 p. Department of Fisheries and Oceans, Ottawa, Canada.
- Beamish, R.J., G.A. McFarlane and D.E. Chilton. 1983. Use of oxytetracycline and other methods to validate a method of age determination for sablefish, p. 95-118. In Proceedings of the International Sablefish Symposium. Alaska Sea Grant Program, Alaska University, Alaska.
- Edwards, R.R.C., J.H.S. Baxter, V.K. Gopalan, C.V. Mathews and D.M. Finlayson. 1971. Feeding, metabolism, and growth of tropical flatfish. J. Exp. Mar. Biol. Ecol. 6:279-300.
- Manooch, C.S. 1987. Age and growth of snapper and groupers, p. 329-373. In J.J. Polovina and S. Ralston (eds). Tropical snappers and groupers: biology and management. Westview Press, Boulder.
- Pannella, G. 1974. Otolith growth patterns: an aid in age determination in temperate and tropical fish, p. 28-39. In T.B. Bagena (ed.) Proceedings of an International Symposium on the Ageing of Fish. Unwin Brothers, Surrey, England.
- Pannella, G. 1980. Growth patterns in fish sagittae, p. 519-560. In D.C. Rhoads and R.A. Lutz (eds). Skeletal growth of aquatic organisms: biological records of environmental change. Plenum Press, New York, USA.
- Scholander, P.F. 1953. Climatic adaptation in arctic and tropical poikilotherms. Physiol. Zool. 26:67-92.
- Tucker, J.W., P.G. Bush and S. Slaybaugh. 1993. Reproductive patterns of Cayman Islands Nassau grouper (*E. striatus*) populations. Bull. Mar. Sci. 52(3):961-968.

ENTERED IN NAGA

APR 14 1998

Age Validation, Movements and Growth Rates of Tagged Gag (*Mycteroperca microlepis*), Black Sea Bass (*Centropristes striata*) and Red Porgy (*Pagrus pagrus*)

M.R. COLLINS

S.B. VAN SANT

G.R. SEDBERRY

Marine Resources Research Institute

South Carolina Wildlife and Marine Resources Department

P.O. Box 12559 Charleston, South Carolina

USA 29422-2559

COLLINS, M.R., S.B. VAN SANT and G.R. SEDBERRY. 1996. Age validation, movements and growth rates of tagged gag (*Mycteroperca microlepis*), black sea bass (*Centropristes striata*) and red porgy (*Pagrus pagrus*) [*Movimientos y tasa de crecimiento a partir de datos de marcado del cuna agujaí (Mycteroperca microlepis), del Serrano Estriado (Centropristes striata), y del Pargo (Pagrus pagrus)*], p. 158-162. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Ages of fishes are commonly estimated by counting opaque bands in the otoliths, but direct evidence to validate the annual nature of these bands is lacking for most species. Therefore, gag (*Mycteroperca microlepis*), black sea bass (*Centropristes striata*), and red porgy (*Pagrus pagrus*) were tagged, injected intramuscularly with oxytetracycline (OTC) and released. Otoliths were acquired from eleven gag at large for 225-603 days, five black sea bass at large for 206-355 days, and one red porgy at large for 341 days. Transverse sections of the otoliths were examined microscopically under white and ultraviolet light. Numbers of opaque bands distal to the fluorescent OTC mark were consistent with the hypothesis that these opaque bands are produced annually. Most individuals were recaptured at or near the two study sites. Growth rates were calculated for comparison with previous estimates.

Resumen

La edad de los peces es comúnmente estimada por conteo de bandas opacas en los otolitos, pero se carece de evidencias directas para validar la naturaleza anual de estas bandas para la mayor parte de las especies. En consecuencia el cuna agujaí (*Mycteroperca microlepis*), el serrano estriado (*Centropristes striata*) y el pargo (*Pagrus pagrus*) fueron marcados, injectados intramuscularmente con oxitetraciclina (OTC), y liberados. Después de 225-603 días los otolitos de once cuna agujaí fueron obtenidos, cinco del serrano estriado después de 206-355 días, y uno del pargo después de 341 días. Secciones transversales de los otolitos fueron analizadas al microscopio bajo luz blanca y luz ultravioleta. El número de bandas opacas distales de la marca fluorescente de OTC fueron consistentes con la hipótesis de que estas bandas opacas son producidas anualmente. La mayoría de los peces fueron recapturados dentro o cerca de los sitios de estudio. Las tasas de crecimiento fueron calculadas para comparación con estimaciones previas.

Introduction

Validation of the annual nature of marks (annuli) in hard parts of fishes ensures the accuracy of age estimates generated by counting the marks (Beamish and McFarlane 1983). Validation is usually based on indirect evidence, most commonly on marginal increment analyses of monthly samples of fish (e.g., Wenner et al. 1986; Collins et al. 1987) (see also Manickhand-Heileman and Philipp, this vol.). Direct evidence can be produced by examination of hard parts of known-age fish or by marking hard parts and examining them after a known period of time. One common method of marking hard parts is by injecting, feeding or immersing fish in the antibiotic oxytetracycline (OTC), which is incorporated into bony parts and fluoresces when the structure is examined under ultraviolet light (Hettler 1984; Foreman 1987; Marking et al. 1988) (see also Bush et al., this vol.).

Age and growth of most species of economically important reef fishes from the Atlantic coast of the southeastern United States have been described, but evidence for validation has been indirect. The primary objective of this study was to directly validate ages for several species of reef fishes. Secondary objectives were to gather information on growth rates and movements.

Methods

Reef fishes were captured by angling and trapping during 1987-1990 at two natural reef sites in 22-m and 27-m depths near Charleston, South Carolina, USA. Prior to tag application, the swim bladder was deflated with a hypodermic needle, total lengths (TL) were measured to the nearest mm, and a weight-dependent dosage of OTC was injected intramuscularly (McFarlane and Beamish 1987). Weights were estimated from length-weight relationships [(gag *Mycteroperca microlepis*) Manooch and

Haimovici 1978; red porgy (*Pagrus pagrus*) Dias et al. 1972; black sea bass (*Centropristes striata*) Wenner et al. 1986)]. During 1987, Petersen disk tags were attached below the dorsal fin and approximately 70 mg OTC per kg body weight of Liquamycin LA-200 was injected into the dorsal musculature. During 1988-1990, internal anchor tags were inserted into the abdomen and approximately 50 mg OTC per kg body weight of Anchor Oxy-Tet 100 was injected into the dorsal musculature. The address of our laboratory and instructions to save the tag and head were printed on all tags.

When recaptures of tagged fish were reported by commercial or recreational fishers we asked for the fish's length and the re-capture date and location, and we attempted to acquire the head or sagittal otoliths. In most cases, however, only the date and location were provided. When fish were recaptured by project personnel during tagging operations, those that had been at large for less than six months were generally measured and released. Some fish that were at large for more than six months and all that were at large for more than 12 months were sacrificed, measured and the otoliths removed and stored dry. Further processing was restricted to otoliths from fish recaptured after at least 200 days at large. Only fish at large for at least 90 days with lengths measured by project personnel were used in calculations of growth rates (recapture length - tagging length) / days at large).

Otoliths were embedded in paraffin, and transverse sections (ca. 0.5-mm thick) through the core of one otolith per fish were cut with a Buehler Isomet low speed saw. Sections were placed in nonfluorescing immersion oil and examined under white light and ultraviolet light at 40x and 100x using a Nikon Labophot microscope with an epifluorescence attachment. Age estimates were based on the number of opaque zones visible on the otolith section.

Results and Discussion

The brand and/or dosage of OTC used during the first year of this study caused lesions to form in the vicinity of the injection site, at least for gag. In addition, several fish were recaptured with the Petersen disk tags deflected posteriorly and torn partially through the musculature, and a few recaptured fish had evidence of OTC injection but only a scar or wound at the site of tag insertion (Van Sant et al. 1994). These problems were apparently eliminated in subsequent years by changing the tag type and the brand and dosage of OTC.

Validation analyses were restricted to otoliths of 11 gag, five black sea bass and one red porgy since otoliths were not acquired or the time at large was less than 200 days for most of the recaptured fish. Gag, black sea bass, and red porgy used in analyses were at large for 225-603 days, 206-355 days, and 341 days, and their otoliths displayed 2-7, 4-7, and 4 opaque zones, respectively. A fluorescent OTC mark was visible in all otoliths examined, and all otoliths showed growth beyond the OTC mark. Six gag, four black sea bass, and the red porgy had formed one opaque zone distal to the OTC mark.

Our results agreed with the periods of peak annulus formation, as determined from marginal increment analyses, reported in previous studies from this geographic area (May-August for gag, Collins et al. 1987; April-June for black sea bass, Wenner et al. 1986; and March-April for red porgy, Manooch and Huntsman 1977). Because our fish were tagged and recaptured during various months, including months of peak annulus formation, comparing the number of observed opaque zones distal to the OTC mark with the number to be expected if they were deposited annually is not straightforward. For all gag, two black sea bass, and the red porgy, the expected number is a range of two (e.g., 0-1).

However, in no case does the observed number of opaque zones disagree with the expected number or range, supporting the hypothesis that the zones are annual marks in the age groups examined (Fig. 1).

The scarcity of tag returns from locations other than the study sites suggests that most gag, red porgy, and black sea bass moved little. Most tag returns were from within 7 km of the tagging site, confirming results from previous tagging studies that reported little movement by reef fish in this region (Parker et al. 1979; Ansley and Davis 1981; Parker 1990). However, a few fish moved substantial distances. One red porgy at large for 62 days moved 17 km northwest, and another at large for 24 days moved 54 km northwest. A black sea bass at large ≥ 90 days was recaptured at an artificial reef 22 km northeast of the study site. One small gag at large for 1 021 days moved 54 km southwest, and another that was at large for 646 days moved 93 km northeast. The greatest movements were by large (> 75 cm TL) gag. Long distance movements of three large individuals suggested a possible spawning migration to southern Florida (Van Sant et al. 1994).

To minimize the effects of handling stress and possible measurement error on mean growth rate estimates, only fish that were at large ≥ 90 days and that were measured upon recapture by project personnel were utilized in calculations of mean growth rates. Mean growth rates ($\pm SD$) in terms of TL were 0.15 (0.08) mm/day for gag, 0.17 (0.08) mm/day for black sea bass, and 0.17 (0.05) mm/day for red porgy (Table 1). Our growth rates for gag and red porgy are similar to daily growth increments estimated from mean back-calculated (Manooch and Haimovici 1978) and mean observed (Collins et al. 1987) lengths for gag, and from mean back-calculated lengths for red porgy (Manooch and Huntsman 1977). However, our growth rate for black sea bass appears to be substantially greater than daily growth

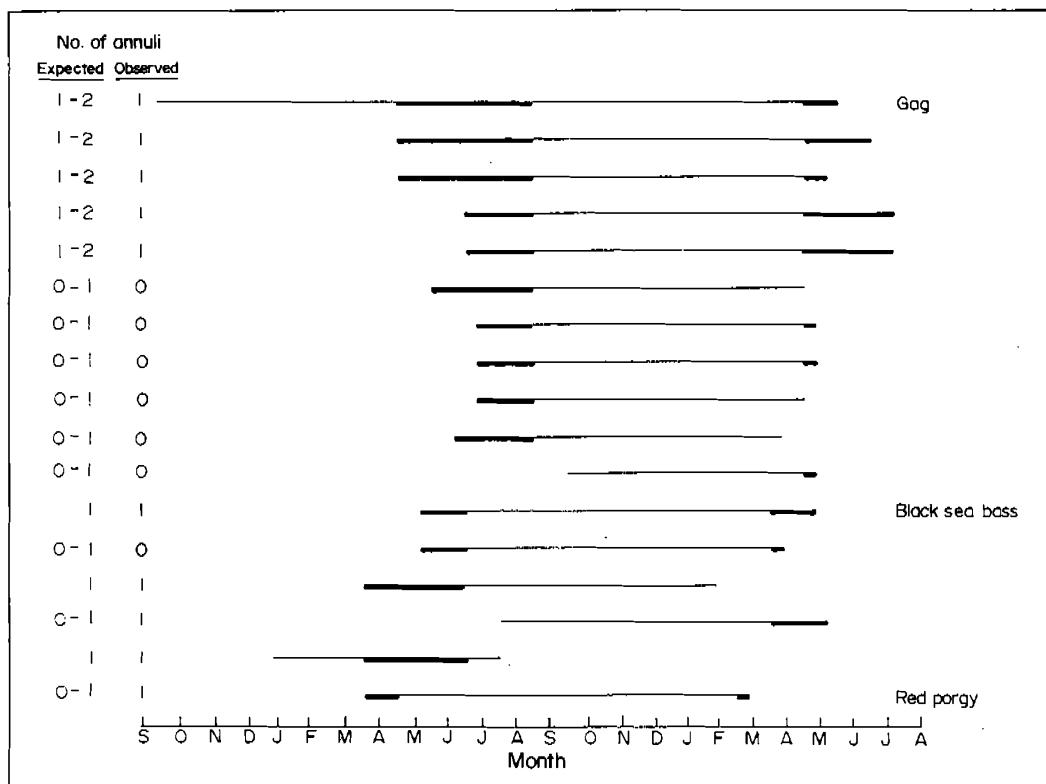


Fig. 1. Months at large (years pooled) and numbers of expected and observed annuli distal to the tetracycline mark for each fish used in validation analyses, with months of peak annulus formation (from the literature) indicated by bold line segments. [Meses (año promedio) y número esperado y observado de annull distales de la marca de tetraciclina para cada pez utilizado en el análisis de validación, con meses pico de formación de annull (tomado de la literatura) indicado por la línea gruesa.]

Table 1. Number of individuals, and mean (\pm SD) total length (TL, in mm), days of freedom, and growth rate (mm/day), of gag (*Mycteroperca microlepis*), black sea bass (*Centropristes striata*), and red porgy (*Pagrus pagrus*) tagged off South Carolina. Only individuals measured by project personnel at recapture and at large for at least 90 days were used in growth rate analyses. [Número de individuos, longitud total (LT, en mm) media (\pm D.S.), días de libertad, y tasa de crecimiento (mm/día) del cuna aguaí (*Mycteroperca microlepis*), serrano estriado (*Centropristes striata*), y pargo (*Pagrus pagrus*) marcados en aguas afuera de Carolina del Sur. Sólo individuos medidos por personal del proyecto al momento de la recaptura, y con el tiempo de liberación >90 días fueron usados en la estimación de la tasa de crecimiento.]

Item	Gag	Black sea bass	Red porgy
No. tagged	155	270	121
No. recaptured	43	45	8
No. for analysis	19	15	2
TL at release	613 ± 119	349 ± 40	350 ± 12
TL at recapture	656 ± 130	381 ± 35	395 ± 11
Days free	300 ± 152	197 ± 72	284 ± 81
Growth rate	0.15 ± 0.08	0.17 ± 0.08	0.17 ± 0.05

increments calculated from mean back-calculated lengths (Wenner et al. 1986).

We suggest two modifications to our methodology for future validation studies. Greater emphasis on public relations (e.g., news releases, presentations to fishing groups) might increase the number of recaptured fish from which otoliths are obtained, as the necessity of retaining heads would be better understood by the public. Concentrating mark and recapture efforts at times other than peak annulus formation would allow the expected number of opaque zones distal to the OTC mark to be a single number rather than a range. This would simplify comparisons of observed and expected numbers.

Acknowledgements

We appreciate the assistance in our tagging operations provided by the crew members of the *R/V Palmetto* and *R/V Lady Lisa* and by numerous MARMAP personnel. Charles A. Barans and Charles A. Wenner provided valuable comments on the manuscript. This study was funded by the National Marine Fisheries Service (Southeast Fisheries Center) and the South Carolina Wildlife and Marine Resources Department through the MARMAP contract. This is Contribution No. 311 from the South Carolina Marine Resources Center.

References

- Ansley, H.L.H. and C. D. Davis. 1981. Migration and standing stock of fishes associated with artificial and natural reefs on Georgia's outer continental shelf. Georgia Department of Natural Resources, Brunswick. 38 p.
- Beamish, R.J. and G.A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. *Trans. Am. Fish. Soc.* 112:735-743.
- Collins, M.R., C.W. Waltz, W.A. Roumillat and D.L. Stubbs. 1987. Contribution to the life history and reproductive biology of gag, *Mycteroperca microlepis* (Serranidae), in the South Atlantic Bight. *Fish. Bull. U.S.* 85:648-653.
- Dias, R.K., J.K. Dias and W.D. Anderson, Jr. 1972. Relationships of lengths (standard, fork, and total) and lengths to weight in the red porgy, *Pagrus sedecim* (Perciformes, Sparidae), caught off South Carolina. *Trans. Am. Fish. Soc.* 101:503-506.
- Foreman, T. 1987. A method of simultaneously tagging large oceanic fish and injecting them with tetracycline. *Fish. Bull. U.S.* 85:645-647.
- Hettler, W.F. 1984. Marking otoliths by immersion of marine fish larvae in tetracycline. *Trans. Am. Fish. Soc.* 113:370-373.
- Manooch, C.S., III and M. Haimovici. 1978. Age and growth of the gag, *Mycteroperca microlepis*, and size-age composition of the recreational catch off the southeastern United States. *Trans. Am. Fish. Soc.* 107:234-240.
- Manooch, C.S., III and G.R. Huntsman. 1977. Age, growth, and mortality of the red porgy, *Pagrus pagrus*. *Trans. Am. Fish. Soc.* 106:26-33.
- Marking, L.L., G.E. Howe and J.R. Crowther. 1988. Toxicity of erythromycin, oxytetracycline, and tetracycline administered to lake trout in water baths, by injection, or by feeding. *Prog. Fish-Cult.* 50:197-201.
- McFarlane, G.A. and R.J. Beamish. 1987. Selection of dosages of oxytetracycline for age validation studies. *Can. J. Fish. Aquat. Sci.* 44:905-909.
- Parker, R.O., Jr. 1990. Tagging studies and diver observations of fish populations on live-bottom reefs of the U.S. southeastern coast. *Bull. Mar. Sci.* 46:749-760.
- Parker, R.O., Jr., R.B. Stone and C.C. Buchanan. 1979. Artificial reefs off Murrells Inlet, South Carolina. *Mar. Fish. Rev.* 8(1):31-49.
- Van Sant, S.B., M.R. Collins and G.R. Sedberry. 1994. Preliminary evidence from a tagging study for a gag (*Mycteroperca microlepis*) spawning migration with notes on the use of oxytetracycline for chemical tagging. *Proc. Gulf Carib. Fish. Inst.* 43:417-428.
- Wenner, C.A., W.A. Roumillat and C.W. Waltz. 1986. Contributions to the life history of black sea bass, *Centropristes striata*, off the southeastern United States. *Fish. Bull. U.S.* 84:723-741.

ENTERED IN NAGA

APR 14 1998

The Validity of Length-based Methods for Estimating Growth and Mortality of Groupers, as Illustrated by Comparative Assessment of the Creole Fish (*Paranthias furcifer*) (Pisces: Serranidae)

J.M. POSADA
R.S. APPELDOORN
Department of Marine Sciences
University of Puerto Rico
Mayagüez 00681-5000, Puerto Rico

POSADA, J.M. and R.S. APPELDOORN. 1996. The validity of length-based methods for estimating growth and mortality of groupers, as illustrated by comparative assessment of the creole fish, (*Paranthias furcifer*) (Pisces: Serranidae) [Validez de los métodos para estimar crecimiento y mortalidad en meros basados en frecuencia de longitudes, a partir de la evaluación comparativa de la cuna lucero (*Paranthias furcifer*) (Pisces: Serranidae)], p. 163-173. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Several length-based methods for the analysis of growth and mortality of the creole fish (*Paranthias furcifer*) (Valenciennes) were used and results compared to see how they were affected by distortion of the length-frequency distribution due to ontogenetic offshore migration. Data were from fish caught using pole spears (≈ 40 ind/month, 20 months) at the edge of the insular shelf off southwestern Puerto Rico. Two methods were used to estimate growth parameters (K , L_{∞}): ELEFAN I, and Wetherall's method (L_{∞}) coupled with a ϕ' -value to estimate K . Four methods were used to estimate mortality ($Z=M$): Z/K , Ralston's and Pauly's equations, and length-converted catch curve. Only the ELEFAN I method gave realistic results for growth parameters ($L_{\infty} = 31.4$ cm and $K = 0.282$ year $^{-1}$), and these gave reasonable estimates for mortality using Ralston's equation (0.647 year $^{-1}$) and Z/K (0.637 year $^{-1}$). Wetherall's method underestimated L_{∞} , and hence led to an overestimate of K . All subsequently derived mortality estimates were biased upwards by a factor of 2. Catch-curve analyses also resulted in overestimations of mortality. These results are all consistent with those expected under the scenario of ontogenetic migration out of the sampling area.

Resumen

Diferentes métodos basados en longitud fueron utilizados para estimar los parámetros de crecimiento y mortalidad de la cuna lucero (*Paranthias furcifer*) (Valenciennes) y los resultados fueron comparados para determinar como la migración ontogenética fuera de la costa distorsiona la distribución de frecuencia de tallas. Los datos provenían de peces capturados mediante el uso de arpones (≈ 40 ind/mes, 20 meses) al borde de la plataforma insular en el suroeste de Puerto Rico. Dos métodos fueron utilizados para estimar los parámetros de crecimiento (K , L_{∞}): ELEFAN I, y Wetherall (L_{∞}) conjuntamente con el valor de ϕ' para estimar K . Cuatro métodos fueron utilizados para estimar mortalidad ($Z=M$): Z/K , las ecuaciones empíricas de Ralston y Pauly, y curva de captura. Únicamente el método ELEFAN I estimó realísticamente

los parámetros de crecimiento ($L_{\infty} = 31.4$ cm y $K = 0.282$ año $^{-1}$), y éstos condujeron a estimados razonables de mortalidad utilizando la ecuación de Ralston (0.647 año $^{-1}$) y la relación Z/K (0.637 año $^{-1}$). El método de Wetherall subestima L_{∞} , y por tanto induce a una sobreestimación de K. Todos las derivaciones subsecuentes de mortalidad resultaron sesgados por un factor de 2. El análisis de curva de captura también resultó en sobreestimaciones de mortalidad. Todos los resultados son consistentes con lo esperado bajo el escenario de migración ontogenética fuera del área de muestreo.

Introduction

Groupers (Subfamily: Epinephelinae) are very important components of commercial fisheries in tropical reef environments. Despite their importance, few quantitative stock assessments have been conducted (see compilation in Munro and Williams 1985, and see also Arreguín-Sánchez et al., this vol.). This results from a combination of the nature of the fishery (usually multispecies and artisanal with a high diversity of gear and landing sites) and the limited resources available on the part of management agencies. Length-frequency analysis has been suggested as a potentially valuable tool for the stock assessment of tropical fishes (Munro 1983), and recent interest in this approach has led to considerable development and testing of length-based techniques (see, e.g., Pauly and Morgan 1987).

Length-frequency analysis (LFA) has two general constraints when applied to groupers. First, discrete modes in the length-frequency distribution must be detectable if growth rate is to be determined. Detection of modes is favored where growth is rapid (usually correlated with short lifespan) and spawning is restricted to a short season. While groupers often show a quite restricted spawning season (Shapiro 1987), they are slow growing and long lived. Nevertheless, LFA has been successfully applied to some important species of groupers where a clear modal progression of size classes can be followed over time (Manooch

1987). Second, in general, large sample sizes are required to adequately represent the location of modes in the length-frequency distribution (Erzini 1990). Considering the nature of these fisheries, large sample sizes are often difficult to obtain during a restricted period of time, although sampling strategies can be adjusted to maximize the quality of these limited data with respect to LFA (Dennis 1988; Acosta and Appeldoorn 1992).

If growth rate determination is the goal of LFA, sampling need not be random relative to the underlying population (Hoenig et al. 1987). All that is required is that modes be detectable and their location be relatively unbiased; the relative size of the modes is unimportant. A variety of techniques, e.g., polymodal breakdown (Cassie 1954; Bhattacharya 1967; Macdonald and Pitcher 1979; Schnute and Fournier 1980; Akamine 1985) and ELEFAN I (Pauly and David 1981) can be used to determine growth under these conditions.

More restrictive assumptions of a steady-state population and an unbiased sample of the population are necessary when using techniques dependent upon the shape of the distribution (Hoenig et al. 1987). These include techniques for estimating mortality, such as Beverton and Holt's (1956) method and length-converted catch curves (Pauly 1984) and some methods for estimating growth parameters (Wetherall et al. 1987). These assumptions are rarely assessed when applying length-based techniques, yet there is good evidence that

these assumptions are, at times, poorly met with respect to groupers. Two sources of deviation from these assumptions are of particular concern: recruitment variations, and nonrandom spatial distribution with respect to size.

Marked, nonrandom changes in the recruitment of two species of grouper were found by Appeldoorn et al. (1992), and these caused considerable interannual variation in the shape of their respective length-frequency distributions. These changes were detected only after long time-series of length-frequency distributions had been obtained and growth rate via otolith analysis had been determined; this is an infrequent situation in most tropical fisheries.

Shifts in length-frequency distributions toward larger sizes in deeper, offshore habitats are known for many reef species (see Parrish 1987; Williams 1991), reflecting ontogenetic migrations from shallow/inshore areas to deeper/offshore areas. Similar behavior is known for groupers (Bullock and Smith 1991). This can lead to two problems. First, it is much more difficult to obtain an unbiased population length-frequency distribution. While a wide depth range can be easily stratified and sampled, such sampling is costly and time-consuming, and the pooling of samples among strata is made difficult because differences in habitat abundance among strata will affect fish abundance within strata. This problem can be ameliorated somewhat if sampling is limited to the deeper strata where larger fish are found. However, this leads to the second problem, which is a reduction in the number of size classes available for estimating parameters. Also, because size is a poor indicator of age in large fish, these data will be of lesser quality.

The purpose of this study is to compare the results of different length-based methods to see if they are subject to invalid assumptions. This is illustrated with an analysis of

the creole fish (*Paranthias furcifer*) (Valenciennes) off the southwest coast of Puerto Rico. Since our orientation is primarily methodological, we will restrict our analyses and comparisons to mean estimates of parameters. A more detailed analysis of this species, including estimation of parameter variances, is currently being conducted using otolith analysis.

The creole fish is a small grouper and one of the few species of fishes found at both sides of the Atlantic and in the eastern Pacific (Snodgrass and Heller 1905; Meek and Hildebrand 1925; Fowler 1936, 1945; Briggs 1967; Randall 1968; Hoese and Moore 1977; Thomson et al. 1979; Quero et al. 1990). It is reported to occur in the open waters over reefs 20 m and deeper, beyond outer emergent reefs (Smith 1971; Davis and Birdsong 1973; Kimmel 1985).

At the moment, *P. furcifer* lacks significant commercial importance due to its small size (30-cm maximum size, according to Smith 1971). However, it is occasionally found in party-boat catches from the Florida Middle Grounds (Bullock and Smith 1991) and is gaining value in Bermuda as the catch of larger groupers declines (Butler et al. 1993). Given this, and its wide geographic distribution, we consider that *P. furcifer* represents a potentially important fisheries resource. Age, growth and mortality have been estimated by Nelson et al. (1986) at the Flower Gardens Bank (Gulf of Mexico) using scales and otoliths. Significantly, using remote video transects at depths beyond the reach of scuba divers, the maximum size they observed was in excess of 34.0 cm fork length (FL), while the largest size sampled by divers was 28.0 cm FL. Similarly, one of us (J.M. Posada) has observed small individuals of *P. furcifer* to recruit to a shallow water/inshore habitat in Bermuda. Although limited, these observations indicate that creole fish undergo an ontogenetic offshore migration.

Methods

The study area was located in depths of 16-34 m at the edge of the Insular shelf off southwestern Puerto Rico, at approximately 17°53'86"N, 66°57'35"W. This is southwest of Guanica with the nearest land being Punta Jorobada, 4 km to the north (Fig. 1).

Collections, oriented to reproduction studies, were made using SCUBA diving. Fish were caught (approx. 40 ind.) monthly between March 1992 and October 1993 with a pole spear fitted with a three-pronged tip; extreme care was taken to collect all fish encountered so as not to bias the sample towards particular size classes. Divers felt that it was equally difficult to catch a 13-cm TL fish as one 27-cm TL, although the former was more scarce. For all individuals, total length (TL) was measured to the nearest 0.1 cm.

To increase modal definition for LFA, samples were pooled bimonthly without weighting and assigned a single collection date. Sample size varied from 62 to 92 individuals and the total number of fish sampled was 842. Our analysis assumes von Bertalanffy growth:

$$L_t = L_{\infty}(1 - \exp(-K(t-t_0)))$$

where L_t = length at time t (years), L_{∞} = asymptotic length, K = growth coefficient, and t_0 = hypothetical age when length would be zero. To obtain an idea of the range of growth parameters that could be expected, a literature search was made on the growth of small groupers.

Estimates of K and L_{∞} were made using two different techniques. The first technique was the ELEFAN I method as implemented in the Compleat ELEFAN (Gayanilo et al. 1989). ELEFAN I does not assume a

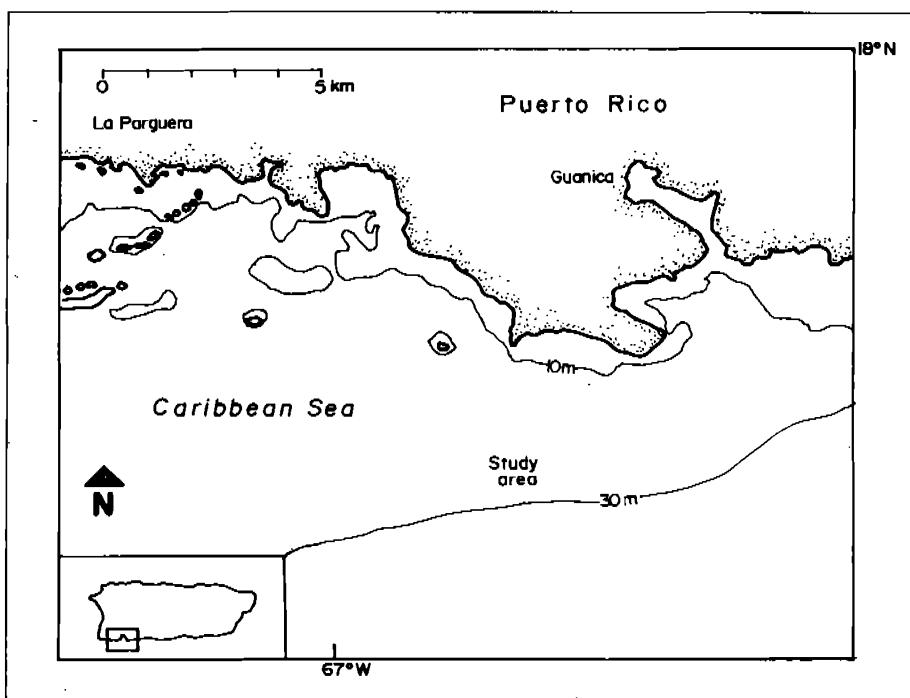


Fig. 1. Map showing study area on the shelf edge off southwestern Puerto Rico (from Colin and Clavijo 1988). [Mapa mostrando el área de estudio sobre el borde de la plataforma continental al suroeste de Puerto Rico.]

steady-state population and only requires an unbiased sample of the catch. Using ELEFAN I, L_{∞} and K were first allowed to vary, and a response surface of R_n (goodness-of-fit) values was generated. The logic of ELEFAN I implies that one should pick the value of L_{∞} and K associated with the highest R_n -value, however some constraints were imposed considering the biology of groupers in general. Over a narrow range defined by the response surface (subject to the above constraints), all parameters (K, L_{∞} , starting point and sample) were allowed to vary, and optimum values were obtained.

The second technique used Wetherall's method (also implemented using the Compleat ELEFAN) to estimate L_{∞} and Z/K, where Z is instantaneous total mortality. Wetherall's method assumes a steady-state population and unbiased sample. To smooth out possible recruitment variations, all data (over two years) were pooled, without weighting, into a single length-frequency analysis. The growth parameters for *P. furcifer* presented by Nelson et al. (1986) were used to estimate ϕ' (Pauly and Munro 1984), where $\phi' = \log_{10}(K) + Z \log_{10}(L_{\infty})$. The value of L_{∞} obtained from Wetherall's method was then substituted into the ϕ' equation for *P. furcifer* to estimate K, and hence Z. In addition, the estimate of Z/K was combined with the estimate of K derived from ELEFAN I to estimate Z. The difference between these two estimates of Z is that the former is done while attempting to maintain a known relationship between the growth parameters (i.e., ϕ') while the latter does not.

Estimation of instantaneous natural mortality (M) was done by substituting the estimated values of L_{∞} and K values derived from the ELEFAN method into the equations:

$$\begin{aligned} \text{Log}(M) &= -0.0066 + 0.6543 \text{ Log}(K) - \\ &\quad 0.279 \text{ Log}(L_{\infty}) + 0.4634 \\ &\quad \text{Log}(T) \text{ (Pauly 1980), and} \\ M &= -0.0666 + 2.53 K \text{ (Ralston 1987)} \end{aligned}$$

where T = annual mean water temperature at the sampling site (27.9°C). Instantaneous total mortality (Z) was calculated using a length-converted catch curve (Pauly 1984), again implemented using the Compleat ELEFAN. For this analysis, all data were pooled, without weighting, into a single length-frequency sample. A regression line was fitted to points immediately to the right of the highest point on the catch curve. The slope of the regression line is an estimate of Z. The L_{∞} and K values used for the catch curve were those determined using the ELEFAN method. Since the creole fish is not commercially or recreationally exploited in the study area, the estimates of total mortality should reflect only natural mortality.

Results

Length-frequency distributions used for the estimation of growth parameters for *Paranthias furcifer* are presented in Table 1. Table 2 presents the results of the analyses. The estimate of ϕ' for *P. furcifer* from Nelson et al. (1986) was 2.60. Wetherall's method (Fig. 2) resulted in an estimate of L_{∞} of 25.9 cm and a value of 2.261 for Z/K. Using the former with the estimated value of ϕ' resulted in an estimate of K of 0.593 year⁻¹ and a high estimate for Z of 1.34 year⁻¹. Fig. 3 shows the ELEFAN-derived growth curve superimposed on the length-frequency data. The estimated parameters were $L_{\infty} = 31.4$ cm and $K = 0.282$ year⁻¹. Using this K-value with the Z/K estimate from Wetherall's method resulted in a markedly lower Z-value of 0.637 year⁻¹.

Natural mortality (M) estimates derived from the Pauly and Ralston equations and the ELEFAN parameters were 0.769 and 0.647 year⁻¹, respectively. Natural mortality estimates derived from the Pauly and Ralston equations and the Wetherall parameters were 1.320 and 1.435 year⁻¹,

Table 1. Length-frequency data on *Paranthias furcifer* collected between March 1992 and October 1993 at the shelf edge off southwestern Puerto Rico. [Datos de frecuencia de longitudes de *Paranthias furcifer* colectados entre Marzo y Octubre de 1993 en el borde de la plataforma continental, al suroeste de Puerto Rico.]

Length class (TL; cm)	M-A/ 92	M-J	J-A	S-O	N/D	J-F/ 93	M-A	M-J	J-A	S-O
13.0-13.9	-	-	-	1	-	-	1	-	-	-
14.0-14.9	-	-	1	-	-	-	-	-	-	-
15.0-15.9	1	1	4	2	-	-	-	1	-	1
16.0-16.9	1	-	2	3	2	-	-	1	-	-
17.0-17.9	1	6	3	12	7	4	-	-	-	-
18.0-18.9	15	6	11	16	7	10	4	2	-	3
19.0-19.9	17	14	11	12	14	12	9	8	3	13
20.0-20.9	11	18	8	8	16	18	16	9	9	15
21.0-21.9	8	11	10	8	14	16	16	13	29	32
22.0-22.9	14	10	15	7	10	10	18	15	25	13
23.0-23.9	9	6	8	6	9	12	10	9	18	12
24.0-24.9	8	9	11	8	7	5	2	4	7	2
25.0-25.9	3	2	-	1	2	1	4	-	1	1
26.0-26.9	-	-	-	1	-	-	-	-	-	-
Total	88	83	84	85	88	88	80	62	92	92

Table 2. Growth and mortality of *Paranthias furcifer* using various methods (all instantaneous rates in year⁻¹). [Crecimiento y mortalidad de *Paranthias furcifer* usando varios métodos (todas las tasas instantáneas son anuales).]

Source of estimates	Growth					Mortality		
	L ^a	K	ϕ ^b	Z/K	Z ₁ ^c	Z ₂ ^d	M ₁ ^e	M ₂ ^f
Nelson et al. (1986)	42.4	0.22	2.60	-	-	-	-	-
This study								
ELEFAN I	31.4	0.282	2.44	-	-	2.777	0.769	0.647
Wetherall plot	25.9	0.593	(2.60)	2.26	1.340	1.416	1.320	1.435

^a TL; cm

^b $\phi' = \log_{10}K + 2\log L_{\infty}$; value for Nelson et al. 1986 used to infer K in Wetherall plot estimate

^c based on (Z/K)·K

^d Length-converted catch curve estimates

^e M from Pauly's equation

^f M from Ralston's equation

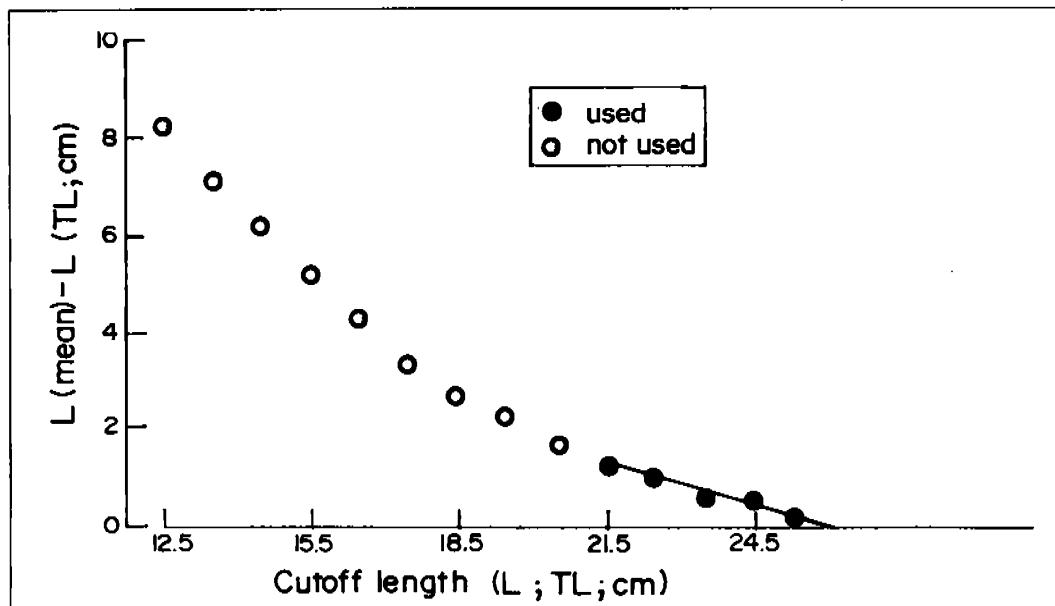


Fig. 2. Wetherall plot used to estimate L_{∞} in *Paranthias furcifer* from southwestern Puerto Rico. [Gráfico de Wetherall usado para estimar L_{∞} en *Paranthias furcifer* del Suroeste de Puerto Rico.]

respectively. The estimates of total mortality from catch curve analysis using the ELEFAN and Wetherall parameters were $Z = 2.777$ and $Z = 1.416 \text{ year}^{-1}$, respectively.

Discussion

The maximum size commonly recorded for *Paranthias furcifer* in the literature is near 30 cm TL (Metzelaar 1919; Meek and Hildebrand 1925; Smith 1958, 1971; Randall 1968; Took 1978; Cervigón 1991), a value that is close to the estimate of L_{∞} derived using ELEFAN I. However, Hoese and Moore (1977) reported a 36-cm TL fish in waters adjacent to the Gulf of Mexico, and Nelson et al. (1986) observed fish in excess of 34 cm FL at the Flower Garden Banks (Gulf of Mexico) and predicted an asymptotic length of 37.2 cm FL (42.4 cm TL). Pauly (1981) suggested that a given species attains a larger asymptotic size and lower growth coefficient (K) in cooler regions.

Considering the above, and that Nelson et al. (1986) found larger individuals at greater depths, plus our own observations of juvenile recruitment into shallow waters, it is likely that, in our study, Wetherall's method underestimated L_{∞} . If larger fish are found in depths deeper than sampled, then the shape of the right-hand side of the length-frequency distribution would be dependent upon, not only growth and mortality, but migration (to deeper waters) as well. Thus, the slope on this side of the distribution would be increased, leading to an underestimation of L_{∞} ; however, the estimate of Z/K would be unaffected (Wetherall et al. 1987). Using this L_{∞} to estimate K would lead to an overestimation of K , and this is evident in our results. In contrast, the ELEFAN I method appears to provide a better estimator of L_{∞} . This indicates that the length-frequency data are suitable for estimating growth parameters using methods with less restrictive assumptions, i.e., modes are apparent and they shift position over time (Fig. 3).

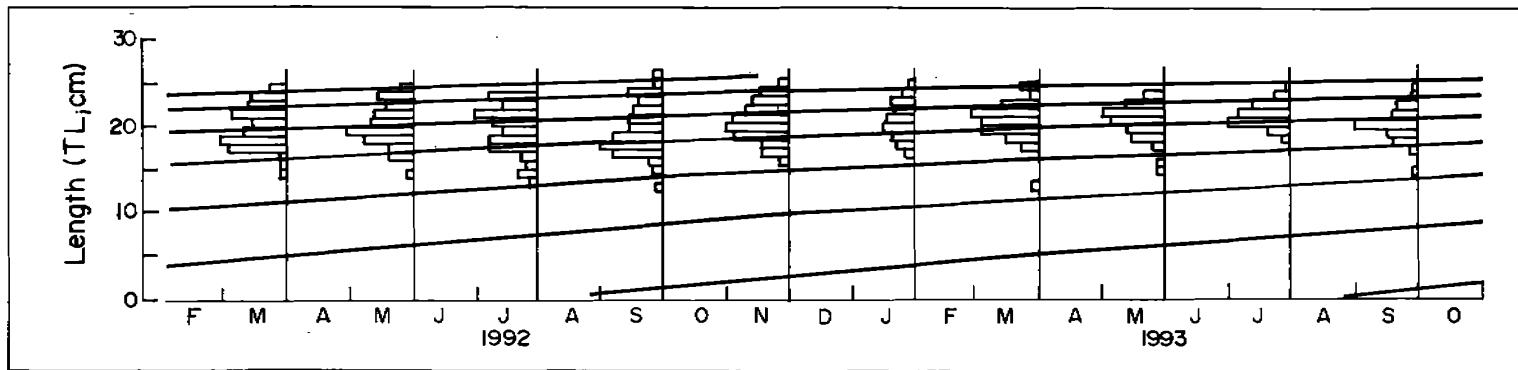


Fig. 3. Growth curve obtained using ELEFAN I for *Paranthias furcifer* caught at the shelf edge off southwestern Puerto Rico superimposed on length-frequency data. [Curva de crecimiento obtenida usando ELEFAN I, para *Paranthias furcifer* capturado en el borde de la plataforma continental al suroeste de Puerto Rico, superpuesta a los datos de frecuencia de longitudes.]

Four methods were used for mortality ($Z=M$) estimation: length-converted catch curve, Z/K ratio, and the Pauly and Ralston equations. The latter two gave similar results when used with the ELEFAN I growth parameters, with the results from the Pauly equation being slightly higher. Nelson and Manooch (1982), Brouard and Grandperrin (1984) and Ralston (1987) indicate that Pauly's equation tends toward overestimation of M for slow-growing species. This is consistent with our results and the estimate of mortality reported by Nelson et al. (1986) ($M = 0.61 \text{ year}^{-1}$). If our length-frequency distribution was affected by ontogenetic migration of larger individuals into deeper water, then we would also expect that mortality rates derived from the catch-curve would be overestimated (Pinto 1986), and this was clearly evident in our results. The amount of bias is dependent upon the magnitude of the K and L_{∞} values and will be greater when K is low and L_{∞} is high, i.e., to account for a given shape of the right-hand side of the length-frequency distribution, continued growth must be offset by greater mortality. For this reason, the results using the ELEFAN I parameters show greater overestimation of mortality.

The underestimation of L_{∞} and subsequent overestimation of K using Wetherall's method resulted in extreme overestimations of mortality for all methods. The results with Pauly's equation were surprising, as it was thought that, with the inverse linear log-log relationship between K and L_{∞} , overestimation in one parameter would be offset by underestimation of the other. However, a closer examination reveals that if L_{∞} is underestimated, and K thus overestimated, then M will be overestimated without compensatory effect.

It has been suggested that Wetherall's method could be used to first estimate L_{∞} and that a different method (e.g., ELEFAN I) be used to estimate K (e.g., Pauly 1986);

this suggestion is based on the good statistical properties of the method (Wetherall et al. 1987) and its ease of use. However, we believe its application to reef fish must be done with caution and the validity of its assumptions ascertained. In a similar manner, Ralston's (1987) equation has been recommended to predict natural mortality for snappers and groupers. We agree with this recommendation; however, in relying only on a single parameter, this method is more sensitive than Pauly's equation to biases in growth-parameter estimation.

Acknowledgements

We are indebted to G. López, M. Rosado and A. Nazario for assistance in collecting specimens; M. Reigle kindly facilitated the use of boats and personnel. This research was supported by the Department of Marine Sciences, University of Puerto Rico and by a fellowship to J.M. Posada from the National Council for Scientific and Technological Research (CONICIT, by its Spanish abbreviation), Venezuela.

References

- Acosta, A. and R.S. Appeldoorn. 1992. Estimation of growth, mortality and yield per recruit for *Lutjanus synagris* (Linnaeus) in Puerto Rico. Bull. Mar. Sci. 50:282-291.
- Akamine, T. 1985. Considerations of the BASC programs to analyse the polymodal frequency distributions into normal distributions. Bull. Japan Sea Reg. Fish. Res. Lab. 35:129-160.
- Appeldoorn, R.S., J. Beets, J. Bohnsack, S. Bolden, D. Matos, S. Meyers, A. Rosario, Y. Sadovy and W. Tobias. 1992. Shallow water reef fish stock assessment for the U.S. Caribbean. NOAA Tech. Mem. NMFS-SEFC-304, 70 p.
- Bhattacharya, C.G. 1967. A simple method of resolution of a distribution into Gaussian components. Biometrics 23:115-135.

- Beverton, R.J.H. and S.J. Holt. 1956. A review of methods for estimating mortality rates in fish populations with special reference to sources of bias in catch sampling. *Rapp. P.-v. Réun. CIEM* 140:67-83.
- Briggs, J.C. 1967. The relationship of the tropical shelf regions. *Stud. Trop. Oceanogr.* Miami 5:569-578.
- Brouard, F. and R. Grandperrein. 1984. Les poissons profonds de la pente récifale extérne à Vanuatu. Notes et documents d'océanographie, Mission ORSTOM, Port-Vila, Vanuatu, No. 11, 131 p.
- Bullock, L.H. and G.B. Smith. 1991. Memoirs of the Hourglass cruises: seabasses (Pisces: Serranidae). Florida Marine Research Institute, Dept. Nat. Resources, St. Petersburg, Florida. 3(2):1-243.
- Butler, J.N., J. Burnett-Herkes, J.A. Barnes and J. Ward. 1993. The Bermuda fisheries: a tragedy of the commons averted? *Environment* 35(1):7-33.
- Cassie, R.M. 1954. Some uses of probability paper in the analysis of size frequency distributions. *Aust. J. Mar. Freshwat. Res.* 5:13-522.
- Cervigon, F. 1991. Los peces marinos de Venezuela, Vol. I, 2da. edición. Fund. Cient. Los Roques, Caracas. 425 p.
- Colin, P.L. and I.E. Clavijo. 1988. Spawning activity of fishes producing pelagic eggs on a shelf edge coral reef, Southwestern Puerto Rico. *Bull. Mar. Sci.* 43(2):249-279.
- Davis, W.P. and R.S. Birdsong. 1973. Coral reef fishes which forage in the water column. *Helgoländer wiss. Meeresunters* 24:292-306.
- Dennis, G.D. 1988. Commercial catch length-frequency data as a tool for fisheries management with an application to the Puerto Rico trap fishery. *Mém. Soc. Cienc. Nat. La Salle* 48(suppl. 3):289-310.
- Erzini, K. 1990. Sample size and grouping of data for length-frequency analysis. *Fish. Res.* 9:355-366.
- Fowler, H.W. 1936. The marine fishes of west Africa, part II. *Bull. Am. Mus. Nat. Hist.* 70(2):1493 p.
- Fowler, H.W. 1945. Los peces del Peru. *Mus. Hist. Nat. Javier Prado, Univ. Nac. Mayor de San Marcos, Lima.* 298 p.
- Gayanilo, F.C., Jr., M. Soriano and D. Pauly. 1989. A draft guide to the Compleat ELEFAN. *ICLARM Software* 2, 67 p.
- Hoenig, J.M., J. Csirke, M.J. Sanders, A. Abella, M.G. Andreoli, D. Levi, S. Ragonese, M. Al-Shoushani and M.M. El-Musa. 1987. Data acquisition for length-based stock assessment: Report of Working Group I, p. 343-352. In D. Pauly and G. Morgan (eds.) *Length-based methods in fisheries research*. ICLARM Conf. Proc. 13, 468 p.
- Hoese, H.D. and R.H. Moore. 1977. *Fishes of the Gulf of Mexico, Texas, Louisiana and adjacent waters*. Texas A & M University Press, College Station. 327 p.
- Kimmel, J.J. 1985. A characterization of Puerto Rican fish assemblages. University of Puerto Rico, Mayaguez, Puerto Rico. 106 p. Ph.D. dissertation.
- Manooch, C.S. III. 1987. Age and growth of snappers and groupers, p. 329-374. In J.J. Polovina and S. Ralston (eds) *Tropical snappers and groupers: biology and fisheries management*. Westview Press, Boulder.
- Macdonald, P.D.M. and T.J. Pitcher. 1979. Age groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. *J. Fish. Res. Board Can.* 36:987-101.
- Meek, S.F. and S.F. Hildebrand. 1925. The marine fishes of Panama, part II. *Field Mus. Natur. Hist. Pub.* 226, Zool. Ser. 15:331-707.
- Metzelaar, J. 1919. *Fishes of the Dutch West Indies. Report on the fishes collected by Dr. J. Boeke in the Dutch West Indies 1904-1905, with comparative notes on marine fishes of Tropical West Africa by Dr. J. Metzelaar*. A. Asher and Co., Amsterdam.
- Munro, J.L. 1983. A cost-effective data acquisition system for assessment and management of tropical multispecies, multi-gear fisheries. *Fishbyte* 1(1):7-12.
- Munro, J.L. and D.McB. Williams. 1985. Assessment and management of coral reef fisheries: biological, environmental and socio-economic aspects, p. 545-578. In C. Gabrie and B. Salvat (eds.) *Proceedings of the Fifth International Coral Reef Congress, 27 May-1 June 1985, Tahiti*. Vol.

4. Antenne Museum-EPHE, Moorea, French Polynesia.
- Nelson, R.S. and C.S. Manooch III. 1982. Growth and mortality of red snappers in the west-central Atlantic Ocean and northern Gulf of Mexico. *Trans. Am. Fish. Soc.* 111:465-475.
- Nelson, R.S., C.S. Manooch III and D.L. Mason. 1986. Ecological effects of energy development on reef fish of the Flower Garden Banks: Reef fish bioprofiles. Final report. Southeast Fish. Cent. Beaufort Lab., Natl. Mar. Fish. Serv., NOAA, Beaufort, North Carolina. 251 p.
- Parrish, J.D. 1987. The trophic biology of snappers and groupers, p. 405-463. *In* J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. J. Westview Press, Boulder.
- J Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and the mean environmental temperature in 175 fish stocks. *J. Cons. C.I.E.M.* 39(3):175-192.
- J Pauly, D. 1981. The relationships between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Meeresforsch.* 28:251-282.
- J Pauly, D. 1984. Fish population dynamics in tropical waters: a manual for use with programmable calculators. ICLARM Stud. Rev. 8, 325 p.
- J Pauly, D. 1986. Improving operation and use of the ELEFAN programs. Part II. Improving the estimation of L_{∞} . *Fishbyte* 4(1):18-20.
- J Pauly, D. and N. David. 1981. ELEFAN I, a BASIC program for the objective extraction of growth parameters from length-frequency data. *Meeresforsch.* 28:205-211.
- J Pauly, D. and G.R. Morgan, Editors. 1987. Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.
- J Pauly, D. and J.L. Munro. 1984. Once more on growth comparison in fish and invertebrates. *Fishbyte* 2(1):21.
- Pinto, L. 1986. Use of ELEFAN programs for emigrating species. *Fishbyte* 4(1):14-15.
- Quero, J.C., J.C. Hureau, C. Karrer, A. Post and L. Saldanha. 1990. Check-list of the fishes of the eastern tropical Atlantic. Vols. I-III. UNESCO, Paris. 1492 p.
- Ralston, S. 1987. Mortality rates of snappers and groupers, p. 375-404. *In* J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Randall, J.E. 1968. Caribbean reef fishes. T.F.H. Publications, Neptune City, New Jersey. 318 p.
- Schnute, J. and D. Fournier. 1980. A new approach to length-frequency analysis: growth structure. *Can. J. Fish. Aquat. Sci.* 37:1337-1351.
- Shapiro, D.Y. 1987. Reproduction in groupers, p. 295-327. *In* J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Smith, C.L. 1958. The groupers of Bermuda, p. 4-17, 37-59. *In* J. E. Bardach, C. L. Smith and D.W. Menzel (eds.) Final report of the Bermuda Fisheries Research Program. Bermuda Trade Development Board, Hamilton, Bermuda.
- Smith, C.L. 1971. A revision of the American groupers: *Epinephelus* and allied genera. *Bull. Am. Mus. Natur. Hist.* 146(2):67-242.
- Snodgrass, R.E. and E. Heller. 1905. Shore fishes of the Revillagigedo, Clipperton, Cocos and Galapagos Islands. *Proc. Wash. Acad. Sciences*, 6:33-427.
- Thomson, D.A., L.T. Findley and A.N. Kerstitch. 1979. *Reef fishes of the Sea Cortez*. John Wiley and Sons, New York. 302 p.
- Took, I. F. 1978. *Fishes of the Caribbean Reef*. Macmillan Publishers Ltd., London. 92 p.
- J Wetherall, J.A., J.J. Polovina and S. Ralston. 1987. Estimating growth and mortality in steady-state fish stocks from length-frequency data, p. 53-74. *In* D. Pauly and G. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.
- Williams, D.McB. 1991. Patterns and processes in the distribution of coral reef fishes, p. 437-474. *In* P.F. Sale (ed.) *The ecology of fishes on coral reefs*. Academic Press, New York.

ENTERED IN NAGA

APR 14 1998

Spawning and Annual Fecundity of the Red Snapper (*Lutjanus campechanus*) from the Northeastern Gulf of Mexico

L.A. COLLINS

A.G. JOHNSON

C.P. KEIM

National Oceanic and Atmospheric Administration

National Marine Fisheries Service

Southeast Fisheries Science Center

Panama City Laboratory

3500 Delwood Beach Road

Panama City, Florida 32408, USA

COLLINS, L.A., A.G. JOHNSON and C.P. KEIM. 1996. Spawning and annual fecundity of the red snapper (*Lutjanus campechanus*) from the northeastern Gulf of Mexico [Desove y fecundidad anual del pargo del Golfo (*Lutjanus campechanus*) del noreste del Golfo de México], p. 174-188. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

We used batch fecundity and spawning frequency methods to provide information on spawning and annual fecundity for the red snapper (*Lutjanus campechanus*), an indeterminate spawner. These estimates were based on 923 females sampled during February 1991 through November 1993, from northwest Florida landings. Spawning occurred from May through September or early October. Oocytes >0.16 mm in diameter were homogeneously distributed in hydrated ovaries. The smallest (349 mm total length (TL) and 0.60 kg total weight (TW)) female contained 458 hydrated oocytes, while the largest (820 mm TL and 9.00 kg TW) and oldest (age 12 years) female contained 1 704 736 hydrated oocytes. Batch fecundity was predicted well by age ($r^2=0.642$) and TL ($r^2=0.584$). Estimates of the spawning frequency were 26 in 1991, 21 in 1992, and 35 in 1993. Estimates of annual fecundity ranged from 0.012 to 59.666 million per female, assuming that spawning frequency was constant for all sizes/ages. However, estimates of spawning frequency by age for $n>11$ suggested that age 8 females spawn more often than age 3, 4, 5 and 6 females. Previous estimates of annual fecundity (based on number of oocytes ≥ 20.20 mm in diameter) were strongly correlated with improved estimates incorporating batch fecundity and spawning frequency methods (based on number of hydrated oocytes). This relationship was described by the equation: improved annual fecundity estimate = $(5.401 \cdot \text{previous annual fecundity estimate}) + 2.054 \cdot 10^5$ ($r^2 = 0.956$; $n = 21$; TL range from 349 to 810 mm). This equation will allow adjustment of previous fecundity estimates, making previous spawning potential ratios more accurate and useful.

Resumen

El presente trabajo tiene por objeto proporcionar información sobre desove y fecundidad anual del pargo del Golfo (*Lutjanus campechanus*) utilizando un método de pulsos de fecundidad y un método de frecuencia de desove. Estas estimaciones fueron basadas en 923 hembras muestreadas en el periodo de febrero 1991 hasta Noviembre de 1993, de desembarques al noroeste de Florida. Los desoves ocurrieron

de Mayo a Septiembre-inicio de Octubre. Los oocitos mayores de 0.16 mm de diámetro estaban homogéneamente distribuidos en ovarios hidratados. Las hembras más pequeñas (349 mm de longitud total (LT) y 0.60 kg de peso total (PT)) presentaron 458 oocitos hidratados, mientras que las hembras más grandes (820 mm LT y 9.0 kg PT) y más viejas (12 años de edad) presentaron 1 704 736 oocitos hidratados. Las estimaciones de frecuencia de desove fueron 26 en 1991; 21 en 1992 y 35 en 1993. Las estimaciones de fecundidad anual variaron de 0.012 a 59.666 millones por hembra, suponiendo que la frecuencia de desove fué constante para todas las tallas/edades. Sin embargo, la frecuencia de desove por edad sugiere que las hembras de 8 años de edad desovan más a menudo que las hembras de edades 3, 4, 5 y 6 años. Estimaciones previas de fecundidad anual (basada en el número de oocitos (≥ 0.20 mm de diámetro) fueron fuertemente correlacionadas con las estimaciones mejoradas incorporando los métodos de fecundidad por pulsos y frecuencia de desove (basados en el número de oocitos hidratados). Esta relación fué descrita por la ecuación: estimación mejorada de la fecundidad anual = $(5.401 \cdot \text{estimación previa de la fecundidad anual}) + 2.054 \cdot 10^6$ ($r^2=0.956$; $n=21$; LT variando de 349 a 810 mm). Esta ecuación permitirá ajustar las estimaciones previas de fecundidad, haciendo que las relaciones de desove sean más precisas y útiles.

Introduction

The red snapper (*Lutjanus campechanus*) is one of many valuable marine fish species of the southeastern United States for which there is inadequate information on reproduction. Information on spawning and annual fecundity are needed to assess the status of stocks. Minimum target level spawning potential ratios (SPRs) are used to assure maintenance of an adequate spawning stock. Accurate estimation of SPR requires the number of spawns per year by age (GMFMC 1989). Fecundity and sexual maturity estimates are important in population dynamics (Hunter et al. 1992). Age/size at maturity and spawning are other aspects of reproduction that are useful for management.

Red snapper occur only along the continental shelf of the Atlantic coast of the US and the Gulf of Mexico (Briggs 1958). Commercial landings of red snapper in the US have been generally declining since 1983 and a closure of this fishery occurred in 1991, 1992 and 1993 (Bennett 1993).

Although estimates of fecundity for red snapper have been developed (Collins et al. unpubl.) and published (Grimes 1987), their accuracy is now questionable given recent developments in methods of estimating batch fecundity and spawning frequency (Hunter et al. 1985; Hunter and

Macewicz 1985). However, these previous estimates were considered to be the best available (Nelson 1988) and were used for red snapper stock assessment (Goodyear and Phares 1990).

This paper provides the first estimates of red snapper annual fecundity using batch fecundity/spawning frequency methods. Information on sex ratio, spawning frequency by age, and length/age at spawning is also given. In addition, an analysis of the relationship between previous and improved estimates provides a means to judge the accuracy of past SPRs, calculated using previous estimates of fecundity, as well as a formula for adjusting those estimates.

Methods

Red snapper were sampled mainly from recreational and commercial landings in Panama City, Florida. Fork length (FL) and total length (TL) were measured to the nearest cm or mm, and total wet weight (TW) was usually taken to the nearest 0.01 kg for each fish sampled. Gonads were removed and placed dry into plastic bags and stored on ice. Also, a sagittal otolith was removed and stored dry for ageing.

Gonads were processed as soon as possible in the laboratory. Excess tissue was removed and a small sample of each gonad was microscopically examined before

preservation. Preliminary sex and maturation stage were assigned, and a maximum oocyte diameter recorded for females in order to compare these data with those from histology. Gonad weight was recorded to the nearest 0.1 g before selected gonads were preserved in a plastic bag with 5-10 times the gonad's volume of 10% buffered histological grade formalin. Large gonads were usually cut longitudinally to promote preservation.

We tested for homogeneity of oocyte diameter distributions throughout the ovary with the Kolmogorov-Smirnov test (Sokal and Rohlf 1981). This was done to allow selection of a single sample within an ovary for accurate determination of maturation stage and batch fecundity. Three late-stage ovaries were divided into 6 regions and a wedge-shaped sample was cut out in cross section to represent the periphery and center of each region. We teased apart all oocytes in each sample and measured the diameter of 300+ randomly selected oocytes in each region.

We also tested for differences in hydrated oocyte counts among regions and between lobes with an analysis of variance (SAS 1988). Six hydrated ovaries were divided into 6 regions and wedge-shaped samples taken as above.

A simple gonadosomatic index ($GSI = (\text{gonad weight}/\text{total weight}) \times 100$) was used to generally delineate the spawning season by month. We also looked for relationships between length and GSI, since they are usually related allometrically (deVlaming et al. 1982).

Late-stage ovaries selected from the microscopic examination of fresh, whole oocyte samples were prepared for final sexing and staging through histology. Histological preparation (after the selected ovaries had been fixed in formalin for at least 2 weeks) was identical to that described by Fitzhugh et al. (1993). Ovarian stage judged from the most advanced stage of oocytes recorded from both the fresh material and histological

slides was: 1-primary growth, 2-cortical alveolar, 3-vitellogenic, and 4-hydrated (Wallace and Selman 1981) and 5-spent (West 1990). Only Stage 4 ovaries, with no postovulatory follicles, were selected for fecundity estimation.

Ovaries selected for fecundity estimation were randomly sampled as follows. A wedge-shaped sample representing the periphery and center of each ovary in cross sections was weighed to the nearest 0.001 g and placed in a 2 dram vial with 33% glycerol. Sample size was usually 0.1-0.3 g. After at least 2 hours, the hydrated oocytes within the sample were carefully separated with teasing needles. We made at least two independent counts of all hydrated oocytes on each selected sample and used the mean as the final estimate. The batch fecundity estimate (BFE) was calculated gravimetrically, by multiplying the final estimate of the number of hydrated oocytes by the weight of the whole ovary, then dividing this product by the sample weight. Batch fecundity was regressed on TL, TW and age for all hydrated ovaries (SAS 1988).

The spawning frequency estimate (SFE), required for calculating annual fecundity (Hunter and Macewicz 1985), was found by dividing the duration of the spawning season (DOSS) in days by the number of days between spawning for all females. DOSS was the number of days between the first and last occurrence of hydrated oocytes or postovulatory follicles each year. The number of days between spawning for all females ($\geq TL$ of the smallest hydrated fish) was 100% divided by the percentage of hydrated females. SFE is the number of times that the species spawned each year.

Age was determined from sections of sagittal otoliths following the method of Johnson (1983). Nelson (1980) validated rings on red snapper otoliths as annular marks.

Spawning frequency by age was estimated using 1993 females $\geq TL$ of the smallest

hydrated female. As with the SFE, only females collected during the spawning season were included for this estimate.

The relationship between previous and improved annual fecundity estimates was determined. Previous estimates were represented by counts of all yolked oocytes (≥ 0.20 mm) from some of the same ovaries from which improved estimates were made. The previous method's formula was annual fecundity = (number of oocytes ≥ 0.20 mm \times ovary weight)/sample weight. To determine the relationship between the two estimates of fecundity, we regressed the improved estimate on the previous estimate using SAS (1988).

Results

A total of 1 475 red snapper gonads were sampled from northwest Florida waters during February 1991 through November 1993. Most fish came from charterboats during the summer months. The largest portion of fish (629, or 43%) was collected in 1993 when we sampled almost daily most of the summer, while 484 (33%) were sampled in 1992, and 362 (24%) in 1991. Sampling in 1991 was biased toward females, but

unbiased sampling in 1992 and 1993 showed 59% and 50% females, respectively.

Most fish were caught, iced, landed and sampled the same day, which allowed adequate preservation of gonads. Preservation of gonads in formalin usually occurred within 12 to 48 hours of the fish's death.

Red snapper spawned serially from May-June through September-early October, according to GSIs (Fig. 1 and Tables 1 and 2). Peaks of spawning apparently occurred in June, July and August. Monthly mean-GSIs were similar in each of the 3 years, except for females in June 1993, when the estimate was much higher than the 1991 and 1992 values. The greater mean GSI in June 1993 was explained by the fact that significantly larger females were sampled in June 1993 (mean TL = 528 mm) than in June 1991 (mean TL = 389 mm) and June 1992 (mean TL = 433 mm).

Examinations of gonads revealed that red snappers are gonochorists. The lobes of the ovaries and testes were symmetrical. Large amounts of adipose tissue were usually attached to both ovaries and testes.

The test for homogeneity of oocyte diameter distributions throughout each of 3 hydrated ovaries showed no significant differences for oocytes > 0.16 mm in diameter (Tables 3 and 4). This result allowed

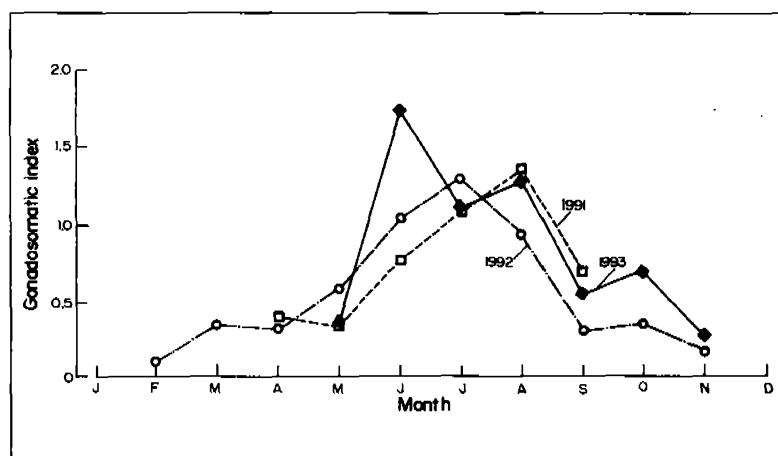


Fig. 1. Mean GSI of female red snapper from the NE Gulf of Mexico, 1991-1993. N = 646 (months with n > 10). [Indice gonadosomático (GSI) medio de hembras de pargo del Golfo del noreste del Golfo de México, 1991-1993. N = 646; meses con n > 10.]

Table 1. Gonosomatic index (GSI) and total length (TL in mm) for female red snapper by month, 1991-1993; s.d. = standard deviation, c.v. = coefficient of variation, N = number of individuals. [*Indice gonadosómico (GSI) y longitud total (TL, en mm) para hembras de pargo del Golfo, por mes, durante 1991-1993; s.d. = desviación estandar; c.v. = coeficiente de variación, N = numero de individuos.*]

Year	Month											
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	N
1991												
n	0	1	8	35	39	16	24	24	10	6	5	168
Min GSI	-	1.09	0.13	0.03	0.04	0.11	0.10	0.09	0.07	0.15	0.10	
Max GSI	-	1.09	0.93	1.77	4.21	3.69	2.71	3.13	2.03	0.59	0.81	
Mean GSI	-	1.09	0.43	0.39	0.34	0.78	1.09	1.36	0.71	0.35	0.35	
s.d.	-	-	0.26	0.29	0.67	1.00	0.90	0.87	0.75	0.15	0.28	
c.v.	-	-	59.12	74.36	199.39	128.41	82.12	64.25	106.10	43.46	82.41	
Min TL	-	795	460	350	330	340	350	350	305	355	357	
Max TL	-	795	710	670	740	550	560	640	550	630	580	
Mean TL	-	795	567	460	454	389	462	482	436	484	469	
s.d.	-	-	87.05	61.72	81.27	67.77	57.38	66.18	73.88	94.47	83.77	
c.v.	-	-	15.36	13.42	17.89	17.41	12.43	13.74	16.96	19.51	17.85	
1992												
n	0	10	17	16	16	22	25	33	32	12	26	209
Min GSI	-	0.04	0.10	0.09	0.07	0.03	0.19	0.14	0.11	0.18	0.03	
Max GSI	-	0.26	0.55	0.75	2.25	2.93	3.41	2.62	2.37	0.78	0.72	
Mean GSI	-	0.11	0.34	0.31	0.59	1.04	1.29	0.94	0.31	0.36	0.18	
s.d.	-	0.06	0.15	0.18	0.62	0.91	1.01	0.77	0.40	0.18	0.15	
c.v.	-	57.49	42.55	57.94	105.50	87.75	78.05	82.12	128.80	51.63	83.82	
Min TL	-	359	336	366	355	331	358	342	359	393	336	
Max TL	-	638	730	654	607	785	810	736	651	709	662	
Mean TL	-	427	546	497	429	433	469	497	444	516	433	
s.d.	-	79.83	109.11	90.91	79.74	114.37	116.62	114.28	63.72	114.53	77.44	
c.v.	-	18.69	19.98	18.30	18.59	26.44	24.85	22.97	14.35	22.18	17.88	
1993												
n	2	0	3	7	39	44	57	40	56	31	19	298
Min GSI	0.14	-	0.29	0.20	0.07	0.04	0.08	0.19	0.07	0.14	0.06	
Max GSI	0.43	-	0.60	0.34	2.05	10.09	4.83	7.21	2.41	2.08	0.61	
Mean GSI	0.29	-	0.43	0.27	0.36	1.74	1.11	1.28	0.56	0.71	0.28	
s.d.	0.21	-	0.16	0.05	0.40	2.17	1.20	1.52	0.57	0.42	0.17	
c.v.	72.62	-	36.37	18.06	109.76	125.17	108.89	119.17	100.49	58.44	62.20	
Min TL	455	-	431	372	334	320	326	345	335	366	325	
Max TL	710	-	575	715	642	869	852	750	744	741	692	
Mean TL	583	-	506	464	431	528	477	469	463	543	474	
s.d.	180.31	-	72.19	114.23	68.08	141.43	140.24	94.26	94.19	109.69	93.76	
c.v.	30.96	-	14.27	24.64	15.81	26.78	29.40	20.10	20.33	20.21	84.73	
1991-93N	2	11	28	58	94	82	106	97	98	49	50	675

Table 2. Gonadosomatic index (GSI) and total length (TL in mm) for male red snapper by month, 1991-1993; s.d. = standard deviation, c.v. = coefficient of variation, N = number of individuals. [Indice gonadosomático (GSI) y longitud total (TL, en mm) para machos de pargo del Golfo, por mes durante 1991-1993, s.d. = desviación estándar; c.v. = coeficiente de variación, N = numero de individuos.]

Year	Month												N
	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov		
1991													
n	0	0	1	14	1	0	0	0	0	0	0	0	16
Min GSI	-	-	0.17	0.04	0.26	-	-	-	-	-	-	-	-
Max GSI	-	-	0.17	0.51	0.26	-	-	-	-	-	-	-	-
Mean GSI	-	-	0.17	0.19	0.26	-	-	-	-	-	-	-	-
s.d.	-	-	-	0.17	-	-	-	-	-	-	-	-	-
c.v.	-	-	-	88.90	-	-	-	-	-	-	-	-	-
Min TL	-	-	630	386	440	-	-	-	-	-	-	-	-
Max TL	-	-	630	570	440	-	-	-	-	-	-	-	-
Mean TL	-	-	630	454	440	-	-	-	-	-	-	-	-
s.d.	-	-	-	44.06	-	-	-	-	-	-	-	-	-
c.v.	-	-	-	9.71	-	-	-	-	-	-	-	-	-
1992													
n	0	1	3	1	13	21	22	15	26	8	7	117	
Min GSI	-	0.04	0.09	0.70	0.02	0.02	0.05	0.05	0.05	0.04	0.03	0.02	-
Max GSI	-	0.04	0.22	0.70	1.33	3.81	1.86	1.65	1.20	0.40	0.10	-	-
Mean GSI	-	0.04	0.17	0.70	0.43	0.56	0.48	0.41	0.24	0.15	0.06	-	-
s.d.	-	-	0.07	-	0.43	0.88	0.49	0.44	0.27	0.13	0.03	-	-
c.v.	-	-	43.26	-	101.23	158.11	101.46	108.78	110.62	85.07	52.79	-	-
Min TL	-	652	406	733	332	330	345	365	342	306	354	-	-
Max TL	-	652	574	733	702	750	780	709	590	735	448	-	-
Mean TL	-	652	504	733	513	466	430	491	461	581	418	-	-
s.d.	-	-	87.43	-	129.55	110.79	99.69	111.12	60.71	152.47	35.88	-	-
c.v.	-	-	17.35	-	25.25	23.79	23.16	22.64	13.16	26.24	8.58	-	-
1993													
n	3	1	1	3	25	33	59	59	47	46	16	293	
Min GSI	0.03	0.04	0.05	0.03	0.03	0.05	0.03	0.04	0.06	0.04	0.05	-	-
Max GSI	0.23	0.04	0.05	0.09	0.61	3.17	4.46	3.91	2.77	1.35	0.24	-	-
Mean GSI	0.15	0.04	0.05	0.06	0.18	0.60	0.63	0.57	0.63	0.53	0.11	-	-
s.d.	0.11	-	-	0.03	0.15	0.75	0.85	0.67	0.75	0.32	0.06	-	-
c.v.	71.01	-	-	46.11	85.24	124.02	135.23	116.84	118.26	61.04	55.65	-	-
Min TL	515	790	511	358	350	350	316	336	327	247	345	-	-
Max TL	703	790	511	478	700	792	744	676	695	870	592	-	-
Mean TL	593	790	511	423	464	479	453	463	465	510	484	-	-
s.d.	98.17	-	-	60.71	77.97	92.13	106.83	94.43	93.60	132.94	74.89	-	-
c.v.	16.56	-	-	14.34	16.80	19.23	23.57	20.40	20.15	26.06	15.47	-	-
1991-93 N	3	2	5	18	39	54	81	74	73	54	23	426	

us to sample just one location on each ovary to determine maturation stages and maximum oocyte diameter.

Hydrated oocyte counts per unit of weight did not differ significantly by region or lobe (Table 5). The 6 ovaries selected for this ANOVA represented June through October, 1993.

Percentage frequencies of 588 Stage 1-4 ovaries (unpreserved, examined microscopically) varied by month (Fig. 2 and Table 6) and basically showed the same spawning peaks as had GSI. Stage 1-2 ovaries were prominent in January through May, and November. Stage 3 ovaries were found from May through November. Stage 4 ovaries occurred from May through September or October, but were most prominent in June through September.

Means of maximum oocyte diameter for 576 ovaries indicated that spawning occurred from June through October (Fig. 3 and Table 6). Greatest means of maximum oocyte diameter were 0.51, 0.67 and 0.55 in June, July and August of 1992, respectively.

A total of 237 Stage 3-4 ovaries was examined histologically from red snapper collected during the period May 1991 through October 1993. Physical appearance of Stage 1-4 oocytes was identical to those of sheepshead described and illustrated by Render and Wilson (1992). Only one ovary with fresh postovulatory follicles was found, in June 1992. Sixty-six ovaries weighing 1.2 to 908 g were hydrated and intact, and thus were used for BFEs (Table 7). These BFE fish were 349 to 820 mm TL, 0.60 to 9.10 kg TW and, age 3 to 12 years old. Early stage hydrated (including yolk coalescence) and late stage hydrated oocytes were included in Stage 4 ovaries used for BFEs. Atresia of yolked oocytes occurred in many Stage 4 ovaries; this may have been an effect of delayed preservation.

Batch fecundity estimates (BFEs) ranged from 458 to 1 704 736, for the smallest and largest fish, respectively (Table 7). BFEs

by year were not significantly different ($F = 1.43$, $p = 0.237$), therefore data for all years were combined for analysis. TL, TW and age all proved to be useful predictors of batch fecundity, with simple linear models providing the best fits. These relationships were described by the following equations:

$$\text{BFE} = (1.949 \times 10^3(\text{TL})) - 8.055 \times 10^5 \\ (r^2 = 0.584);$$

$$\text{BFE} = (1.363 \times 10^5(\text{TW})) - 1.315 \times 10^5 \\ (r^2 = 0.741); \text{ and}$$

$$\text{BFE} = (1.278 \times 10^5(\text{AGE})) - 4.375 \times 10^5 \\ (r^2 = 0.642);$$

with TL in mm, TW in kg and age in years.

SFEs per year ranged from 21 to 35 (Table 7). The smallest hydrated females were 400, 362 and 344 mm TL in 1991, 1992 and 1993, respectively. Percentage of hydrated females was 25.2, 16.8 and 22.7 in 1991, 1992 and 1993, respectively. Days between spawning were 3.97, 5.95 and 4.41 in 1991, 1992 and 1993, respectively. DOSS was 102, 119 and 154 in 1991, 1992 and 1993, respectively. All estimates for 1993 are probably the most accurate because of the greater sampling intensity during that year.

Annual fecundity estimates ranged from 11 613 to 59 665 760 assuming that SFE was the same for all females by year (Table 7). Again, 1993 estimates are probably the most accurate.

We aged 502 of 526 red snapper of both sexes collected in 1993. The remaining fish had confusing marks.

Estimates of SFE by age were made with all aged females ≥ 344 mm TL collected from 2 May through 3 October 1993 (Table 8). A comparison of samples with $n > 10$ was possible for only ages 3, 4, 5, 6, and 8. The SFE for ages 3, 4, 5, and 6 were 28, 30, 41 and 14, respectively. The SFE for age 8 was 112. Sample size was much greater for ages 3-5 ($n > 43$) than for age 6 and 8 ($n = 11$), however.

The relationship between AFEs using previous (Collins et al., unpubl.) and improved (Hunter et al. 1985) methods was determined

Table 3. Oocyte diameter frequency distributions by region of red snapper for two fully hydrated ovaries (I and II) and one partially hydrated ovary (III). Oocyte diameter given as ocular micrometer units (OMU = 0.04 mm). [Distribución de frecuencia del diámetro de los oocitos por región de ovarios de pargo del Golfo para dos ovarios totalmente hidratados (I y II), y un ovario parcialmente hidratado (III). El diámetro de los oocitos está dado en unidades de micrómetro ocular (OMU). (Un OMU=0.04 mm).]

OMU	I						II						III					
	A ^a	B	C	D	E	F	A	B	C	D	E	F	A	B	C	D	E	F
1	69	73	79	65	82	69	82	72	73	59	102	67	51	93	93	101	105	57
2	127	104	99	117	101	97	83	100	101	98	102	78	66	51	66	97	64	91
3	43	45	43	61	60	40	36	22	31	34	22	25	81	64	60	53	60	24
4	10	21	21	21	18	12	17	8	14	14	9	16	30	50	32	16	19	9
5	14	10	9	8	14	17	16	9	15	16	9	10	31	15	5	10	7	4
6	5	10	5	12	7	10	14	10	18	9	8	10	3	6	6	5	8	5
7	12	8	2	2	13	6	12	14	12	11	8	17	9	4	4	2	2	9
8	9	2	3	1	6	7	22	28	17	11	13	21	4	4	4	3	2	14
9	12	2	9	8	2	6	12	17	8	14	14	14	5	1	4	5	4	12
10	12	4	12	2	6	17	4	16	16	3	10	11	12	1	7	3	7	21
11	9	6	5	3	7	6	9	4	8	5	4	18	4	7	8	3	9	25
12	3	1	3	2	3	1	4	8	4	3	3	3	10	1	8	3	10	21
13	1	0	1	1	0	1	4	5	0	0	1	3	3	2	3	0	2	6
14	0	0	1	0	0	1	4	5	5	3	1	2	0	0	0	0	1	2
15	0	0	1	0	1	0	12	11	14	8	9	16	0	0	0	0	0	0
16	0	0	2	0	1	0	4	10	10	7	4	9	0	0	0	0	0	0
17	1	3	2	0	0	2	6	13	7	9	9	9	0	1	0	0	0	0
18	3	1	0	2	2	1	2	4	2	9	8	2	0	0	0	0	0	0
19	4	3	3	5	3	3	1	3	5	1	2	2	0	0	0	0	0	0
20	5	2	2	6	7	2	0	0	0	0	0	2	0	0	0	0	0	0
21	6	2	1	1	3	1	0	0	0	0	0	0	0	0	0	0	0	0
22	2	2	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Total ^b	347	301	305	318	336	300	344	359	360	314	338	335	309	300	300	301	300	300

^aOvary regions:

A = right lobe, anterior one-third

D = left lobe, anterior one-third

B = right lobe, middle one-third

E = left lobe, middle one-third

C = right lobe, posterior one-third

F = left lobe, posterior one-third

^bNumber of oocytes sampled.

Table 4. Regions of three red snapper ovaries where significantly different oocyte diameter frequencies were found by the Kolmogorov-Smirnov test. See previous table for location of regions. One OMU = 0.04 mm. [Regiones de tres ovarios de pargo del Golfo donde se encontraron diferencias significativas en la frecuencia del diámetro de los oocitos, al aplicar la prueba de Kolmogorov-Smirnov. Ver tabla anterior para localización de las regiones. Un OMU= 0.04 mm.]

OMU	I (fully-hydrated)	II (fully-hydrated)	III (partially-hydrated)		
			$d_{0.05}$	d	
1	None	D vs E $(d^{0.05} = 0.1064,$ $d = 0.1139)$	A vs B	0.1103	0.1450
-	-	-	A vs C	0.1103	0.1450
-	-	-	A vs D	0.1100	0.1705
-	-	-	A vs E	0.1034	0.1850
-	-	-	C vs F	0.1103	0.1200
-	-	-	D vs F	0.1108	0.1455
-	-	-	E vs F	0.1103	0.1600
2	None	None	B vs D	0.1108	0.1523
3	None	None	A vs F	0.1103	0.1821
-	-	-	C vs F	0.1103	0.1200
4	None	None	B vs F	0.1103	0.1367
5-27	None	None	None	-	-

Table 5. Effect of location of red snapper tissue samples for hydrated oocyte counts per unit of weight (g). Locations are anterior (1), middle (2), and posterior (3) of ovarian lobes. Analysis of variance indicates significance of location within a lobe for number of hydrated oocytes per gram of tissue. [Efecto de la localización de las muestras del tejido del pargo del Golfo para conteo de oocitos hidratados por unidad de peso (g). Las localizaciones fueron anterior (1), media (2), y posterior (3) de los lóbulos ováricos. El análisis de varianza indica significancia de localización dentro de un lóbulo para el número de oocitos hidratados por gramo de tejido.]

Positions of sample in ovary	Mean number and standard deviation of oocytes per gram of ovarian tissue								
	Lobe 1			Lobe 2			Both lobes		
	X	s.d.	n	X	s.d.	n	X	s.d.	n
1	2 333	767	6	2 427	792	6	2 380	745	12
2	2 357	887	6	2 454	942	6	2 405	874	12
3	2 423	856	6	2 387	782	6	2 405	782	12
Total	2 371	788	18	2 423	791	18	2 379	779	(36)

ANOVA of oocytes/gram of ovarian tissue.

Source	df	SS	MS	F	PR>F
Lobe 1 vs 2	1	23 883.54	23 883.54	0.04	0.85
Region	11	3 616.64	3 616.64	0.01	0.94
Interaction	1	25 206.79	25 206.79	0.04	0.85
Error	32	21 173 908.34	661 684.84	-	-
Total	35	21 226 615.31	-	-	-

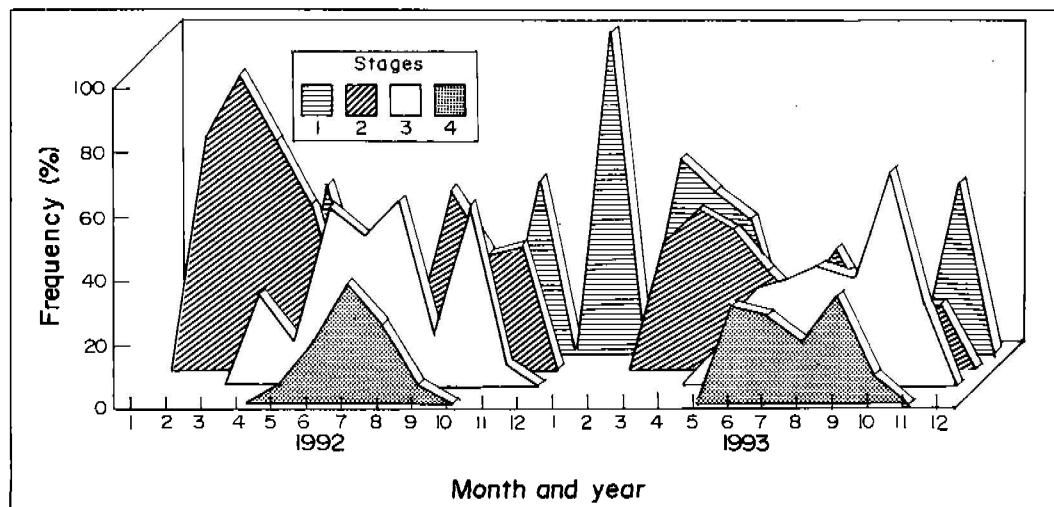


Fig. 2. Percentage frequency of red snapper ovary stages, 1992 (N=275) and 1993 (N=313). [Frecuencia porcentual de los diferentes estadios de desarrollo de los ovarios de pargo del Golfo, 1992 (N=275) y 1993 (N=313).]

Table 6. Relative frequency in % of female red snapper by maturation stage and maximum oocyte diameter from microscopic examination of unpreserved, whole oocytes by month for 1992 and 1993. [Frecuencia porcentual del estado de maduración de hembras, y diámetro máximo del oocito, del examen microscópico de oocitos completos sin preservar, por mes, para 1992 y 1993.]

Month/year	Stage				N	\bar{x}	s.d.	N
	1	2	3	4				
Jan '92	-	-	-	-	0	-	-	0
'93	100	0	0	0	2	0.12	0	2
Feb '92	27	73	0	0	33	0.18	0.08	31
'93	-	-	-	-	0	-	-	0
Mar '92	8	92	0	0	24	0.13	0.06	21
'93	60	40	0	0	5	0.22	0.13	5
Apr '92	0	71	29	0	17	0.25	0.17	15
'93	50	50	0	0	8	0.15	0.05	8
May '92	29	52	14	5	21	0.29	0.18	21
'93	42	44	12	2	43	0.22	0.20	42
Jun '92	6	19	56	19	32	0.51	0.21	32
'93	9	31	29	31	45	0.48	0.27	44
Jul '92	0	15	47	38	34	0.67	0.20	33
'93	18	22	32	28	60	0.47	0.23	60
Aug '92	3	14	58	25	36	0.55	0.18	36
'93	5	38	38	19	42	0.41	0.21	42
Sep '92	22	56	17	6	36	0.31	0.23	36
'93	14	18	34	34	56	0.45	0.25	56
Oct '92	7	36	57	0	14	0.38	0.21	13
'93	6	18	67	9	33	0.47	0.21	33
Nov '92	54	39	7	0	28	0.15	0.11	27
'93	53	21	26	0	19	0.22	0.20	19
Dec '92	-	-	-	-	0	-	-	0
'93	-	-	-	-	0	-	-	0
All '92	16	44	28	12	275	-	-	265
'93	20	28	31	20	313	-	-	311

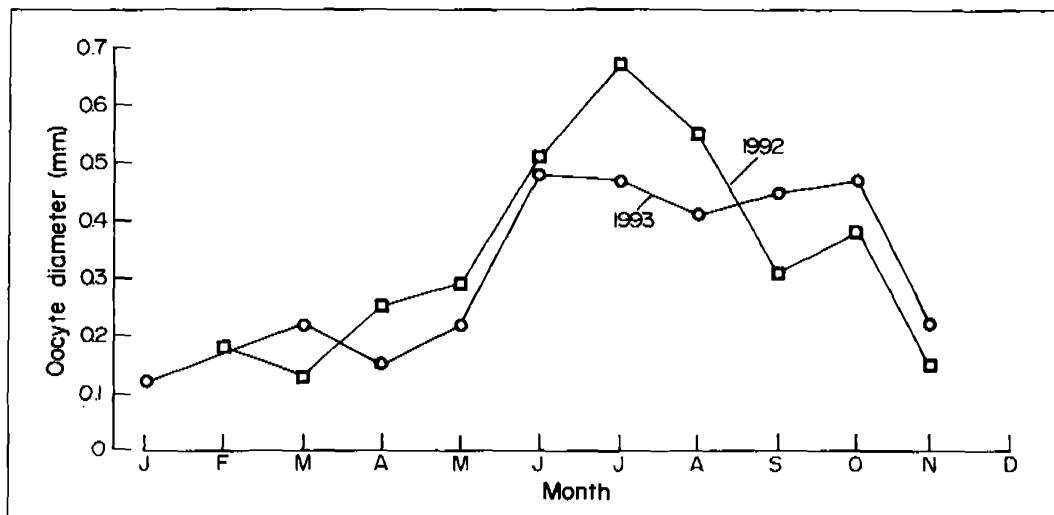


Fig. 3. Mean maximum oocyte diameter of red snapper, 1992 (N=265) and 1993 (N=311). [Diámetro máximo promedio (en mm) de los oocitos del pargo del Golfo, 1992 (N=265) y 1993 (N=311).]

from 21 fish from 349 to 810 mm TL (Table 9). This relationship was: Improved AFE = $(5.401 \cdot \text{previous AFE}) + 2.054 \cdot 10^5$ ($r^2 = 0.956$). Since previous AFEs are strongly correlated to improved AFEs, adjustments can now be made on previous AFEs to improve stock assessments. However, an assumption of no significant difference in AFE between years would have to be made in order to make these adjustments to previous years' AFEs.

Discussion and Recommendations

Dockside sampling of charterboat catches provided an adequate first measurement of red snapper spawning and annual fecundity off northwest Florida. The delay in preserving gonads was necessary because of the need to examine unpreserved material (to inspect and measure the oocytes before they were affected by formalin), and the fact that periodic backups in processing occurred with our intensive sampling.

Intensive sampling at sea with rapid examination and preservation of ovaries is needed

to identify spawning time and better define rates of ovarian development and atresia for red snapper. This species probably spawns at night (Grimes 1987; B. Thompson, pers. comm.), which could explain why ovaries in our collections used for BFE had both early and late hydration. The charterboats usually fished throughout the day and landed their catch in the late afternoon. Spawning of red snapper may occur in the early evening off northwest Florida, since more than half of the ovaries used for BFE were late-stage hydrated. Post-ovulatory follicles apparently deteriorated rapidly after spawning.

Studies are also needed on large numbers of large, old snappers to better estimate annual fecundity and frequency of spawning. Fish of this greater size are not common off northwest Florida, but are relatively common off Louisiana.

Acknowledgements

We thank many individuals in the Panama City, Florida, area for allowing us to sample their catch, in particular commercial Captains Sigurd Smeby, Mark Raffield, Mike

Table 7. Data used for red snapper annual fecundity estimates (AFEs), 1991-1993.
[Datos usados para la estimación de fecundidad anual del pargo del Golfo (AFEs), 1991-1993.]

Date dd/mm/yy	Length TL (mm)	Weight (kg)	Age (years)	Ovary weight (g)	Counts of hydrated oocytes			B F E	S F E	A F E
					n	mean	s.d.			
19/06/91	420	2.10	4	35.7	3	1 238	76	155	622	26 4 046 172
06/07/91	440	1.30	5	32.9	5	546	49	117	408	26 3 052 608
14/07/91	470	1.40	4	32.8	3	330	57	82	000	26 2 132 000
26/07/91	450	1.10	3	28.6	3	469	117	74	107	26 1 926 782
04/08/91	440	1.40	4	28.9	3	640	55	117	809	26 3 063 034
04/08/91	470	1.70	5	24.5	4	539	177	83	053	26 2 159 378
09/08/91	400	1.10	3	3.9	3	31	16	1	950	26 50 700
09/08/91	470	1.50	3	18.1	3	683	40	75	380	26 1 959 880
09/08/91	480	1.60	5	50.0	3	950	62	165	505	26 4 303 130
07/09/91	420	1.00	3	33.1	3	484	35	103	357	26 2 687 282
28/05/92	418	0.84	-	5.4	3	50	16	8	710	21 182 910
11/06/92	525	2.00	-	131.4	3	497	64	349	229	21 7 333 809
15/06/92	580	3.10	4	150.8	2	1 834	26	397	938	21 8 356 698
20/06/92	362	0.70	3	4.5	3	79	11	10	456	21 219 576
27/06/92	665	4.65	8	72.2	3	325	46	153	366	21 3 220 686
09/07/92	475	1.70	4	43.5	3	743	95	176	615	21 3 708 915
11/07/92	380	-	-	4.0	3	29	21	1	902	21 39 942
18/07/92	475	1.22	4	33.2	3	652	55	117	643	21 2 470 503
18/07/92	431	1.04	4	27.1	3	557	41	75	098	21 1 577 058
18/07/92	810	8.85	9	302.1	5	468	42	817	242	21 17 162 082
19/07/92	606	2.90	5	60.0	2	1 516	86	236	875	21 4 974 375
01/08/92	362	0.80	3	4.1	3	45	1	5	766	21 121 086
12/09/92	651	3.88	6	92.1	3	734	62	254	141	21 5 336 961
23/09/92	426	1.25	5	4.9	3	7	2	553	-	21 11 613
15/06/93	692	5.00	8	180.0	2	1 067	61	741	544	35 25 954 040
15/06/93	718	5.50	-	197.7	2	743	21	676	918	35 23 692 130
15/06/93	820	9.00	12	908.2	3	687	57	1 704	736	35 59 665 760
22/06/93	435	1.30	3	22.7	2	773	14	74	669	35 2 613 415
22/06/93	445	1.30	5	18.5	2	578	30	70	349	35 2 462 215
23/06/93	645	3.80	10	168.5	2	764	30	531	959	35 18 618 565
24/06/93	765	9.10	10	546.5	3	882	139	1 456	499	35 50 977 465
26/06/93	425	1.20	4	13.4	2	668	54	53	600	35 1 876 000
27/06/93	430	1.00	4	4.2	3	450	107	6	279	35 219 765
06/07/93	541	2.40	4	35.0	3	689	115	141	023	35 4 935 805
06/07/93	648	3.75	4	84.4	3	746	47	234	061	35 8 192 135
11/07/93	708	4.60	8	173.9	2	789	15	766	520	35 26 828 200
11/07/93	787	6.30	8	302.2	3	759	125	697	173	35 24 401 055
12/07/93	485	1.50	4	43.6	3	459	45	122	775	35 4 297 125
12/07/93	505	1.50	5	72.5	3	815	61	252	511	35 8 837 885
18/07/93	395	0.90	4	6.7	3	567	56	22	087	35 773 045
18/07/93	407	1.00	3	11.7	2	342	35	42	120	35 1 474 200
24/07/93	538	2.35	5	16.0	2	237	1	37	920	35 1 327 200
24/07/93	704	4.80	8	117.4	2	535	13	269	567	35 9 434 845
29/07/93	655	4.90	8	81.1	2	413	30	178	161	35 6 235 635
09/08/93	410	0.80	3	13.5	3	424	10	48	923	35 1 712 305
14/08/93	640	3.80	-	136.4	2	791	23	531	490	35 18 602 150
28/08/93	553	2.55	5	26.4	2	530	18	39	525	35 1 383 375
28/08/93	349	0.60	-	1.2	2	37	3	458	-	35 16 030
01/09/93	504	2.10	4	15.3	3	184	19	25	828	35 35 903 980
04/09/93	428	1.20	4	13.4	2	469	38	44	890	35 1 571 150
04/09/93	362	0.75	-	2.9	3	195	22	3	512	35 122 920
11/09/93	419	1.20	5	11.2	3	416	37	31	061	35 1 087 135
15/09/93	530	2.30	-	36.6	2	616	43	131	846	35 4 614 610
15/09/93	479	1.59	-	18.6	2	467	29	55	681	35 1 948 835
15/09/93	454	1.40	4	6.3	3	162	22	13	608	35 476 280
15/09/93	455	1.36	-	26.0	3	567	85	108	397	35 3 793 895
17/09/93	515	1.78	-	23.5	2	498	6	70	927	35 2 482 445
18/09/93	413	1.05	4	4.6	3	120	13	5	633	35 197 155
21/09/93	744	4.90	6	118.1	2	523	1	383	642	35 13 427 470
25/09/93	370	0.60	-	7.1	2	409	14	22	338	35 781 830
25/09/93	456	1.30	4	3.4	2	82	0	1	991	35 69 685
29/09/93	376	0.70	3	3.6	2	283	16	10	396	35 363 860
01/10/93	615	3.50	5	38.2	2	256	27	72	979	35 2 554 265
01/10/93	540	2.30	4	30.5	3	198	27	45	067	35 1 577 345
01/10/93	408	1.10	3	6.3	2	203	18	12	662	35 443 170
03/10/93	705	5.00	8	23.1	2	42	1	10	002	35 350 070

Table 8. Spawning frequency estimates by age of female red snapper with hydrated oocytes from 2 May 1993 to 3 October 1993. [Estimación de la frecuencia de desove por edad de las hembras más pequeñas de pargo del Golfo con oocitos hidratados, de Mayo 2 de 1993 a Octubre 3 de 1993.]

Age (years)	Length (TL; mm)	n	n with hydrated oocytes	Spawning frequency
2	344-389	4	1	39
3	345-470	44	10	35
4	344-734	76	15	30
5	350-618	45	12	41
6	456-744	11	1	14
7	646-750	2	0	0
8	530-852	11	7	98
9	755	1	0	0
10	645-765	2	2	154
11	-	0	-	-
12	820	1	1	154
13-24	-	0	-	-
25	869	1	0	0
2-25	344-869	198	51	40

Table 9. Data used for analyzing relationships of previous and improved annual fecundity estimates (AFEs) for red snapper. [Datos usados para analizar las relaciones de las estimaciones de fecundidad anual, previa y mejorada (AFEs) para el pargo del Golfo.]

Date (dd/mm/yy)	Length (TL; mm)	Weight (kg)	Age (years)	Mean count of oocytes ≥0.20 mm	Previous AFE	Mean count of hydrated oocytes	Improved AFE
19/06/91	420	2.10	4	4 965	654 919	1 238	4 046 172
26/07/91	450	1.10	3	3 023	486 200	469	1 926 782
04/08/91	440	1.40	4	2 342	453 564	640	3 063 034
11/06/92	525	2.00	-	3 183	2 147 371	497	7 333 809
27/06/92	665	4.65	8	1 875	1 073 090	325	3 220 686
18/07/92	810	8.85	9	2 327	4 332 428	468	17 162 082
01/08/92	362	0.80	3	487	60 347	45	121 086
12/09/92	651	3.88	6	4 009	1 465 290	734	5 336 961
23/09/92	426	1.25	5	301	27 898	7	11 613
15/06/93	820	9.00	12	4 807	8 166 356	687	59 665 760
23/06/93	645	3.80	10	3 510	2 519 145	764	18 618 565
24/06/93	765	9.10	10	4 585	7 914 966	882	50 977 465
06/07/93	541	2.40	4	2 936	691 333	689	4 935 805
24/07/93	538	2.35	5	1 373	242 560	237	1 327 200
28/08/93	349	0.60	-	1 311	17 035	37	16 030
28/08/93	553	2.55	5	3 780	340 814	530	1 383 375
21/09/93	744	4.90	6	2 257	1 742 158	523	13 427 470
25/09/93	370	0.60	-	1 326	82 578	409	781 830
25/09/93	456	1.30	4	1 359	37 181	82	69 685
01/10/93	615	3.50	5	1 051	397 109	256	2 554 265
03/10/93	705	5.00	8	992	250 052	42	350 070

Raffield, and Ray Ward. Jerry and Carl Anderson allowed us to routinely sample their seafood markets at Panama City Beach. Charterboat captains Bill Archer and Charles Paprocki also participated in our sampling. Special thanks are extended to National Marine Fisheries Service Fishery Reporting Specialist Debbie Fable, who routinely interrupted her schedule to assist our sampling.

Bruce Thompson, Cheryl Crowder and Jeff Render of Louisiana State University in Baton Rouge provided valuable advice on ovarian histology. Lew Bullock, Ron Taylor and Ruth Reece of the Florida Marine Research Institute in St. Petersburg helped with sampling methodology and histology.

Marc Remy, Sean Murray and James McClain processed gonads and participated in batch fecundity estimation. John Dahl assisted with efficient processing of otoliths.

This research was funded by the MARFIN (Marine Fisheries Initiative) Program of the NMFS, Southeast Region.

References

- Bennett, J. 1993. Automated landings assessment for responsive management (ALARM) report. October 1993. NOAA, NMFS, SEFSC, Res. Manage. Div. Contrib. MIA-93/94-18, 49 p.
- Briggs, J.C. 1958. A list of Florida fishes and their distribution. Bull. Fla. State Mus. (Biol. Sci.) 2:223-318.
- Collins, L.A., J.H. Finucane and H.A. Brusher. Reproductive biology of red snapper, *Lutjanus campechanus* (Poey), from three areas along the southeastern coast of the United States. 21 p.
- deVlaming, V.L., G. Grossman and F. Chapman. 1982. On the use of the gonadosomatic index. Comp. Biochem. Physiol. 73A:31-39.
- Fitzhugh, G.R., B.A. Thompson and T.G. Snider III. 1993. Ovarian development, fecundity, and spawning frequency of black drum, *Pogonias cromis*, in Louisiana. Fish. Bull. US 91:244-253.
- Goodyear, C.P. and P. Phares. 1990. Status of red snapper stocks of the Gulf of Mexico Report for 1990. NOAA, NMFS, SEFSC, Coast. Res. Div.. Contrib. 89/90-05.
- Grimes, C.B. 1987. Reproductive biology of the Lutjanidae: a review, p. 239-294. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- GMFMC. 1989. Amendment Number 1 to the reef fish fishery management plan. Gulf of Mexico Fishery Management Council, Tampa, Florida. 356 p.
- Hunter, J.R., N.C.H. Lo and R.J.H. Leong. 1985. Batch fecundity in multiple spawning fishes, p. 67-77. In R. Lasker (ed.) An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. NOAA/NMFS Tech. Rep. 36.
- Hunter, J.R. and B.J. Macewicz. 1985. Measurement of spawning frequency in multiple spawning fishes, p. 79-94. In R. Lasker (ed.) An egg production method for estimating spawning biomass of pelagic fish: application to the northern anchovy, *Engraulis mordax*. NOAA/NMFS Tech. Rep. 36.
- Hunter, J.R., B.J. Macewicz, N.C.H. Lo and C.A. Kimbrell. 1992. Fecundity, spawning, and maturity of female Dover sole, *Microstomus pacificus*, with an evaluation of assumptions and precision. Fish. Bull. US 90:101-128.
- Johnson, A.G. 1983. Age and growth of yellowtail snapper from south Florida. Trans. Am. Fish. Soc. 112:173-177.
- Nelson, R.S. 1980. Growth and mortality aspects of natural populations of the red snapper *Lutjanus campechanus*, in the West Central Atlantic and Gulf of Mexico. North Carolina State University. 73 p. M.S. thesis.
- Nelson, R.S. 1988. A study of the life history, ecology, and population dynamics of four sympatric reef predators (*Rhomboplites aurorubens*, *Lutjanus campechanus*, Lutjanidae; *Haemulon melanurum*, Haemulidae; and *Pagrus pagrus*, Sparidae) on the East and West Flower Garden Banks, northwestern Gulf of Mexico. North Carolina State University. 163 p. Ph.D. thesis.

- Render, J.H. and C.A. Wilson. 1992. Reproductive biology of sheepshead in the northern Gulf of Mexico. *Trans. Am. Fish. Soc.* 121:757-764.
- SAS. 1988. Release 6.03. SAS Institute, Inc., Cary, North Carolina.
- Sokal, R.R. and F.J. Rohlf. 1981. *Biometry*. W.H. Freeman and Co., New York. 859 p.
- Wallace, R.A. and K. Selman. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. *Am. Zool.* 21:325-343.
- West, G. 1990. Methods of assessing ovarian development in fishes: a review. *Aust. J. Mar. Freshwat. Res.* 41:199-222.

ENTERED IN NAGA

APR 14 1998

Reproductive Biology of the Gray Snapper (*Lutjanus griseus*), with Notes on Spawning for other Western Atlantic Snappers (Lutjanidae)

M.L. DOMEIER*

*California Department of Fish and Game
Marine Resources Division*

330 Golden Shore, Suite 50, Long Beach, California 92648, USA

C. KOENIG

F. COLEMAN

*Florida State University, Department of Biological Sciences
Conradi Building, Tallahassee, Florida 32306, USA*

DOMEIER, M.L., C. KOENIG and F. COLEMAN. 1996. Reproductive biology of the gray snapper (*Lutjanus griseus*), with notes on spawning for other Western Atlantic snappers (Lutjanidae) [*Biología reproductiva del pargo prieto (Lutjanus griseus), con notas sobre el desove de otros pargos (Lutjanidae) del Atlántico Occidental*], p. 189-201. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) *Biology and culture of tropical groupers and snappers*. ICLARM Conf. Proc. 48, 449 p.

Abstract

Specimens of *Lutjanus griseus* were collected from four sites off Key West, Florida, from May 1991 to January 1992. Two sites were in shallow inshore waters and two were offshore reef sites. Gonads from all specimens were macroscopically examined, and a subset was examined microscopically. A few sexually active males were found as early as late March, but females were not observed with active ovaries until mid-June. Spawning peaked in July and August and tapered off in September. The minimum size at maturity was found to be 182 mm SL for males and 198 mm SL for females. Examination of otoliths from newly settled *L. griseus* revealed that actual spawning was occurring during the new moon phases. Adult fish were observed to migrate from inshore to offshore waters during the peak of the spawning season. Observations of other species of *Lutjanus* suggest that some spawn in annual aggregations at specific sites, while others have protracted spawning seasons with no apparent spawning migration.

Resumen

Especímenes de Lutjanus griseus fueron colectados de cuatro sitios fuera de Key West, Florida, de Mayo de 1991 a Enero de 1992. Dos sitios fueron en aguas interiores de baja profundidad y dos fueron en arrecifes de aguas marinas. Las góndadas de todos los peces fueron examinadas macroscópicamente y una submuestra fué examinada microscópicamente. Unos pocos machos sexualmente activos fueron encontrados al inicio y al final de Marzo, pero no fueron observadas hembras con ovarios activos hasta

* Present address: Hubbs-Seaworld Research Institute, 2595 Ingraham Street, San Diego, California 92109, USA; e-mail 103727.3530@compuserve.com

la mitad de junio. El desove presentó su máximo en Julio y Agosto, culminando en Septiembre. El tamaño mínimo de madurez fue de 182 mm de longitud estandar (SL) para machos y 198 mm SL para hembras. El examen de los otoñitos de *L. griseus* recientemente reclutados reveló que el desove actual ocurrió durante las fases de luna nueva. Se observó que los peces adultos presentan una migración de aguas costeras a aguas marinas durante el pico de la época de desove. La observación de otras especies de *Lutjanus* sugiere que algunas desovan en agregaciones anuales en sitios específicos, mientras que otros presentan una época de desove protáctil sin migración aparente para desovar.

Introduction

Snappers are a major component of the commercial, sport and subsistence fisheries in the tropical Western Atlantic and Gulf of Mexico. Although gray snapper (*Lutjanus griseus*) (Domeier and Clarke, unpubl.), red snapper (*L. campechanus*) (Arnold et al. 1978; Minton et al. 1983) (see also Collins et al., this vol.), lane snapper (*L. synagris*) (Domeier and Clarke 1992; Clarke et al. in prep.) (see also Rivera-Arriaga et al., this vol.), yellowtail snapper (*L. chrysurus*) (Soletchnik et al. 1989; Domeier and Clarke 1992; Clarke et al. in prep), and mutton snapper (*L. analis*) (Clarke et al. in prep) have been spawned in captivity, little is known of the reproductive biology and spawning habits of this group (see also Manickchand-Heileman and Philipp, this vol.). Details of reproduction and early life history are critical to effective fisheries management. Here we present new data regarding the reproductive biology of the gray snapper and report observations on the spawning habits of several other species of Western Atlantic snapper.

The gray snapper is of considerable commercial importance in Florida, where hook-and-line landings for 1978 amounted to 337 t worth an estimated US \$426 000 (Bortone and Williams 1986). Catches dropped to 230 t by 1990 but the economic value remained high at \$731 000 (preliminary data: O'Hop, pers. comm.). The economic value of the sport fishery

probably far exceeds that of the commercial fishery (Starck 1971). Peak commercial landings occur during the summer months in Florida, with the Florida Keys taking 25% of the annual catch in July alone (Burton 1992). This peak of commercial activity coincides with the peak of gray snapper spawning activity reported by Jordan and Evermann (1923) to occur in July and August, and Starck (1971) (working in south Florida) from June to September with peak spawning in June and July.

Actual spawning has not been observed but the evidence suggests that it takes place at offshore reefs and wrecks (Springer and Woodbum 1960; Starck 1971). Starck (1971) suggested that spawning periods followed a lunar cycle, occurring around the full moon. Eggs and larvae are planktonic (Barans and Powles 1977). Larvae remain in the plankton for three weeks (Domeier and Clarke, unpubl.) and settle as early juveniles in estuaries (Bortone and Williams 1986), primarily in shallow seagrass beds in Florida (Starck 1971). Gray snapper larvae have been described from laboratory-reared individuals (Richards and Saksena 1980; Clarke et al. in prep.).

Starck's (1971) comprehensive study of gray snapper covered many aspects of the life history. However, important details regarding spawning were left unanswered. This study investigates spawning season, spawning periodicity, spawning behavior, and sexual pattern of gray snapper. Data were also collected regarding certain aspects of early juvenile biology.

Materials and Methods

Site selections

Gray snapper were collected from four sites near Key West, Florida, two shallow inshore sites and two offshore reef sites representative of the wide range of habitat types known for this species. Specific sites were chosen after visually identifying areas (using SCUBA) with large numbers of gray snapper. The following are site descriptions.

Inshore Site 1 (IS1) - A large patch reef (20 m long, 7 m wide, and 3 m high in a depth of 5 m) consisting of living boulder, brain, and star coral, surrounded by sand and seagrass beds. Visibility varied greatly from poor to good (2-12 m).

Inshore Site 2 (IS2) - Boca Grande Channel between Boca Grande Keys (west of Key West in a depth of 6 m) with soft corals, sponges and one small isolated coral head. This site was subject to strong tidal currents restricting sampling to slack tides. Visibility was poor (1-6 m).

Offshore Site 1 (OS1) - A large area of reef with overhanging ledges and sand channels at a depth of 9 m, adjacent to a sloping dropoff into deepwater. The top of the reef was covered with soft corals. Visibility ranged from 10 to 20 m. Although this site produced relatively few gray snappers during initial surveys, it was selected because it was known by fishers to be a spawning ground for these fish.

Offshore Site 2 (OS2) - A large area of spur and groove reef, locally referred to as Boca Grande Bar at a depth of 15 m). Visibility ranged from 10 to 30 m.

Miscellaneous Sites - The data set was supplemented by specimens opportunistically collected at a variety of locations in southern and western Florida. Many of these collections were made by fishers unwilling to reveal the exact location of the site.

Sampling of adults

Ten gray snappers were collected by spearfishing at each of the four sites at regular intervals between 14 May 1991 and 12 September 1991, the extent of the spawning season. Collections were made at one-week intervals during the peak of spawning activity, and at two-week intervals at all other times. These sites were periodically sampled outside the spawning season until January 1992. All specimens were sexed, measured to the nearest mm standard length (SL), and gonads were removed for subsequent analysis. Most of the specimens were also weighed to the nearest gram. A subset of fish were not weighed due to faulty equipment; weights were calculated for these specimens using a derived length (cm)-weight (g) relationship (weight= $0.0281(\text{SL}^{2.998})$; n=1 026).

The large variability in visibility between sites and between sampling periods precluded reliable density comparisons between sites and sampling periods. Densities of gray snapper changed over time on a magnitude that could not be explained by repeated sampling.

Gonad analysis

Gonads removed in the field were macroscopically examined to determine sex, if possible, and either placed on ice for transport to the laboratory, or placed in Davidson's solution for subsequent histological work (n=122). In the laboratory, gonads were weighed to the nearest 0.1 g and frozen.

Squashes of thawed gonad tissue were microscopically examined to determine sex, identify stages of oocyte development (Moe 1969), range of oocyte size per stage, and presence or absence of atresia. Quick hematoxylin and eosin stains of new squashes

were made (see Link (1980)) when sex could not be determined from unstained squashes.

Histological preparations of gonads were made following the procedures of Moe (1969) to determine gonadal development. Preserved tissue was sectioned at 10 m, mounted on slides, and stained with hematoxylin and eosin. Such preparations were required for identification of pre- or post-spawning individuals and early atritic stages. Gonads were evaluated histologically for the following:

1. Minimum size of sexual maturation and sexual differentiation;
2. Sexual pattern;
3. Description of stages of gonadal maturation; and
4. Timing of annual spawning activity.

Spawning season and periodicity

The extent and peaks of spawning activity were determined by calculating a gonadosomatic index (GSI) for all specimens, and plotting them against capture dates. Spawning dates were also back-calculated by counting daily increments of otoliths from juvenile gray snapper ($n=68$) collected from seagrass beds by otter trawl, benthic scrape and roller frame trawl. Collections were made in 1992 between late July and mid-September. The specimens were measured to the nearest mm (SL) and either frozen or fixed in 95% ethanol to ensure preservation of otoliths. Otoliths were subsequently removed and stored in 95% ethanol. Lapilli were ground and polished, then viewed under oil immersion at 1000x. Daily increment counts (following Brothers and McFarland 1981) were made using a video-enhanced microscope.

Daily growth increments of juvenile otoliths were validated by comparing our counts with the known age of juveniles reared from the egg by Richards and Saksena (1980).

A subset of 10 otoliths were read and counts confirmed by Dr. Ed Brothers.

Spawning behavior

Many dive trips were made during the summers of 1991 and 1992 in an attempt to observe courtship and spawning. Dives were made between first light and dark. These dives were made primarily during the days before and after the full moon, since Starck (1971) stated that gray snapper spawn at this time.

Observations on spawning behavior of several other Western Atlantic snappers were opportunistically made by one of us (MLD). Although this information is not quantitative, it is a valuable contribution to our knowledge of these little known species. Observations on *L. analis*, *L. synagris*, *L. chrysurus*, *L. jocu*, *L. apodus*, and *L. cyanopterus* were made on SCUBA, and additional information was gained through collecting (hook and line, spearfishing, fish trapping) and through interviewing fishers.

Results

Gonad analysis

Gonad developmental stages of gray snapper were described by histological examination of gonads. All oocyte and spermatocyte stages follow those described by Moe (1969).

- Sexually undifferentiated - Gonad is small, compact and contains undifferentiated stroma. No oocytes, seminiferous tubules, spermatogenic tissue or lumen are visible. All gonads have attached fat.

- Immature female - Gonads are small and compact with a distinct lumen. The gonads contain much stroma and scattered small previtellogenic oocytes, or many small previtellogenic oocytes. The ovarian wall is generally thin. All gonads have attached fat.
- Immature male - Gonads are small and compact with no lumen. The gonads contain developing seminiferous tubules and scattered early stages of spermatogenesis, interspersed with stroma.
- Mature inactive female - In addition to a lumen and previtellogenic oocytes, the ovaries contain a number of stage 3 oocytes (early vitellogenic) and/or indications of prior spawning. Prior spawning is indicated by a thickened ovarian wall, degenerating oocytes, or internal muscle bundles that contract the expanded ovary after spawning.
- Mature inactive male - The testes predominantly consist of the early stages of spermatogenesis, which are particularly evident at the gonad margins. A few scattered cysts of later spermatogenic stages may be present.
- Mature active female - Ovaries have a lumen and a mixture of previtellogenic oocytes and vitellogenic oocytes of stages 3,4 and 5 in varying proportions. The diameter of the gonad is relatively thin and stretched.
- Mature active male - The testes consist predominantly of later stages of spermatogenesis (stage 2 spermatocytes, spermatocids and spermatozoa). The gonad is enlarged and may contain large areas of sperm.

If spawning has occurred, empty lobules may be visible and the testes will appear to be disrupted in areas.

Gonads were generally undifferentiated in fish smaller than 140 mm SL. The smallest sexually differentiated male was 120 mm SL, and the smallest sexually differentiated female was 140 mm SL. The size of first maturity was 182 mm SL for males and 198 mm SL for females. Although small sample size precluded separate analyses of maturation by sex, we calculated a combined maturity curve for both sexes for size classes 100-300 mm SL (n=80) because both sexes mature at about the same size. Ninety percent of gray snappers mature by the time they reach 200 mm SL and 100% are mature at 240 mm SL.

All gray snapper gonads have stored fat attached to the gonads during the non-reproductive season; during the spawning season sexually mature fish lose this fat as it is mobilized for gametogenesis and spawning.

Sexual pattern

Gray snapper are clearly gonochorists, based on the similarity in size of sexual maturation of the sexes, the overlap between the sexes in size-frequency distributions, and the absence of individuals undergoing sexual transition. Testes had a typical gonochore structure lacking the ovarian-type lumen characteristic of many hermaphroditic (protogynous) species. One adult male exhibited a few, very small previtellogenic oocytes within the testes, but this characteristic is found in many gonochoristic species (Sadovy and Shapiro 1987), and is assumed to be unrelated to sexual pattern in the absence of any other indications of sex change.

The sex ratio of gray snapper was slightly skewed towards females at 1.2 females:1 male ($n=889$; size range 145-497 mm). A subset of all fish greater than 350 mm also had a sex ratio of 1.2:1.

Spawning season

Spawning began in late May and continued into early September (Fig. 1; $n=664$). A few ripe males were found as early as late May, but most males were ripe by late June. Females were never collected running ripe, although microscopic examination of ovaries revealed a few hydrated eggs in several specimens during the months

of July and August. Clear peaks in GSI appear to be related to the lunar cycle for fish collected at the offshore sites. The first peak coincides with the new moon in mid-June, a second peak occurs on the following full moon late in June, and a third peak with the new moon in July. Each of these three peaks is successively larger than the previous one. The fourth and largest peak occurs on the last quarter moon in early August. The mean GSI of inshore specimens are lower than those of offshore specimens collected at the same time and do not show any pronounced peaks until the last quarter moon in August, although GSI gradually increases from June through August.

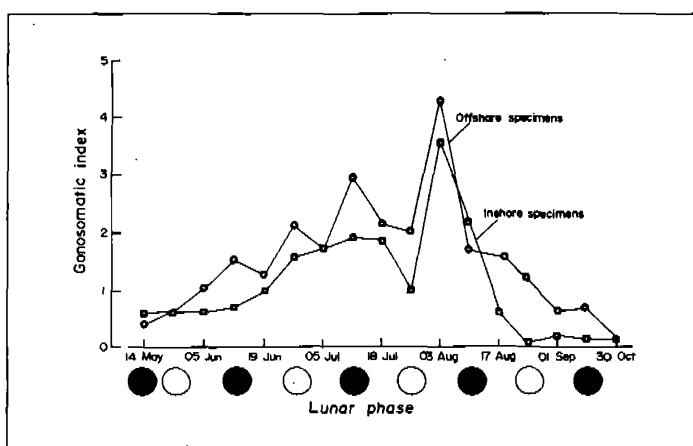


Fig. 1. Mean gonadosomatic Index (GSI) of *Lutjanus griseus* in inshore and offshore waters of Florida. [Indice gonadosomático medio (GSI) de *Lutjanus griseus* en aguas Interiores y aguas marinas de Florida.]

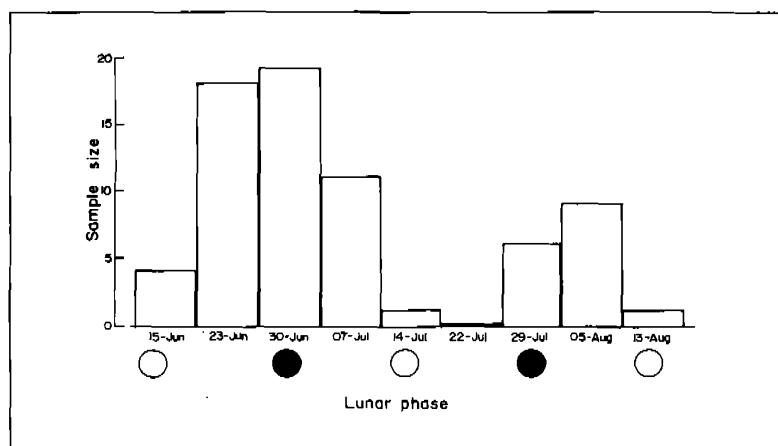


Fig. 2. Back-calculated spawning dates of *Lutjanus griseus* relative to date and lunar phases. [Fechas de desove retrocalculadas de *Lutjanus griseus* asociada a fechas y fases lunares.]

Spawning dates back-calculated by reading daily increments of juvenile gray snapper otoliths (Fig. 2) corroborated spawning periods delimited by GSIs. Spawning takes place in June, July and August, with peaks of spawning around the new moon and a decline in spawning activity around the full moon of each month. The relatively small number of samples from spawnings in July and August is due to decreased sampling effort. Since sampling was discontinued in mid-September, representative specimens from the new moon spawning in August were not obtained.

Spawning migration

During the course of this study, movement of adult gray snapper from inshore to offshore sites was observed. Initially, large

fish were especially numerous at IS2 while very few gray snappers were present at OS1. As the spawning season progressed large specimens disappeared from the inshore sites and began to appear at the offshore sites. Movement of gray snappers from inshore areas to offshore areas became clear as the time required to attain our weekly samples increased at the inshore sites and decreased at the offshore sites. Fig. 3 plots the mean standard length for each sampling period at inshore and offshore sites (two inshore sites were combined and two offshore sites were combined; $n=664$). Prior to the onset of the spawning season, the mean SL of inshore samples was actually higher than that of offshore samples; as the spawning season progressed the mean standard length of the samples increased at offshore sites. At the end of the spawning season, the means are again similar. This

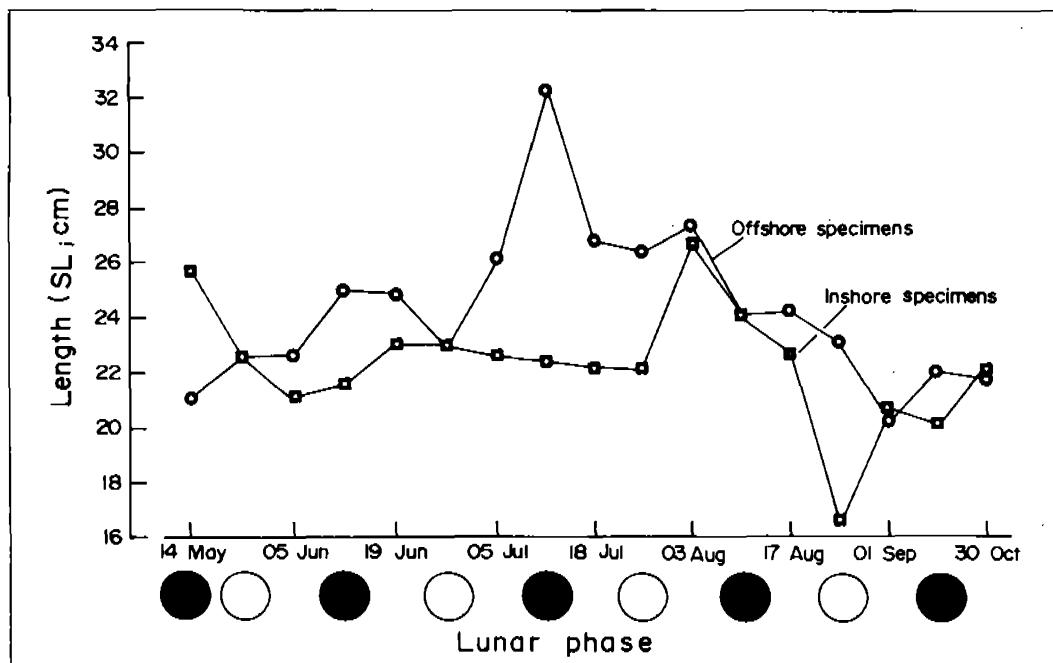


Fig. 3. Average standard length of *Lutjanus griseus* captured in inshore and offshore waters in Florida relative to date and lunar phases. [Longitud estándar promedio de *Lutjanus griseus* capturado en aguas Interiores y aguas marinas en Florida, asociada a fechas y fases lunares.]

supports our observation that many adult gray snappers migrate to offshore reefs to spawn.

Despite repeated diving, actual spawning behavior was never observed.

Reproductive strategies of other western Atlantic snappers

As discussed in the methods section, observations of spawning strategies for several Western Atlantic lutjanids were made over the last several years (by MLD). Each species for which we have information to add is reviewed and updated relevant to its specific reproductive biology.

Mutton Snapper (*Lutjanus analis*)

Adult *L. analis* are found in a variety of habitats, from shallow grass beds and patch reefs to deep barrier reefs. They are a solitary fish, rarely found in groups or schools outside the spawning season. However, during the spawning season, they form dramatic spawning aggregations that may persist for several weeks. They exhibit high site-fidelity, spawning at exactly the same location and on the same days of the lunar calendar year after year. Aggregations may form and dissipate at a particular site during two consecutive months of the late spring. Three such aggregations were observed: one at Riley's Hump in the Dry Tortugas near the time of the full moon in May and June; one off West Caicos, Turks and Caicos, during the full moons of April and May; and the third off English Cay, Belize, between the full and last quarter moons of April and May. All three sites are located on the edge of a steep drop-off.

Many mutton snappers were collected by spearfishing and a single female with expressable hydrated eggs was collected at dusk near Riley's Hump, suggesting that

spawning occurs near this time. Several evening dives made at West Caicos and the Dry Tortugas to observe spawning were unsuccessful. Thousands of snappers were observed milling around the bottom and in the water column but none spawned. It may be that mutton snapper spawn after dark.

Several fish were collected by hook-and-line at West Caicos and brought back to the laboratory where they were induced to spawn via hormone injection, confirming that the fish observed in the aggregation were in spawning condition.

Dog Snapper (*Lutjanus jocu*)

Dog snappers are solitary reef fish that appear to occupy a home range; individual specimens of dog snappers inhabited the same ledge or crevice of a reef over extended periods of time. Based on a single observation of a spawning aggregation off English Cay, Belize, on 19 July 1992 (between full and last quarter moon), it appears that dog snappers spawn in large aggregations. The site consisted of a spur of reef that began in 5 m of water and sloped down to over 35 m.

During two dives at this site in the early afternoon, several large groups of fish, totalling over a thousand individuals, were observed schooling on the bottom and occasionally forming tight balls that rose up into the water column approaching the surface. Ten fish were collected by spear, 6 males and 4 females. All the males were running ripe and the females had large, well developed ovaries but no observable hydrated eggs. The lack of a laboratory and a means of refrigeration precluded a more detailed study of the ovaries. Experience in collecting ovaries and inducing spawning in other species of snapper allow the conclusion that females present in this aggregation were ready to spawn.

Cubera Snapper (*Lutjanus cyanopterus*)

This is the largest species of Western Atlantic snapper, attaining weights in excess of 57 kg (Robins et al. 1986). Despite its size, it is perhaps the least studied species of this region. It is one of the few snappers that enters water that is nearly fresh (e.g., the intra-coastal waterway on the east coast of Costa Rica). Cubera snappers are also found on both shallow and deep reefs, and in mangroves.

According to anecdotal accounts by fishers and divers, this species also spawns in aggregations. Three aggregation sites have been found by fishers off the coast of south Florida. Two of these sites (Key West and Dry Tortugas) are wrecks located in 67-85 m of water. The third is a deep reef in the Miami area. D. DeMaria (pers. comm.) has observed and collected Cubera snapper from these wrecks during spawning aggregations. The aggregations of Cubera snapper in Florida have far fewer fish, less than 100 to a few hundred, than aggregations of other snapper species reported here.

Similar aggregations occur in Belize off Buttonwood Cay and Cay Bokel (Cabral, pers. comm.). The Belizean sites are in much shallower water (10-30 m) than the Florida sites and may contain greater numbers of individuals. Both the Florida and Belizean aggregations occur during the months of June and July (full moon to last quarter).

Yellowtail Snapper (*Lutjanus oxyurus*)

This is a small planktivorous species of *Lutjanus* (= *Ocyurus*, see Domeier and Clarke 1992), abundant throughout the tropical western Atlantic. Although juvenile yellowtail snapper can be found over sandy bottom inshore, adults occur primarily over coral reefs. This species can be found feeding well off the bottom in large schools, or seen swimming over the reef as a solitary fish.

Extensive year-round collecting of this species shows a protracted spawning season lasting from March through September in south Florida. Other investigators have found this species to have a protracted, if not year-round spawning season in other parts of the Caribbean (Piedra 1965; Munro et al. 1973; Thompson and Munro 1974/1983; Erdman 1976; Soletchnik et al. 1989).

Yellowtail snappers do not exhibit any migration or aggregation related to spawning.

Lane Snapper (*Lutjanus synagris*)

This is a small, reef-dwelling species that occurs in tight schools close to the bottom.

Extensive collecting of this species at all times of the year reveals a similar spawning pattern to that of the *L. chrysurus* snapper. In south Florida, *L. synagris* have been found in spawning condition from March through August. Other investigators have found this species to have a protracted and/or continuous spawning season (Rodriguez-Pino 1962; Erdman 1976; Reshetnikov and Claro 1976; Erhardt 1977).

Lane snappers show an interesting pattern of distribution in that they can be common at a particular location year after year, but can be rare at other locations in the vicinity. This suggests that individual schools of lane snappers have strict home ranges and do not migrate or aggregate for the purpose of spawning.

Discussion

Our study of the gray snapper was consistent with previous work for first size of maturity (Croker 1962) and time of spawning season (Jordan and Evermann 1922; Starck and Schroeder 1971). Our finding that they spawn around the new moon is contrary to the findings of Starck and Schroeder (1971) who reported gray snapper spawning on

the full moon. Their conclusions were based upon the presence of spent ovaries in specimens collected shortly after a full moon in early September. Our study suggests that these fish had spawned a few weeks prior to their collection and were finished spawning for the year.

Many dives were made at all times of the daylight hours during the spawning season to observe spawning. Although dives were concentrated around the full moon due to Starck's (1971) report of spawning activity at this time, some diving was accomplished at all phases of the lunar calendar. Our failure to witness spawning may be a result of our concentrated effort around the full moon, or it may suggest that gray snappers spawn at night. The lack of specimens with hydrated eggs supports the suggestion that they spawn at night, since all specimens were collected during the day.

Grimes (1987) concluded that snappers exhibit two basic spawning strategies that are directly related to whether the population occurs over a continental or insular habitat. Continental populations exhibit extended summer spawning seasons, while insular species reproduce year-round with spring and fall peaks (Grimes 1987). This study found a new snapper spawning strategy, the spawning aggregation, that occurs over both insular and continental habitats. It is true that habitat differences can cause variation of occurrence and length of spawning season between populations of the same species, but we suggest that spawning strategies are species specific rather than habitat dependent.

Two spawning strategies seem evident among Western Atlantic lutjanids:

1. Schooling species that have protracted spawning seasons and do not migrate or aggregate for the purposes of spawning (e.g., *L. chrysurus* (Piedra 1965; Munro et al. 1973; Thompson and Munro 1974/1983;

Erdman 1976; Soletchnik et al. 1989), *L. synagris* (Rodriguez-Pino 1962; Erdman 1976; Reshetnikov and Claro 1976; Erhardt 1977), *L. apodus* (Munro et al. 1973; Thompson and Munro 1974/1983).

2. Solitary species that migrate and aggregate for the purpose of spawning over a very short time period (i.e., a few days or weeks) (e.g., *L. analis*, *L. jocu*, *L. cyanopterus*).

Mahogany snapper (*L. mahogani*) may be found to be a Strategy 1 spawner due to its similarity in behavior and habitat utilization to *L. synagris*.

Spawning aggregations have been well documented for many species of grouper (Serranidae) (see Sadovy et al., in press), but have not been previously reported for lutjanids. The nature of snapper spawning aggregations is extremely similar to that of groupers. In fact, many sites that are used by groupers for spawning are used by snappers but at different times of the year. For example, the Belize site used by mutton snapper is also used by Nassau grouper (*Epinephelus striatus*), yellowfin grouper (*M. venosum*), and Jewfish (*E. itajara*) (Cabral, pers. comm.). As with groupers, snappers begin to arrive at the spawning site approximately one week prior to the peak spawning activity (deduced from peak density of fish at site) and linger at the site after spawning for another week. Also similar to groupers, an aggregation may occur during two consecutive months of the year, although one month usually has a greater number of fish participating in the aggregation.

In both the Lutjanidae and the Serranidae it is the larger species that aggregate to spawn. These large predators require more spatial and nutritional resources to survive than smaller fish. Increased space between individuals creates difficulty in finding mates during the spawning season. Formation of annual spawning aggregations at permanent

sites provides an efficient mechanism for overcoming this problem. The brevity of the spawning may limit periods of intense conspecific competition for food.

Smaller species of lutjanids require fewer resources per individual and can form schools year-round. Membership in a school enhances reproductive success. Schooling species are limited in the duration of the spawning season only by the availability of food and the physiological constraints of the eggs and larvae.

The gray snapper does not fit well into either of the described spawning strategies. This species has adapted to a variety of habitats, including inshore areas that can vary widely in temperature and salinity. It is possible that the adult stage has evolved to tolerate a wide range of physical conditions, but the larval stage remains intolerant. The spawning migration of this species from inshore to offshore would thereby increase the survival of the offspring. This scenario would make the *L. griseus* snapper a modified Strategy 1 spawner. Another possibility is that the intermediate size of this species has allowed an intermediate spawning strategy. The *L. apodus* is a closely related species that needs further study; it too may exhibit an intermediate spawning strategy.

Spawning behavior has only been reported for two species of snappers worldwide: *L. synagris* which were observed to spawn at dusk in Florida (Wicklund 1969) and *L. kasmira* which were reported to spawn at night in captivity (Suzuki and Hioki 1979). Both species were group spawners. Although *L. chrysurus* (Soletchnik et al. 1989) and *L. campechanus* (Arnold et al. 1978) have been spawned in captivity without the aid of hormone injection, the time of spawning and spawning behavior were not reported. Davis and West (1993) report that *L. vittus* (Australia) spawns during the early afternoon. This conclusion was based on the presence of hydrated eggs between 1100 and 1500 hours, and a peak in the

presence of early post-ovulatory follicles by 1700 hours. *Lutjanus vittus* is probably an unusual example of daytime spawning among a group of primarily dusk or nocturnal spawners.

Both snapper species observed spawning are group- rather than pair-spawners (Wicklund 1969; Suzuki and Hioki 1979). The behavior of *L. jocu* within a spawning aggregation reported here may also indicate group spawning. Some species of aggregating groupers are pair spawners (i.e., *Mycteroperca tigris*: Sadovy et al., in press) while at least one species is a group spawner (*E. striatus*: Colin 1992). It is possible that future studies will find that the lutjanids also have representative group and pair spawning species. The presence of group spawning among lutjanids may also play a role in the formation of spawning aggregations. It is not known whether or not group spawning species can successfully reproduce when populations are severely depleted.

Spawning aggregations of both lutjanids and serranids are often fished out of existence upon discovery by fishers. Although the United States is taking measures to protect the mutton snapper at Riley's Hump, Florida, the annual aggregation is already a tiny fraction of what it once was. Proactive rather than reactive management is called for where aggregation sites exist. As we have seen, specific aggregation sites are often used by more than one species of fish; protecting an aggregation site would serve to protect multiple species in many cases.

Acknowledgements

Captain Don DeMaria and Carl Cabral provided valuable information regarding the locations and habits of snappers that made this study possible. Chris Ninnis and the Fisheries Department of the Turks and Caicos provided their assistance and resources while studying mutton snapper at West Caicos. Grant money from the Florida

Department of Natural Resources and the Caribbean Marine Research Center supported various aspects of this research. Scott Harris provided valuable technical support regarding the manipulation of the large database.

References

- Arnold, C.R., J.M. Wakeman, T.D. Williams and G.D. Teece. 1978. Spawning of red snapper (*Lutjanus campechanus*) in captivity. *Aquaculture* 15:301-302.
- Barans, C.A. and H.W. Powles. 1977. South Carolina MARMAP program: present and future, p. 6-12. In D.M. Cupka, P.J. Eldridge and G.R. Huntsman (eds.) *Proceedings of Workshop on the Snapper/Grouper Resources of the South Atlantic Bight*. South Carolina Marine Resources Center Tech. Rep. 27.
- Bortone, S.A. and J.L. Williams. 1986. Gray, lane, mutton, and yellowtail snappers. Species profiles: life histories and environmental requirements of coastal fishes and invertebrates (South Florida). *Fish Wildl. Serv. Biol. Rep.* 82(11.52) TR EL-82-4:1-18.
- Brothers, E.B. and W.N. McFarland. 1981. Correlations between otolith microstructure, growth, and life history transitions in newly recruited French grunts (*Haemulon flavolineatum* (Desmarest), Haemulidae). *Rapp. P.-v. Réun. CIEM* 178:369-374.
- Burton, M. 1992. The relationship between spawning season and landings of selected reef fishes. Beaufort Laboratory, Southeast Fisheries Science Center, National Marine Fisheries Service, National Oceanic and Atmospheric Administration.
- Clarke, M.E., M.L. Domeier and W.A. Laroche. Development of the larvae and juveniles of mutton snapper (*Lutjanus analis*), lane snapper (*L. synagris*) and yellowtail snapper (*L. ocularis*). *Bull. Mar. Sci.* (In press).
- Colin, P.L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. *Env. Biol. Fish.* 34:357-377.
- Croker, R.A. 1962. Growth and food of the gray snapper, *Lutjanus griseus*, in Everglades National Park. *Trans. Am. Fish. Soc.* 91:379-383.
- Davis, T.L.O. and G.J. West. 1993. Maturation, reproductive seasonality, fecundity, and spawning frequency in *Lutjanus vittus* (Quoy and Gaimard) from the North West Shelf of Australia. *Fish. Bull.* 91:224-236.
- Domeier, M.L. and M.E. Clarke. 1992. A laboratory produced hybrid between *Lutjanus synagris* and *Ocyurus chrysurus* and a probable hybrid between *L. griseus* and *O. chrysurus* (Perciformes: Lutjanidae). *Bull. Mar. Sci.* 50(3):501-507.
- Erdman, D.S. 1976. Spawning patterns of fishes from the northeastern Caribbean. Puerto Rico Dept. Agric., Commer. Fish. Lab., Agric. Fish. Contrib. 8(2):1-36.
- Erhardt, H. 1977. Beiträge zur Biologie von *Lutjanus synagris* (Linnaeus 1758) an der Kolumbianischen Atlantikküste. *Zool. Beitr.* 23(2):235-265.
- Grimes, C.B. 1987. Reproductive biology of the Lutjanidae: a review, p. 239-294. In J.J. Polovina and S. Ralston (eds). *Tropical snappers and groupers: biology and fisheries management*. Westview Press, Boulder.
- Jordan, D.S. and W. Evermann. 1923. American food and game fishes. Doubleday, Page and Co., New Jersey.
- Link, G.W., Jr. 1980. Age, growth, reproduction, feeding, and ecological observations on the three species of *Centropristes* (Pisces: Serranidae) in North Carolina waters. The University of North Carolina, Chapel Hill. 277 p. Ph.D. Dissertation.
- Minton, R.V., J.P. Hawke and W.M. Tatum. 1983. Hormone induced spawning of red snapper, *Lutjanus campechanus*. *Aquaculture* 30:363-368.
- Moe, M. A., Jr. 1969. Biology of the red grouper (*Epinephelus morio* Valenciennes) from the eastern Gulf of Mexico. *Prof. Pap. Ser., Fla. Mar. Lab.* 10, 95 p.
- Munro, J.L., V.C. Gaut, R. Thompson and P.H. Reeson. 1973. The spawning seasons of Caribbean reef fishes. *J. Fish Biol.* 5:69-84.
- Piedra, G. 1965. Materials on the biology of the yellowtail snapper (*Ocyurus chrysurus* Bloch), p. 251-269. In A.S. Bogdanov (ed.) *Soviet-Cuban fishery research. All-Union Sci. Res. Inst. Mar. Fish. Oceanogr., Fish. Res. Cent. Nat. Pisc. Inst. Rep. Cuba*.

- Reshetnikov, Y.S. and R.M. Claro. 1976. Cycles of biological processes in tropical fishes with reference to *Lutjanus synagris*. J. Ichthyol. 16:711-723.
- Richards, W.J. and V.P. Saksena. 1980. Description of larvae and early juveniles of laboratory-reared gray snapper, *Lutjanus griseus* (Linnaeus) (Pisces, Lutjanidae). Bull. Mar. Sci. 30:515-521.
- Robins, C.R., G.C. Ray and J. Douglas. 1986. A field guide to Atlantic Coast fishes of North America. Houghton Mifflin Co., Boston, Massachusetts. 354 p.
- Rodríguez-Pino, Z. 1962. Estudios estadísticos y biológicos sobre la biajaiba (*Lutjanus synagris*). Cent. Invest. Pesq., Notas Sobre Invest. 4, 91 p.
- Sadovy, Y. and D.Y. Shapiro. 1987. Criteria for the diagnosis of hermaphroditism in fishes. Copeia 1:136-156.
- Sadovy, Y., P.L. Colin and M.L. Domeier. Aggregation and spawning in the tiger grouper, *Mycteroperca tigris* (Pisces: Serranidae). Copeia (1994 (2)). (In press).
- Soletchnik, P., M. Suquet, E. Thouard and J.P. Mesdouze. 1989. Spawning of yellowtail snapper (*Ocyurus chrysurus* Bloch 1791) in captivity. Aquaculture 77:287-289.
- Springer, V.G. and K.D. Woodburn. 1960. An ecological study of the fishes of Tampa Bay area. Fla. Dept. Nat. Resour. Prof. Pap. Ser. 1:1-104.
- Starck, W.A. 1971. Biology of the gray snapper, *Lutjanus griseus* (Linnaeus), in the Florida Keys. In W.A. Starck and R.E. Shroeder (eds.) Investigations on the gray snapper, *Lutjanus griseus*. Studies in Tropical Oceanography 10, 224 p.
- Starck, W.A., II and R.E. Schroeder. 1971. Biology of the gray snapper, *Lutjanus griseus*. Studies in tropical oceanography (10), University of Miami Press, Coral Gables, Florida. 224 p.
- Suzuki, K. and S. Hioki. 1979. Spawning behavior, eggs and larvae of the lutjanid fish, *Lutjanus kasmira*, in an aquarium. Jap. J. Ichthyol. 26:161-166.
- Thompson, R. and J.L. Munro. 1974. The biology, ecology, exploitation and management of Caribbean reef fishes. Part V.d. The biology, ecology and bionomics of Caribbean reef fishes: Lutjanidae (Snappers). Res. Rept. Zool. Dept. Univ. West Indies 3(V.d):69 p. reprinted as Thompson, R. and J.L. Munro. 1983. The biology, ecology, and bionomics of snappers, Lutjanidae, p. 94-109. In J.L. Munro (ed.) Caribbean coral reef fishery resources. ICLARM Stud. Rev. 7, 276 p.
- Wicklund, R. 1969. Observations on spawning of lane snapper. Underwater Nat. 6(2):40.

ENTERED IN NAGA

APR 14 1998

Population Dynamics and Stock Assessment of Red Grouper (*Epinephelus morio*) Fishery on Campeche Bank, México^a

F. ARREGUÍN-SÁNCHEZ^b

*Programa de Ecología, Pesquerías
y Oceanografía del Golfo de México
U.A.C. Ap. Postal 520, Campeche 24030
Campeche, México*

M. CONTRERAS

V. MORENO

R. BURGOS

*Centro Regional de Investigación Pesquera de Yucalpetén
Instituto Nacional de la Pesca
Ap. Postal 73, Progreso, Yucatán, México*

R. VALDÉS

*Centro de Investigaciones Pesqueras de Cuba
5a Ave. y 242, Edificio 2
Barlovento Playa C Habana, Cuba*

ARREGUÍN-SÁNCHEZ, F., M. CONTRERAS, V. MORENO, R. BURGOS and R. VALDÉS. 1996. Population dynamics and stock assessment of red grouper (*Epinephelus morio*) fishery on Campeche Bank, México [Dinámica poblacional y evaluación de la pesquería del mero Americano (*Epinephelus morio*) del Banco de Campeche, México], p. 202-217. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

An analysis of information is presented on the current status of the population dynamics and stock assessment of the red grouper (*Epinephelus morio*) fishery from Campeche Bank, Gulf of Mexico. Three fleets participate in the fishery, two from Mexico, and a third one from Cuba. Because of their characteristics, the operations of these fleets constitute a sequential fishery, in which the small-scale fleet mainly exploits juveniles, the mid-sized Mexican vessels target both juveniles and adults; and the technically advanced Cuban fleet mainly captures adult fish. Catch-per-unit-effort indicates a declining population abundance in recent years. Although some authors suggest that overexploitation is the cause, the population decline appears initially to have been related to an important fall in recruitment on the 1980 year class, which was probably combined with changes in suitable habitat which occurred some years later. Results of an age-based VPA analysis indicate a decrease of the population size by 30% after 1980. However, despite this estimate, more detailed studies based on catchability estimates and catch structured data show that population size remained reasonably stable over a period of 17 years. Catchability studies suggest reproductive behavior (maturation and spatial distribution) to be the most important factor affecting yields and fishing strategies.

^a EPOMEX Contribution No. 239.

^b Present address: Centro Interdisciplinario de Ciencias Marinas del IPN, Playa El Conchalito, s/n; Apartado Postal 592, La Paz, 23000, Baja California Sur, México.

Resumen

*El presente documento analiza el estado actual del conocimiento de la dinámica poblacional y de la evaluación del recurso mero (*Epinephelus morio*) del Banco de Campeche, México. En la pesquería participan tres flotas, dos de México y una de Cuba. Debido a sus características, la operación de estas flotas constituye una pesquería secuencial, donde la flota artesanal explota principalmente juveniles, la flota mediana de México captura juveniles y adultos, y la flota tecnificada de Cuba es orientada hacia los adultos. Los datos de captura por unidad de esfuerzo indican que la abundancia del recurso ha decrecido en los últimos años. Aun cuando algunos autores han sugerido una tendencia a la sobrepesca, los decrementos de la población parecen estar asociados a una importante falla del reclutamiento en la clase anual de 1980, lo cual parece estar inicialmente asociado con cambios en la calidad del hábitat ocurrido algunos años más adelante. Los resultados obtenidos utilizando VPA con edades indican un decrecimiento de 30% del tamaño de la población después de 1980. Sin embargo, a pesar de estas estimaciones, estudios detallados sobre la estructura de las capturas indican que la población se ha mantenido razonablemente estable por un período de 17 años. En relación con el éxito de pesca, los estudios de capturabilidad sugieren que el comportamiento reproductivo (maduración y distribución espacial) es un factor de suma importancia que afecta los rendimientos y las estrategias de pesca.*

Introduction

The fishery

Red grouper (*Epinephelus morio*) is a demersal fish constituting the most important fishery resource on the continental shelf of Yucatan, and the second in the Gulf of Mexico, after shrimp. Exploitation is carried out by three fleets (Arreguín-Sánchez et al. 1987a): an artisanal fleet from Mexico and a mid-sized fleet and a fleet of technically-advanced vessels from Cuba. These fleets exhibit important differences in their technical characteristics as well as in their impact on the population. This fishery captures a number of demersal species of which the red grouper amounts to 89% on average from 1980 to 1985. The remaining 11% is composed of about 46 species (Fuentes 1991).

The artisanal fleet consists of about 900 small boats about 10 m long, each carrying two "alijos" and 3-4 fishers (Saenz et al. 1987). It operates to a depth of 22 m (12 fathoms) with long-lines of 50 to 100 hooks, and hand-lines, fishing mostly juveniles and young adults. Catch is landed on the beach and is used mostly for local consumption and also for national and foreign markets. Usually the fishing operation lasts one or two days. This fleet takes 23% of the whole catch.

The mid-sized Mexican fleet is composed of 222 boats (Burgos 1987), 14-22 m long. Each vessel acts as a mother boat with 9-12 fishers and 7-10 small boats, without engines which are locally named "alijos". Each "alijo" fishes with a long-line of 25 to 50 hooks, and two or more hand-lines. The fleet operates mainly between 9 and 109 m (5-60 fathoms) most of the time on 55 m (30 fathoms) or less. The fishing trips last about 15 days (Arceo et al. 1987). Catch is landed as whole fresh fish or fillets, and part of the production is exported. This fleet takes about 52% of the total catch.

The Cuban fleet consists of about 40 mother boats each 22 m long and carrying 18 crew members. Each vessel carries six 5-m boats with an in-board engine. They operate in 27-110 m (15-60 fathoms) with long-lines of 350 hooks (which are checked six or seven times per day). Trips last about 20 to 30 days and the catches, composed mostly of adult fishes, are landed in Havana, Cuba. This fleet takes around 25% of the total catch.

Resource access by the Mexican fleets is unrestricted, while Cuba has a catch quota which was gradually reduced from 10 000 t in 1975 to 3 900 t of demersal fish in 1987. The highest yield was recorded in 1972 with nearly 20 000 t but in recent years it declined to around 11 000 t. Catch trends follow similar annual patterns for both countries.

Biology

Red grouper ranges from Katama Bay, Massachusetts, USA, to Rio de Janeiro, Brazil, including Bermuda, and the West Indies, and found in high densities in Florida and the Gulf of Mexico. Adult fishes are gregarious with a high tendency toward territorialism, and live in caves and on rocky and hard bottoms, to about 275 m (150 fathoms) (Böhlke and Chaplin 1968; Smith 1971; Shapiro 1987). Young fishes live close to the coast and are associated with seagrass beds and reefs. Spawning occurs in aggregations in deepwaters, and in the Gulf of Mexico, usually from December to May, with a peak in January–February in the Campeche Bank (Mexicano-Cíntora 1990); and in March–April in Florida waters (Moe 1969). Fecundity has been estimated to range from $3 \cdot 10^5$ to over $5 \cdot 10^6$ eggs, with a mean value around $1.5 \cdot 10^6$ eggs. Gonad development was described by Moe (1969) for Florida waters, and by Mexicano-Cíntora (1990) for Campeche Bank (see Arreguín-Sánchez and Valero; Brûlé and Dénil; Colin et al., this vol.). This species is protogynous hermaphrodite, reaching female sexual maturity at about 4 years, while the transition to males occurs at 7 to 10 years.

Spatial distribution in the Campeche Bank

Red grouper inhabits the broad continental shelf of Yucatan, also known as Campeche Bank ($100\,000\,\text{km}^2$). Bottom characteristics and type of sediments are typical of reef environments. Some seasonal upwelling (Ruiz and Merino 1989) takes place during late spring and early summer affecting life history and behavior. Oleachea (1975) shows general patterns of abundance and distribution of several demersal fishes on the Campeche Bank; for red grouper there is some evidence of spatial changes in the abundance. Burgos (1987)

established a sampling system for commercial catches which produces valuable data on yields, catch composition (by species), geographic position and other relevant data. This information is continuously reported and displayed on tri-monthly charts. Currently, charts are available for seven years showing the spatial distribution of catch-per-unit-effort (Fig. 1).

Shapiro (1987) compiled information concerning the reproductive behavior of serranid fishes, particularly of the genus *Epinephelus*. The usual behavior of this species is a reproductive aggregation during a specific season of the year. As for *E. morio*, there is no direct evidence of population movements, but its reproductive behavior and seasonal spatial distribution of biomass suggest the existence of seasonal population displacements.

Materials and Methods

This document represents a review of the state of knowledge of the population dynamics and stock assessment for the red grouper in the Campeche Bank, Mexico. Most of this literature originates from Mexican and Cuban investigations on this shared fish resource, and it is complemented by other studies on the environmental factors affecting fish populations in this region.

Results

Population dynamics

Age and Growth

Growth largely conforms to the von Bertalanffy (1938) equation, the age being recorded mostly on hard parts (mainly otoliths and urohyal bones). Ageing techniques vary from simple counting of rings to backcalculations. Works on length composition data are scarce (see Posada and

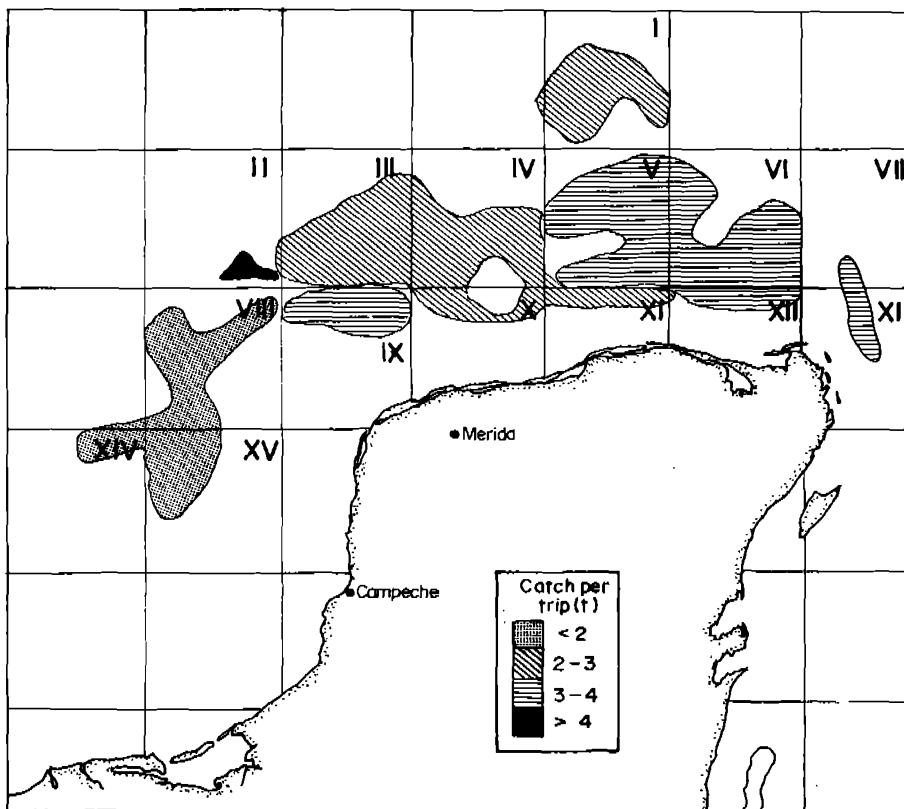


Fig. 1. Spatial distribution of the relative abundance (tons-per-trip) of the red grouper (*Epinephelus morio*), on the continental shelf of Yucatan, México, during the period of January to March of 1986 (from Burgos 1987). [Distribución espacial de la abundancia relativa (tons-por-viaje) del mero americano (*Epinephelus morio*) de la plataforma continental de Yucatan, México, durante el período de Enero a Marzo de 1986 (tomado de Burgos 1987).]

Appeldoorn, this vol.). Table 1 summarizes information on age and growth for *E. morio*.

Rodríguez (1986) analyzed both otoliths and mesopterigoids of *E. morio*, and found that an annulus is laid down in the otolith for every two rings deposited in the mesopterigoids. This relationship has been reported for other species inhabiting the same ecosystem such as the red snapper (*Lutjanus campechanus*) González (1988); and by Ordaz (1993) for mojarra (*Calamus nodosus*). For red grouper, the average time period between two successive otolith rings is one year. However, an important point made by Moe (1969), Claro (1985), Rodríguez (1986) and Arreguín-Sánchez (1989) is that the time between rings may vary between

cohorts (age groups), which can lead to errors in the estimation of the age structure.

Most studies have assumed a normal distribution of age groups with similar variances and a stable growth pattern. However, the possibility of serious errors in mortality estimations has been reported (Arreguín-Sánchez et al. 1987b), particularly because the variance of size increases with age (Zetina 1990; Cabrera 1991; Contreras et al. 1994). A detailed description of the statistical distribution of age groups from backcalculated data provided by Rodríguez (1986) shows normal distributions for age groups, but changing variances between them suggesting that, while growth patterns are

Table 1. Parameters of the von Bertalanffy growth equation estimated for the red grouper (*Epinephelus morio*) from the Campeche Bank, Mexico, by several authors and methods. [Parámetros de la ecuación de crecimiento de von Bertalanffy estimados para el mero americano (*Epinephelus morio*) del Banco de Campeche, por varios autores y métodos.]

Method ^a	L _∞ (TL, cm)	K (year ⁻¹)	ϕ ^b	Reference
Otolith (ml)	79.2	0.179	3.05	Moe (1969)
Urohyal bones	87.5	0.099	2.88	González et al. (1974)
Otolith (ml)	92.8	0.112	2.99	Muhlia (1976)
Otolith (ml)	95.0	0.056	2.70	Valdés and Padrón (1980)
Urohyal bones (bc)	86.0	0.100	2.87	Valdés and Padrón (1980)
Otolith (ml)	80.2	0.159	3.01	Doi et al. (1981)
Otolith (bc)	82.0	0.184	3.09	Rodríguez (1986)
Mesopterigoids (bc)	89.1	0.123	2.99	Rodríguez (1986)
ELEFAN I	98.5	0.171	3.22	Arreguín-Sánchez et al. (1987b)
Otolith (ml)	82.1	0.135	2.96	Salazar (1988)
Otolith	93.6	0.120	3.02	Guzmán (1986)
SLCA	88.8	0.124	2.99	Arreguín-Sánchez (1992)
SLCA	90.0	0.114	2.97	-do-
SLCA	90.6	0.122	3.00	-do-
SLCA	90.0	0.063	2.71	-do-
SLCA	90.5	0.125	3.01	-do-
SLCA	87.7	0.051	2.59	-do-
SLCA	93.3	0.117	3.01	-do-
SLCA	103.0	0.129	3.14	-do-
SLCA	93.5	0.084	2.87	-do-
SLCA	101.5	0.174	3.25	-do-
SLCA	88.5	0.125	2.99	-do-
SLCA	88.9	0.080	2.80	-do-
SLCA	92.0	0.101	2.93	-do-
SLCA	91.6	0.123	3.01	-do-
SLCA	91.2	0.129	3.03	-do-
SLCA	85.6	0.087	2.80	-do-

^a ml = using mean length of age-class; bc = using backcalculated lengths; SLCA = Shepherd's Length Composition Analysis (Shepherd 1987).

^b ϕ = log₁₀ K + 2log L_∞ (Pauly and Munro 1984).

stable, the variability associated with each cohort has an important influence for the identification of population age structure. Moe (1969), Arreguín-Sánchez et al. (1990) and Mexicano-Cíntora (1990) reported variation in spawning season of 4-6 months, another important source of variation.

These difficulties in clearly defining the age structure of the *E. morio* stock are due to its being a long-lived species with longevity of 25-30 years (Manooch 1987) and a relatively slow growth rate. These characteristics, combined with a long spawning season, produce length distributions with great overlap between age groups, and usually showing few modes (Type 4 according to Shepherd et al. 1987). This

explains part of the high variation in growth estimates in Table 1.

Length-based growth studies were undertaken by Arreguín-Sánchez (1992), using several methods, on a comparative basis, including Shepherd's Length Composition Analysis, SLCA (Shepherd 1987b); Projection Matrix method, PROJMAT (Shepherd 1987a; Rosenberg and Beddington 1987; Basson et al. 1988) and the method proposed by MacDonald and Pitcher (1979) for analysis of distribution mixtures, MIX, to obtain age-groups from size-frequency data. Of these methods, only the SLCA offered acceptable results (Table 1); it can thus be expected that the recent improvements proposed by Pauly and Arreguín-Sánchez (1995)

should make it a method of choice for studying the growth of *E. morio*.

Mortality

Few studies on mortality and exploitation rates have been made, most of them assuming constant patterns with age and time, and providing general estimations without a description of their variance or uncertainty. Table 2 shows values obtained by several authors. Moreover, most mortality estimates are based on the catches of the mid-sized Mexican fleet, while only one considers all fleets.

Contreras et al. (1994) used virtual population analysis and found similar exploitation patterns for all the cohorts identified within the period 1973 to 1987, but different values of fishing mortality. According to them, fishing intensity, cohort strength and reproductive behavior have important influences on these patterns.

Arreguín-Sánchez (1992) developed an integrated model of catchability through which fishing mortality can be estimated. For juvenile fish, catchability and its variance can be considered to be constants, up

to age of maturity at four years, but thereafter they increase with age (Fig. 2). This means that fishing mortality is proportional to fishing effort only for immature fishes. As indicated by this author, the importance of the catchability pattern is that young fish are more accessible to fishing because they remain close to the coast, while adult fish catchability increases, because the spawning stock is highly vulnerable to fishing.

Recruitment

There are some isolated reports of recruitment. Arreguín-Sánchez (1987) estimated a recruitment index (r) with the form: $r = \ln((R/A) + 1)$, with R =number of recruits and A =number of adults, for incorporation within the Schaefer (1954, 1957) model according to Walters (1978). In general terms, he found that recruitment fluctuations produced variations of Maximum Sustainable Yield (MSY) of 3 000 t (around 20% of the average value of MSY level). Arreguín-Sánchez (1985) obtained a first estimate of the stock-recruitment relationship by fitting the Ricker (1954) model, and found that density-dependence could be reasonably

Table 2. Estimates of the instantaneous rates of mortality of the red grouper (*Epinephelus morio*) fishery from the Campeche Bank. [Estimaciones de las tasas instantáneas de mortalidad para la pesquería del mero americano (*Epinephelus morio*) del Banco de Campeche.]

Total mortality Z (year ⁻¹)	Natural mortality M (year ⁻¹)	Fishing mortality F (year ⁻¹)	References and remarks
0.485	0.200	-	Muhlia (1976)
0.260	-	-	Valdes and Padrón (1980)
0.542	0.330	0.212	Moreno (1980); mean for 1974 to 1979
0.580	0.330	0.150	Doi et al. (1981); mean for 1972 to 1976
0.819	0.437	0.382	Chávez and Arreguín-Sánchez (1986)
0.680	0.371	0.309	Chávez and Arreguín-Sánchez (1986)
0.680	0.371	(0.309)	Guzmán (1986)
0.987	0.397	0.590	Arreguín-Sánchez et al. (1987a, 1987b)
0.986	0.400	0.586	Salazar (1988)
0.350	-	-	Zetina (1990); estimates vary 26% on both sides
-	0.300	0.1 - 0.7	Contreras et al. (1994); range from age-based VPA
-	-	0.05-1.12	Arreguín-Sánchez (1992); range from a length-catchability pattern and fishing effort

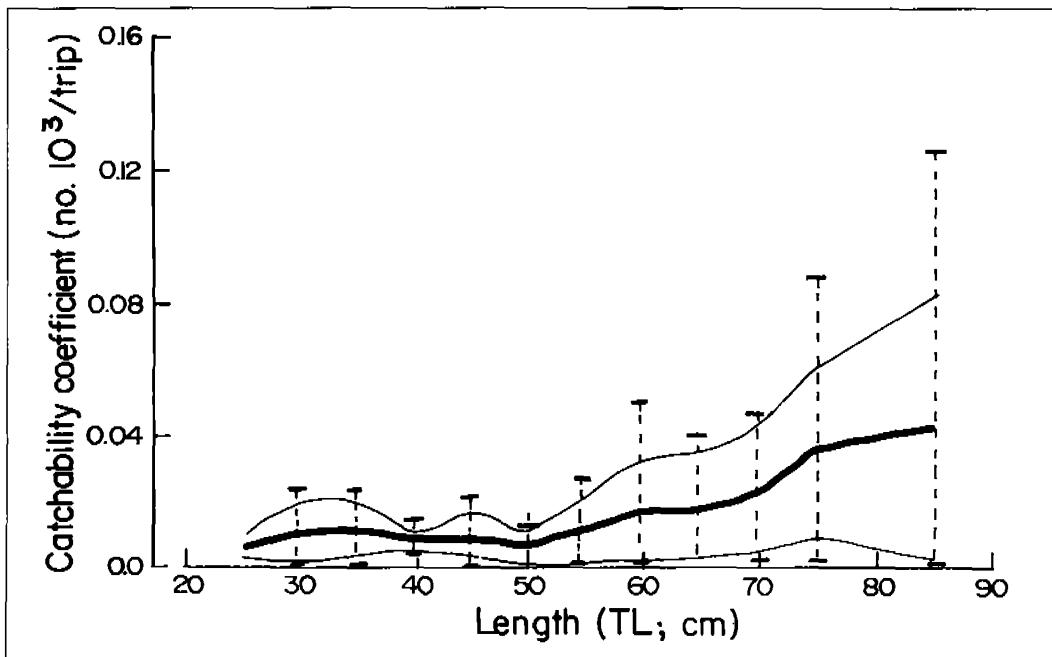


Fig. 2. Catchability-at-length pattern for the red grouper (*Epinephelus morio*) from the Campeche Bank, Mexico. Solid weighted line represents the average pattern over a period of 17 years; solid narrow lines indicate \pm one standard deviation; vertical lines represent the minimum and maximum values for each length class. Note that variance increases significantly from a fish length of 50 cm, which corresponds to the size at first maturity (from Arreguin-Sánchez 1992). [Patrón de cambio de la capturabilidad con la longitud para el mero americano (*Epinephelus morio*) del Banco de Campeche, México. Línea sólida gruesa representa la tendencia promedio para un periodo de 17 años; las líneas sólidas delgadas indican los límites definidos por \pm una desviación estándar; las líneas verticales representan los valores mínimos y máximos para cada clase de longitud. Nótese que la varianza aumenta significativamente a partir de peces con una longitud de 50 cm, la cual corresponde a la talla de primera madurez (tomado de Arreguin-Sánchez 1992).]

explained by the species' habits (i.e., gregarious behavior, territoriality and active predatory behavior). On the other hand, seasonal recruitment patterns obtained by Arreguin-Sánchez et al. (1987b) through the procedure suggested by Pauly (1982), and by simulation experiments (Seijo 1986), show a recruitment timed with spawning during winter and early spring.

A comparative recruitment index (Arreguin-Sánchez 1992) of relative annual abundance of recruits (one-year old fish)

with respect to the average recruitment abundance, showed that during the 17 years analyzed there had been an important fall in recruitment, for the year class of 1980. Also the recruitment index tended to decrease after 1980 with respect to the level observed for the previous years. Because relative abundances are measured as catch-per-unit-effort, it is not possible to define whether this decrease of recruitment (Fig. 3) corresponds to a real decreasing population size, or to another factor affecting fish vulnerability. The most

important point here is that the recruitment fall in 1980 had important consequence for yields. The fall in recruitment during 1980 might have been associated with an oil spill on Campeche Bank which occurred over a period of nine months that included the spawning season of red grouper (and other aquatic organisms).

Stock Assessment

Assessments of the red grouper stocks are not done routinely; however, reports on the state of exploitation at certain times

have agreed with historical catch trends. Fig. 4 shows the trends corresponding to the development stage of the fishery, followed by a level close to the MSY, followed by a decline in catches, suggesting that the resource is being exploited at or beyond its maximum biological capacity (Arreguín-Sánchez 1985, 1987a, 1987b; Fuentes and Contreras 1986; García et al. 1986; Seijo 1986), particularly because fishing intensity has remained fairly constant over the last ten years.

Seijo (1986) developed a simulation model which incorporated biological, economic

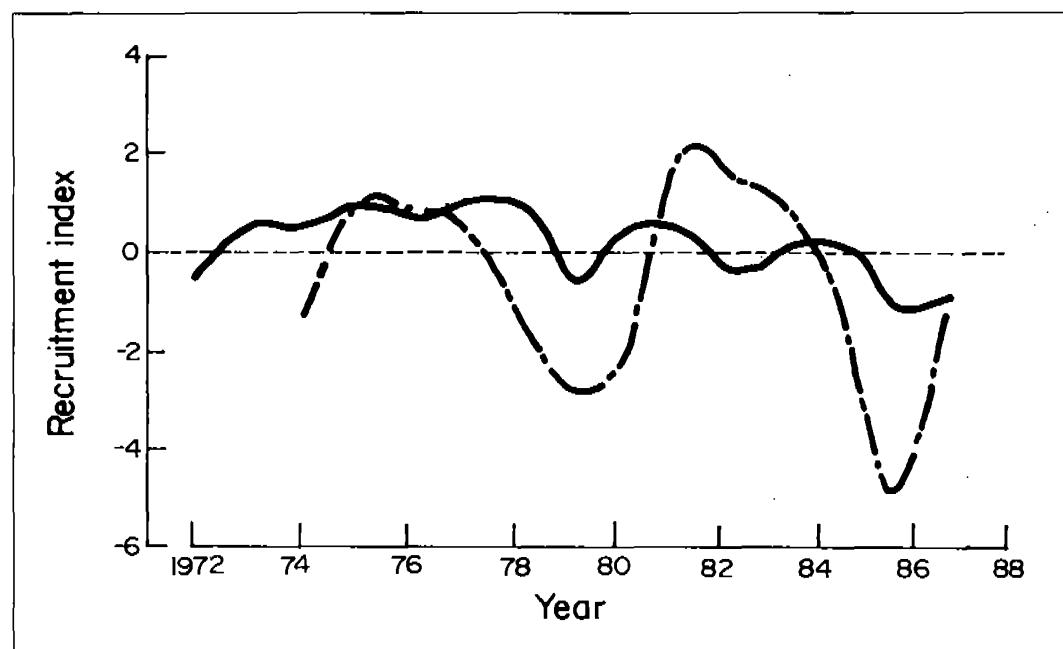


Fig. 3. Recruitment fluctuations of the red grouper stock from the Campeche Bank, as estimated from departure of the annual abundance of juvenile fish, relative to the average population, over a period of 17 years (following Arreguín-Sánchez 1992). Solid line represents recruits to the mid-sized Mexican fleet (one-year old), while dashed line indicates recruits to the Cuban fleet (five-year old). For explanation, see text. [Fluctuaciones del reclutamiento de la población de mero americano del Banco de Campeche, expresado como la diferencia de la abundancia relativa anual de juveniles, con respecto a la estructura promedio de la población obtenida para un período de 17 años (de acuerdo con Arreguín-Sánchez 1992). La línea continua representa los reclutas a la flota mediana de México (peces de un año de edad), y la línea discontinua representa el reclutamiento a la flota cubana (peces de cinco años de edad).]

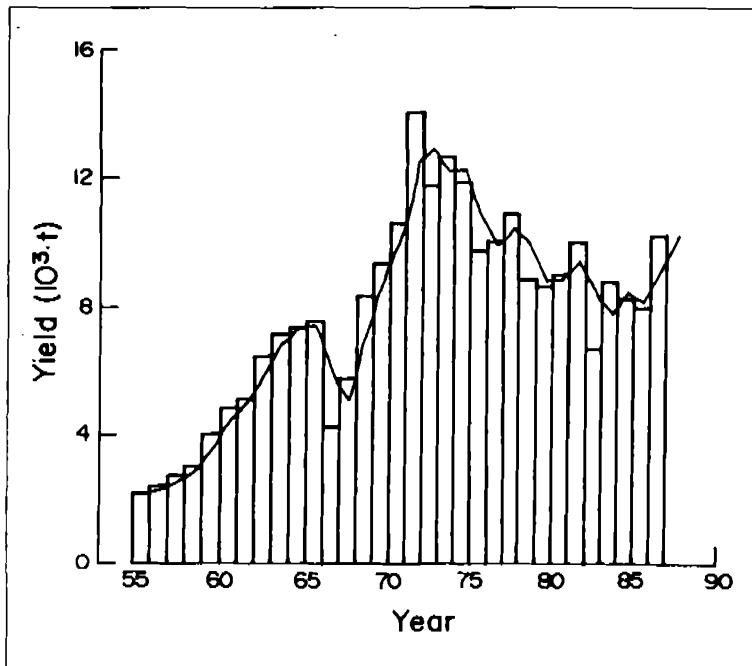


Fig. 4. Historical trends of yields for the red grouper (*Epinephelus morio*) fishery from the Campeche Bank, Gulf of Mexico; 1956-1987. [Tendencia histórica de las capturas de la pesquería del mero americano (*Epinephelus morio*) del Banco de Campeche, Golfo de México; 1956-1987.]

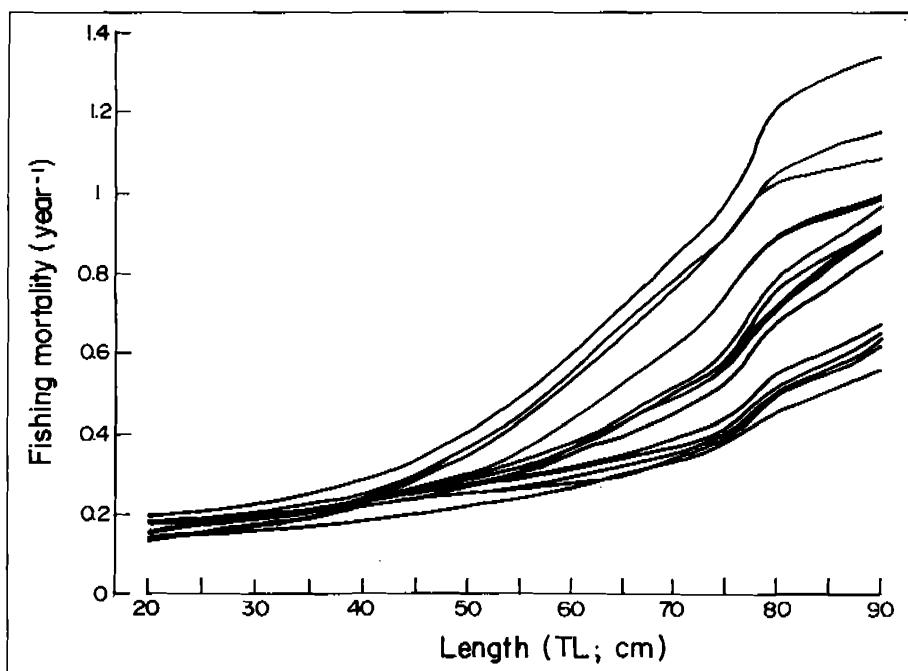


Fig. 5. Annual fishing mortality-at-length within the period of 1973 to 1987, for the middle-sized fleet of Mexico, for the red grouper fishery from the Campeche Bank (from Arreguin-Sánchez 1992). [Patrón de cambio de la mortalidad por pesca anual con la longitud para el período 1973 a 1987, para la flota mediana de México de la pesquería de mero americano del Banco de Campeche (tomado de Arreguin-Sánchez 1992).]

and institutional aspects, taking into account the three fleets participating in this fishery. His conclusions show a clear trend towards overfishing, probably caused by a high pressure on juveniles by the artisanal fleet. (Note that the simulation was started with the estimated age structure of December 1985.) On the other hand, Arreguin-Sánchez (1992) calculated from the logistic model the time of recovery of the exploited population under different fishing intensities. His estimations based on catch and effort data, indicate that in the absence of fishing and at average recruitment levels, the population would need five years to attain a size equivalent to 0.5 of the maximum population which can be sustained by the ecosystem (carrying capacity) 14 years at the exploitation rate prevailing in 1986.

Contreras et al. (1994) using cohort analysis and VPA have shown a decrease of nearly 30% in population size since 1980, at levels of exploitation similar to those estimated for the previous decade. These results do not completely agree with other studies, because the effect of fishing intensity as the cause for the decrease of the population size is not clearly shown.

The integrated catchability model suggested by Arreguin-Sánchez (1992) (involving size, time, density dependence and between-fleet effects) enabled estimation of fishing mortality and population size independently of VPA. The complete model is expressed by the relationship

$$F(l,t,f,E) = q(l,t,f,E) E(t,f)$$

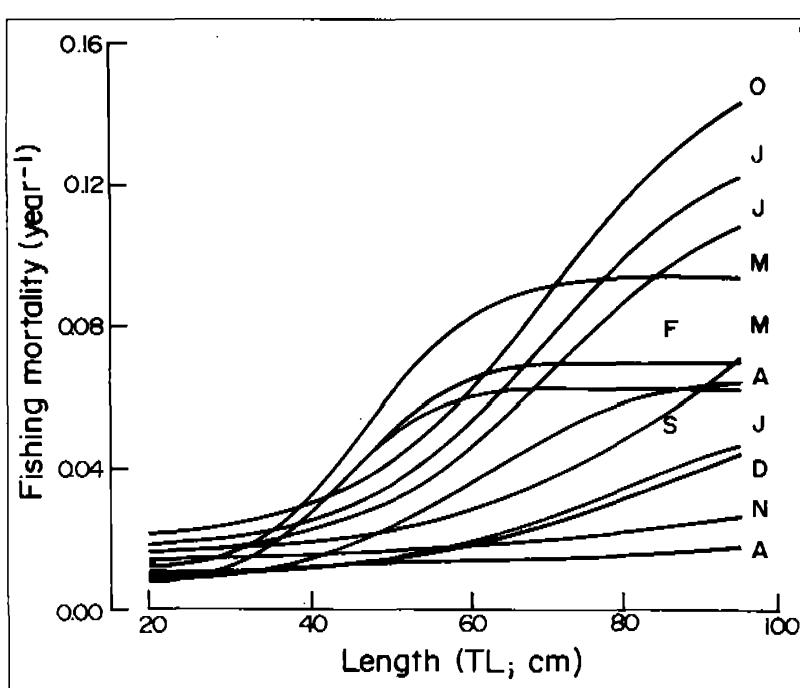


Fig. 6. Monthly fishing mortality-at-length during 1978, for the middle-sized fleet of Mexico, for the red grouper (*Epinephelus morio*) fishery from the Campeche Bank (from Arreguin-Sánchez 1992). [Patrón de cambio mensual de la mortalidad por pesca con la longitud, durante 1978, para la flota mediana de México de la pesquería de mero americano (*Epinephelus morio*) del Banco de Campeche (tomado de Arreguin-Sánchez 1992).]

where l is the length-class, t is the year (y) or month (m) times, f is a fleet index, and E is the amount of fishing, expressed by the fishing effort as the main factor affecting population abundance. Fig. 5 exhibits the annual fishing mortality from 1973 to 1987 for the MCS fleet of Mexico. Fig. 6 shows the pattern of monthly fishing mortality for 1978 for the MDS fleet, while Fig. 7 depicts the monthly fishing mortality rates for ART fleet during 1987.

The size of the fishable stock was estimated by Arreguín-Sánchez (1992) based on the catchability patterns described above, and the fishing effort exerted by each fleet to obtain an estimate for population size per year. Results (Table 3; Fig. 8) indicate that population size varies, but suggest a stable situation of the resource.

Discussion

The growth studies performed to date suggest that more emphasis should be placed on the analysis of hard parts to estimate age and to validate growth estimations. Some otolith-based estimates appear to be outside the region where most values were observed. This could mean that techniques for the analysis of otoliths must be reviewed and improved, to permit adequate definition of the age structure of catches and other population parameters. Length-based methods appear to be an alternative to estimate growth. However, the length-structured data will reflect selection during fishing operations, and the length-frequency distributions will not accurately represent the population structure (Arreguín-Sánchez 1992).

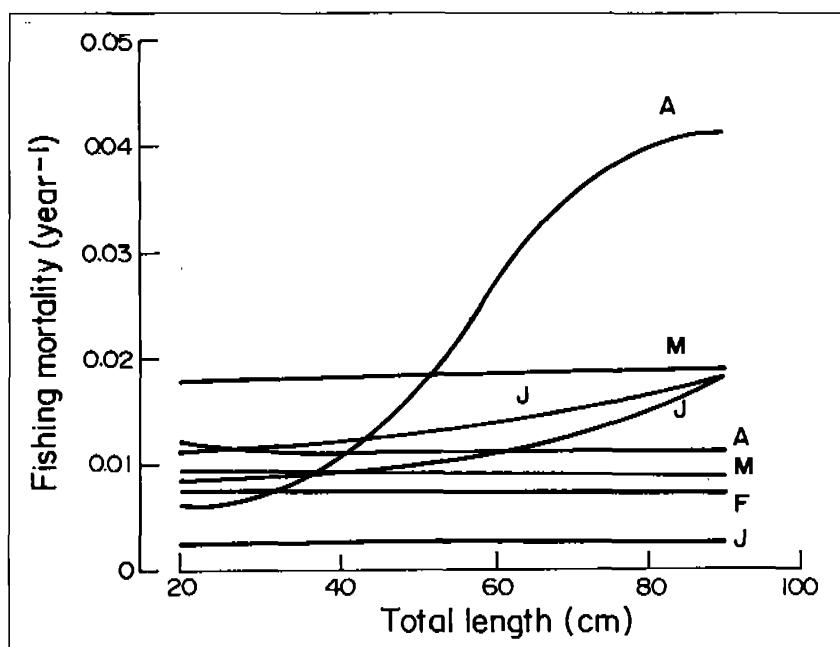


Fig. 7. Monthly fishing mortality-at-length during 1987, for the artisanal fleet of Mexico, for the red grouper (*Epinephelus morio*) fishery from the Campeche Bank (from Arreguín-Sánchez 1992). [Patrón de cambio mensual de la mortalidad por pesca con la longitud, durante 1987, para la flota artesanal de México de la pesquería de mero americano (*Epinephelus morio*) del Banco de Campeche (tomado de Arreguín-Sánchez 1992).]

Table 3. Population size estimated from data of the mid-sized Mexican fleet and the Cuban fleet. [Tamaño de la población estimada a partir de datos de ambas flotas, la de mediano tamaño de México y la flota Cubana.]

Year	Numbers of fish ($\times 10^6$)	
	Without density-dependent effects	With density-dependent effects
1975	111 889	106 003
1976	83 889	82 490
1977	78 135	76 743
1978	77 651	77 578
1979	72 835	80 274
1980	90 207	81 624
1981	82 190	90 603
1982	97 282	110 301
1983	91 825	91 883
1984	81 574	84 742
1985	73 708	76 345
1986	100 878	92 254
1987	87 590	80 157

This could be of particular importance for those species caught while part of spawning aggregations.

Estimates of natural mortality are scarce. In fact, values reported in the literature come from empirical equations or were assumed (Muhlia 1976). This aspect must be emphasized in further population dynamics studies because the estimated range is $0.20 \leq M \leq 0.44 \text{ year}^{-1}$, or, over 200% of the lowest value.

Estimates of fishing mortality, F, have been obtained by different methods. However, detailed analysis has been presented only by Contreras et al. (1994), who used an age-based VPA method, and by Arreguín-Sánchez (1992), who used the catchability method described above. Both studies were applied approximately to the same years and both show that the stocks are exploited and

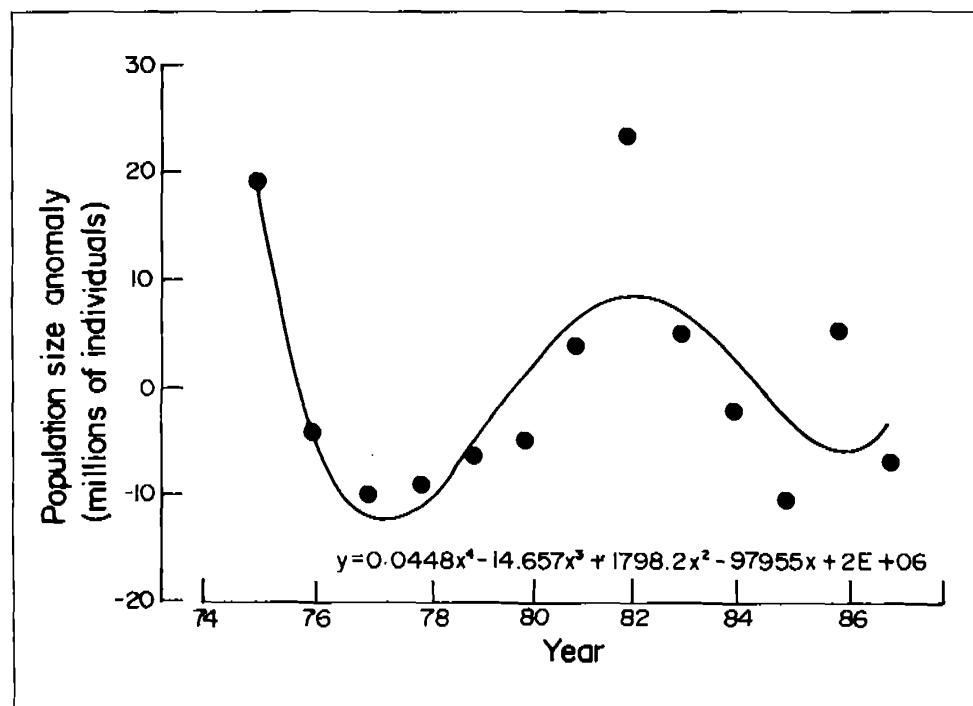


Fig. 8. Fluctuations in population size estimated for the red grouper (*Epinephelus morio*) stock from the Campeche Bank. Notice that cycles tend to be completed in an 8-year period. [Fluctuaciones en el tamaño de la población estimada para el mero americano (*Epinephelus morio*) del Banco de Campeche. Obsérvese que los ciclos tienden a ser completados en un período de ocho años.]

that fishing mortality must be controlled. However, the age-based VPA suggests that the average population decreased by around 30%, while the other study indicates that the population has remained reasonably stable. This matter remains to be resolved.

There is still a lack of quantitative data concerning the sizes of cohorts. This is a serious constraint for a fully exploited resource where the juveniles and sub-adults are subjected to intense exploitation. In terms of management, the Spawning Stock: Recruitment relationship (SSRr) is a very important aspect to be addressed by researchers. Controls on fishing mortality of juveniles (as generated by the artisanal fleet) and on adults (as generated by the mid-sized and Cuban fleets during aggregation) must be established. However they should be based on quantitative information provided by the SSRr.

Red grouper is a gregarious species which has seasonal reproductive aggregations. According to Shapiro (1987), the mechanism which initiates sexual maturity is not well known, but it seems related to environmental changes affecting metabolic processes. Adult fishes mature in response to environmental stimuli, probably more related to spatial distribution than to a specific size. Arreguín-Sánchez (1992) has suggested a probable synchrony with the seasonal upwelling on the eastern end of the continental shelf reported by Ruiz and Merino (1989). Because an important part of the fishing operations are related to the fish aggregation, the SSRr, combined with environmental data and information on vulnerability, might provide information on possible controls and critical times, to determine the number of adults which must escape from fishing to guarantee the stability of the stock. The lack of knowledge on the processes behind the SSRr suggests that they must be included in further research efforts to support management decisions.

Population size estimates suggest that stock abundances fluctuate with an 8-year periodicity. Although there is presently no explanation for these cycles, they are very important in terms of management: most of the studies undertaken during the early 1980s mentioned a declining population abundance, interpreted as evidence of excessive fishing effort. In this case, although the diagnosis was right, the assigned causes were erroneous. However, the most important point here is the management process, because it must consider these variations if restrictions on catch and fishing effort are to be used as main management measures. How these measures will impact the fishery; either positively and encouraging stability or negatively and promoting decline, will depend on the relative situation of the stock. Our recommendation is that a proper fishing management regime must be revisited every year.

References

- Arceo, P., D. Fuentes, R. Puerto, M. Contreras, V. Moreno and L. Juárez. 1987. Sinopsis de datos biológicos del mero (*Epinephelus morio*, Valenciennes). Dcto. Técnico. Centro Regional de Investigaciones Pesqueras, Yucalpetén, Instituto Nacional de Pesca, México.
- Arreguín-Sánchez, F. 1987a. Present status of the red grouper fishery in the Campeche Bank. Proc. Gulf Caribb. Fish. Inst. 38:498-509.
- Arreguín-Sánchez, F. 1987b. Estado actual de la explotación del mero (*Epinephelus morio*) del Banco de Campeche. 25 Aniv. Instituto Nacional de Pesca, Centro Regional de Investigaciones Pesqueras, Yucalpetén, Instituto Nacional de Pesca, México. 23 p.
- Arreguín-Sánchez, F. 1989. Investigaciones para el manejo y administración racional de pesquerías tropicales. Avance y Perspectiva. CINVESTAV-IPN (México) 37(8):31-41.
- Arreguín-Sánchez, F. 1992. An approach to the study of the catchability coefficient with

- application to the red grouper (*Epinephelus morio*) fishery from the continental shelf of Yucatan, Mexico. Centro de Invest. Estudios Avanzados del Instituto Politécnico Nacional, México. 222 p. Ph.D. dissertation.
- Arreguín-Sánchez, F. and E.A. Chávez. How marine shelf fisheries are depending on mangrove ecosystems: the Campeche Bank, Mexico as an example. In A. Yáñez-Arancibia and A.L. Lara-Domínguez (eds.) Valoración económica de los manglares. EPOMEX Serie Científica 6. (In press).
- Arreguín-Sánchez, F., J.C. Seijo, D. Fuentes and M.J. Solís-Ramírez. 1987a. Estado del conocimiento de los recursos pesqueros de la península de Yucatán y región adyacente. Contr. Inv. Pesq. Dcto. Técnico 4. Centro Regional de Investigaciones Pesqueras, Yucalpetén, Instituto Nacional de Pesca, México. 41 p.
- Arreguín-Sánchez, F., M.A. Cabrera and G. Mexicano-Cíntora. 1987b. Dinámica de la pesquería de mero (*Epinephelus morio*) del Banco de Campeche, p. 81-87. In E.M. Ramirez (ed.) Mem. Simp. Biol. Ocean. Pesq. México. La Paz, B.C.S., México. 183 p.
- Arreguín-Sánchez, F., M. Contreras, V. Moreno, M.A. Cabrera and R. Burgos. 1990. Dinámica de la población y evaluación de la pesquería de mero (*Epinephelus morio*) de la plataforma continental de Yucatán. Inf. Téc. Invest. Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional-Mérida, Centro Regional de Investigaciones Pesqueras, Yucalpetén Instituto Nacional de Pesca, México. 62 p.
- Arreguín-Sánchez, F., J.C. Seijo and E. Valero. 1993. An application of ECOPATH II to the north continental shelf ecosystem of Yucatan, Mexico, p. 269-278. In V. Christensen and D. Pauly (eds.) Trophic models of aquatic ecosystems. ICLARM Conf. Proc. 26, 390 p.
- Basson, M., A.A. Rosenberg and J.R. Beddington. 1988. The accuracy and reliability of two new methods for estimating growth parameters from length frequency data. J. CIEM 44:227-285.
- Böhlke, J.E. and C.C.G. Chaplin. 1968. Fishes of the Bahamas and adjacent tropical waters. Acad. Nat. Sci. (Philadelphia) XXI, 771 p.
- Burgos, R. 1987. Operaciones y rendimientos de la flota pesquera mayor de Yucatan durante 1985. Contr. Invest. Pesq. Dcto. Téc. 3. Centro Regional de Investigaciones Pesqueras, Yucalpetén, Instituto Nacional de Pesca, México.
- Cabrera, M.A. 1991. Efectos de cambios en la varianza y tamaño del intervalo en la estimación de los parámetros de crecimiento del mero *Epinephelus morio*. Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Mérida, México. 97 p. Tesis maestría en ciencias.
- Chávez, E.A. and F. Arreguín-Sánchez. 1986. Evaluación de los recursos pesqueros de la península de Yucatán, México. Inf. Téc. Invest. Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Mérida. México.
- Claro, R. 1985. Ecología de los peces marinos de Cuba. Simp. Cienc. Mar. y VII Jornada Cient. Inst. Oceanología. XX Aniv. Acad. Cienc. (Cuba) 1:19-65.
- Contreras, M., F. Arreguín-Sánchez, J.A. Sánchez, V. Moreno and M.A. Cabrera. 1994. Mortality and population size of the red grouper (*Epinephelus morio*) fishery from the Campeche Bank. Proc. Gulf Caribb. Fish. Inst. 43:309-410.
- Doi, T., D. Mendizabal and M. Contreras. 1981. Análisis preliminar de la población de mero *Epinephelus morio* (Valenciennes) en el Banco de Campeche. Cienc. Pesq. (México) 1(1):1-16.
- Fuentes, D. 1991. La pesquería de mero en el Banco de Campeche. Mem. VII Congr. Nal. Oceanol. Ensenada, B.C. (México) 1:361-374.
- Fuentes, D. and M. Contreras. 1986. Situación de la pesquería de mero (*Epinephelus morio*) en Yucatán: Análisis 1985. Inf. Téc. Centro Regional de Investigaciones Pesqueras, Yucalpetén, Instituto Nacional de Pesca, México.
- García, F., P. Arceo and R. Puerto. 1986. Análisis de la pesquería de mero (*Epinephelus morio*) del Banco de Campeche durante el período 1982-1984 según los modelos de Schaefer y Fox. Inf. Téc. Centro Regional de Investigaciones Pesqueras, Yucalpetén, Instituto Nacional de Pesca, México.

- González, M.E. 1988. Análisis de la pesquería de huachinango (*Lutjanus campechanus*) del Banco de Campeche, México. Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Mérida, México. Tesis maestría en ciencias.
- González, P.D., S. Zupanovic and H.E. Ramis. 1974. Biología pesquera de la cherna americana del Banco de Campeche. Centro de Investigaciones Pesqueras, Cuba. Res. Invest. 1:107-111.
- Guzmán, E. 1986. Contribución al conocimiento de la pesquería de mero (*Epinephelus morio*, Valenciennes) de las costas de Yucatán. Escuela Nacional de Estudios Profesionales-Iztacala, Universidad Nacional Autónoma de México. Tesis profesional.
- MacDonald, P.D.M. and T.J. Pitcher. 1979. Age-groups from size-frequency data: a versatile and efficient method of analyzing distribution mixtures. J. Fish. Res. Board Can. 36(8):987-1001.
- Manooch, C.S., III. 1987. Age and growth of snappers and groupers, p. 329-374. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Mexicano-Cíntora, G. 1990. Análisis preliminar de algunos aspectos reproductivos del mero (*Epinephelus morio*) de las costas de Yucatan. Rep. Espec. Acad. Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Mérida, México. 42 p.
- Moe, M.A., Jr. 1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Florida Dept. Nat. Res. Prof. Pap. Ser. 10:95 p.
- Moreno, V. 1980. La pesquería de mero (*Epinephelus morio*) en el Estado de Yucatan. Univ. Autón. Edo. Morelos, México. Tesis profesional.
- Muhlia, A. 1976. Aspectos biológico-pesqueros de *Ephinephelus morio* (Val.): mero. Mem. Primer Simp. al. Rec. Pesq. Mas. México 2:223-265. Instituto Nacional de Pesca, México.
- Oleachea, A. 1975. Distribución y abundancia de peces demersales y su relación con la temperatura de aguas de fondo. Centro de Investigaciones Pesqueras, Cuba. Resúm. Invest. 2:161.
- Ordaz, D. 1993. Estudio sobre la mojarra (*Calamus nodosus*) de las costas de Yucatan. Inst. Tecnol. Mar., Veracruz, México. Tesis profesional.
- Pauly, D. and J.L. Munro. 1984. Once more on the comparison of growth in fish and invertebrates. Fishbyte 2(1):21.
- Pauly, D. 1982. Studying single species on a multispecies context, p. 33-70. In D. Pauly and G.T. Murphy (eds.) Theory and management of tropical fisheries. ICLARM Conf. Proc. 9, 360 p.
- Pauly, D. and F. Arreguín-Sánchez. 1995. Improving Shepherd's length composition analysis (SLCA) method for growth parameter estimation. Naga, ICLARM Q. 18(4):31-33.
- Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 30:409-434.
- Rodríguez, H. 1986. Estudio comparativo de dos estructuras rígidas (otolito y hueso mesopterigoide) para la estimación de edad y crecimiento del mero (*Epinephelus morio*) del Banco de Campeche. Univ. Autón., Nuevo León, México. Tesis profesional.
- Rosenberg, A.A. and J.R. Beddington. 1987. Monte-Carlo testing of two methods for estimating growth from length-frequency data with general conditions for their applicability, p. 283-298. In D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.
- Ruiz, F. and M. Merino. 1989. Upwelling off the north coast of the Yucatan Peninsula, p. 149-160. In E.A. Chávez (ed.) Australia-Mexico Workshop in Marine Science. Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Mérida, Mexico and CSIRO, Australia.
- Saenz, M., F. Mendoza and J.C. Pisté. 1987. Diagnosis de la pesquería artesanal del estado de Yucatán. Centro Regional de Investigaciones Pesqueras, Yucalpetén, Instituto Nacional de Pesca, México. Contr. Inv. Pesq. Dcto. Téc. 5, 43 p.
- Salazar, A.R. 1988. Contribución al conocimiento de la pesquería de mero (*Epinephelus*

- morio*) de la flota menor de las costas de Yucatán. Escuela Nacional de Estudios Profesionales, Iztacala, Universidad Nacional Autónoma de México. Tesis profesional.
- Schaefer, M.B. 1954. Some aspects of the dynamics of populations important to the management of the commercial marine fisheries. Inter-Am. Trop. Tuna Comm. Bull. 1:27-56.
- Shaefer, M.B. 1957. A study of the dynamics of the fishery for the yellowfin tuna in the eastern tropical Pacific Ocean. Inter-Am. Trop. Tuna Comm. Bull. 2:247-268.
- Seijo, J.C. 1986. Comprehensive simulation model of the tropical demersal fishery: red grouper (*Epinephelus morio*) of the Yucatan continental shelf. Michigan State University, East Lansing, Michigan. 210 p. Ph.D. dissertation.
- Shapiro, D.Y. 1987. Reproduction in groupers, p. 295-328. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Shepherd, J.G. 1987a. Towards a method for short term forecasting of catch rates based on length compositions, p. 167-176. In D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.
- Shepherd, J.G. 1987b. A weakly parametric method for estimating growth parameters from length composition data, p. 113-119. In D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.
- Shepherd, J.G., G.R. Morgan, J.A. Gulland and C.P. Mathews. 1987. Methods of analysis and assessment; report of working group II, p. 353-362. In D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.
- Smith, C.L. 1971. Synopsis of biological data on groupers (*Epinephelus morio* and allied genera) of the western north Atlantic. Bull. Am. Mus. Nat. Hist. 146(2):67-242.
- Valdés, E. and G. Padrón. 1980. Pesquerías de palangre. Rev. Cub. Invest. Pesq. 5(2):38-52.
- von Bertalanffy, L. 1938. A quantitative theory of organic growth (inquiries on growth laws II). Hum. Biol. 10(2):181-213.
- Walters, G.G. 1978. A surplus yield model incorporating recruitment and applied to a stock of Atlantic mackerel. J. Fish. Res. Board Can. 35:229-234.
- Zetina, C. 1990. Estudio de la mortalidad del mero (*Epinephelus morio*) en el Banco de Campeche. Centro de Investigación y de Estudios Avanzados del Instituto Politécnico Nacional, Mérida, México. 126 p. Tesis maestría en ciencias.

ENTERED IN NAGA

APR 14 1998

FishBase and AUXIM as Tools for Comparing Life-history Patterns, Growth and Natural Mortality of Fish: Applications to Snappers and Groupers^a

D. PAULY

*International Center for Living Aquatic Resources Management
MCPO Box 2631
0718 Makati City, Metro Manila, Philippines*

*Fisheries Centre, 2204 Main Mall
University of British Columbia, Vancouver, B.C.
Canada V6T 1Z4.*

C. BINOHLAN

*International Center for Living Aquatic Resources Management
MCPO Box 2631
0718 Makati City, Metro Manila, Philippines*

PAULY, D. and C. BINOHLAN. 1996. FishBase and AUXIM as tools for comparing the life-history patterns, growth and natural mortality of fish: applications to snappers and groupers [*FishBase y AUXIM como herramientas para comparación de patrones de estrategias de vida, crecimiento y mortalidad natural de peces: aplicación a pargos y meros*], p. 218-243. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

The FishBase 96 CD-ROM, the computerized encyclopedia of fishes, contains, among other things, 4 434 fully documented sets of growth parameters for 1 115 species, and 170 families of fish. This allows definition of the growth patterns typical of various taxa, and the prediction of likely growth parameters in little studied groups, as well as the identification of outliers in well studied ones. A software tool called AUXIM is presented which, based on growth parameters, facilitates definition and quantification of the "growth space" inhabited by various taxa, here the Lutjanidae (117 cases; 15 spp.) and the Epinephelinae (34 cases; 6 spp.).

It is shown that AUXIM and its underlying concept, the growth performance index ϕ' , can be used to verify ages and/or growth parameter estimates in species for which previous growth parameter estimates exist, and to infer likely growth parameters in unstudied species.

Various predictors of natural mortality (M) in groupers and snappers are examined, and earlier work by S. Ralston is confirmed which suggested that the von Bertalanffy parameter K is a good predictor of M for this very homogenous group of fishes.

FishBase graphs on the longevity of lutjanids and the brain size of serranids are finally used to illustrate the power of FishBase for presenting in fishes previously unconnected aspects of their life-history, and morphology, respectively.

^a ICLARM Contribution No. 1334

Resumen

El CD-ROM de FishBase 96, la enciclopedia computarizada de peces contiene, entre otras cosas, 4 434 conjunto de datos sobre parámetros de crecimiento totalmente documentados para 1 115 especies, y 170 familias de peces. Esto permite la definición de parámetros de crecimiento típicos de varios taxa, y la predicción de valores aproximados para pequeños grupos poco estudiados, así como la identificación de estimaciones erróneas en aquellos bien conocidos. También se presenta un programa llamado AUXIM el cual, con base en los parámetros de crecimiento, facilita la definición y cuantificación del "espacio de crecimiento" en el cual se ubican los diferentes taxa, en este caso los Lutjanidos (117 casos; 15 especies) y los Epinephelidos (34 casos; 6 especies).

Se muestra AUXIM, y el concepto que lo sostiene, el índice de crecimiento ϕ' , puede ser usado para verificar edades y/o estimaciones de parámetros de crecimiento en especies no estudiadas.

Se examinan varios predictores de mortalidad natural (M) para pargos y meros y el trabajo inicial de S. Ralston es confirmado, el cual sugiere que el parámetro K de la ecuación de von Bertalanffy es un buen predictor de M para este muy homogéneo grupo de peces.

Finalmente se utilizan algunas gráficas de FishBase sobre longevidad de lutjanidos y el tamaño del cerebro de serranidos para ilustrar el poder de FishBase para presentar aspectos sobre ciclos de vida y morfología de peces que anteriormente aparecían desconectados entre si.

Introduction

Growth and mortality studies of fish have been crucial to the emergence of fisheries biology as a discipline of its own (Petersen 1891; Baranov 1918; Mohr 1927, 1930, 1943, 1994; Beverton and Holt 1959; Smith 1994). This has resulted in large amounts of size-at-age data, growth curves and growth parameters, and of estimates of natural mortality having been published in a widely scattered literature. However, attempts to derive theories from these data have been few and generally marred by *ad hoc* explanations, suited for only a small subset of the data at hand (e.g., Weatherley and Gill 1987). One reason for this may be that the regularity among species, genera, and families of fish growth and mortality patterns had not been made visible to the practitioners, who are thus left to deal with what they believe are peculiar features of their favorite taxa.

The need to overcome parochialism of this sort, and related considerations led, in the late 1980s to the launching by ICLARM of the FishBase Project, devoted to the creation of a database on fish, which would make available to fishery biologists and other scientists key data on all fish species of the

world, among other things, to provide a basis for new insights and generalizations, e.g., on growth and mortality patterns.

An early version of FishBase was presented at the workshop of which this volume is the proceedings, but the following account is based on the data in FishBase 96, whose CD-ROM was released in June 1996 (Froese and Pauly 1996), and on material extracted from the other contributions in this volume (to be included in the 1997 release of FishBase).

Materials and Methods

Materials

Comparing vectors of sizes-at-age is possible, but is not a straightforward way of comparing the growth parameters of fish, especially when they widely differ in their longevity.

Rather, parameters expressing the shape of a growth curve can be compared, e.g., the parameters L_∞ and K of the von Bertalanffy growth function (VBGF), viz

$$L_t = L_\infty (1 - \exp (-K (t - t_0))) \quad \dots 1$$

where L_t is the mean predicted length at age t , L_∞ is the mean length the fish would

reach if they were to grow forever, K expresses the rate (here always with unit year^{-1}) at which L_∞ is approached, and t_0 is the theoretical age the fish would have at length zero, were they to grow according to the VBGF from the onset on (Bertalanffy 1938; Beverton and Holt 1959; Pauly 1980). Note that t_0 is of no importance to the considerations which follow.

The data for this contribution were all taken from the POPGROWTH table of FishBase, whose layout is detailed in Binohlan and Pauly (1996a). Overall, 250 sets of growth parameters were extracted, pertaining to 41 species of Serranidae (subfamily Epinephelinae, i.e., groupers) and to 43 species of Lutjanidae, i.e., snappers (Table 1). These species' taxonomic status is as defined in the recent revision of Heemstra and Randall (1993) and Allen (1985), respectively.

Also, 29 independent estimates of natural mortality (M ; year^{-1}) were extracted from the relevant fields of the POPGROWTH Table (Table 2).

To ensure comparability of the growth and mortality parameter sets, estimates of asymptotic size initially expressed as fork (FL) or standard length (SL) were re-expressed as total length (TL), based on the taxonomically correct graphs in the above-cited species catalogues. Estimates of W_∞ , the weights corresponding to L_∞ , were obtained by using appropriate length-weight relationships in the LENGTH WEIGHT Table of FishBase 96 (Binohlan and Pauly 1996b).

Methods for growth comparisons

Our first approach for demonstrating the presence of strong patterns among growth parameters uses the plotting routine of FishBase 96, i.e., to output its growth-related graphs, showing all relevant entries in the database (lighter dots), with the entries

for Epinephelinae and Lutjanidae superimposed as black dots.

Our second approach is to compute for each set of growth parameters the corresponding value of the growth performance index ϕ' , defined by

$$\phi' = \log_{10} K + 2 \log_{10} L_\infty \quad \dots 2)$$

where K is year^{-1} and $L_\infty(\text{TL})$ is expressed in cm.

Our third method to document patterns of growth performance in groupers and snappers is to analyze the available growth parameters using AUXIM, a software package documented in Pauly et al. (1996), based on the theory of fish growth of Pauly (1979) and further developed in Pauly (1994) and in Longhurst and Pauly (1987).

This software is built on the observation that in closely related groups (e.g., in population of the same species, and usually in species of the same genus), L_∞ and K not only tend to vary inversely (as has been widely reported in the literature), but that their interrelationship can be more precisely captured by

$$\log K = \phi' - 2 \log L_\infty \quad \dots 3)$$

i.e., the inverse of equation (2), and wherein the slope (2) is the mean of a large number of plots of the same forms as equation (3) (Pauly 1979).

In reality, however, observed pairs of L_∞ , K , pertaining, e.g., to different populations of the same species are not aligned as suggested by equation (3), but form ellipsoid clouds, whose main axis has a mean slope of -2 (Pauly 1979; Moreau et al. 1986; Pauly 1991). Such ellipses can be designed to define the 95% confidence perimeter around the data points representing sets of growth parameters from a given species (Pauly et al. 1996), which can be taken as defining

Table 1. Growth parameters of groupers and snappers in FishBase. [Parámetros de crecimiento de meros y pargos en FishBase.]

	W _∞ (g)	L _∞ (TL, cm)	K (year ⁻¹)	Sex	Data type/ Method	References ^a
Family Serranidae						
Subfamily Epinephelinae						
<i>Cephalopholis crenata</i>						
Curaçao I.	1218	42	0.13	unsexed	1/-	3090
Jamaica	704	34	0.35	unsexed	6/b	3090
Jamaica	690	34	0.34	unsexed	6/b	29
<i>Cephalopholis fulva</i>						
Jamaica	638	34	0.63	unsexed	6/b	29
Virgin Is. US	378	31	0.143	unsexed	5/-	1475
<i>Cephalopholis hemistictos</i>						
Kuwait	1100	34.1	0.11	unsexed	1/f	3639
<i>Epinephelus adscensionis</i>						
Virgin Is. US	1900	49.9	0.11	unsexed	5/-	1475
<i>Epinephelus aeneus</i>						
Egypt	73000	136	0.15	unsexed	-/-	5760
Morocco	1360	85	0.247	male	-/d	312
Morocco	2430	100	0.226	female	-/b	312
Sénégal	47000	144	0.171	unsexed	1/f	2013
<i>Epinephelus areolatus</i>						
Kuwait	697	39.1	0.288	unsexed	1/f	3639
New Caledonia	559	34.3	0.33	unsexed	1/-	3090
<i>Epinephelus chlorostigma</i>						
Seychelles	4070	66.9	0.167	unsexed	6/f	6975
Seychelles	3330	62.7	0.19	unsexed	6/f	6975
<i>Epinephelus coloides</i>						
Kuwait	12900	93	0.167	unsexed	1/-	3627
<i>Epinephelus costae</i>						
Egypt	6050	72.5	0.154	unsexed	-/-	1238
Egypt	11000	86.2	0.12	unsexed	-/-	5760
<i>Epinephelus cyanopodus</i>						
New Caledonia	6299	66.2	0.28	unsexed	1/-	3090
<i>Epinephelus diacanthus</i>						
Yemen	2610	57	0.21	unsexed	3/-	3626
<i>Epinephelus drummondhayi</i>						
USA	14020	97	0.13	unsexed	1/-	3094
<i>Epinephelus fasciatus</i>						
Egypt	4530	72.5	0.154	unsexed	-/-	1238
New Caledonia	402	26.4	0.16	unsexed	1/-	3090
<i>Epinephelus fuscoguttatus</i>						
Papua New Guinea	11900	90.5	0.2	unsexed	-/-	1475
Papua New Guinea	15600	99.1	0.16	unsexed	-/-	1475
<i>Epinephelus guttatus</i>						
Bermuda	1504	51.8	0.18	unsexed	1/-	3090
Jamaica	2113	52	0.24	unsexed	6/b	29
Virgin Is. US	2470	56.8	0.119	unsexed	5/-	1475
<i>Epinephelus itajara</i>						
USA	143166	201	0.126	unsexed	1/d	4841
<i>Epinephelus labriformis</i>						
Mexico	1150	36.4	0.247	unsexed	2/a	7185
<i>Epinephelus latifasciatus</i>						
Kuwait	7870	82.1	0.328	unsexed	1/-	3627
<i>Epinephelus maculatus</i>						
New Caledonia	1817	47.2	0.28	unsexed	1/-	3090
						2290

(continued)

Table 1 (continued)

	W_{∞} (g)	L_{∞} (TL, cm)	K (year ⁻¹)	Sex	Data type/ Method	References ^a	References ^a
<i>Epinephelus marginatus</i>							
Tunisia	18853.7	115	0.09	unsexed	-/-	5533	5550
<i>Epinephelus merra</i>							
New Caledonia	177	21	0.27	unsexed	1/-	3111	2290
<i>Epinephelus merra</i>							
Papua New Guinea	1180	41	0.4	unsexed	-/-	1475	
<i>Epinephelus morio</i>							
Mexico	9353	89.1	0.123	unsexed	3/-	11658	11681
Mexico	6796	80.2	0.159	unsexed	1/-	11658	11676
Mexico	8400	86	0.1	unsexed	3/-	11658	11683
Mexico	14480	96.3	0.1	unsexed	3/-	11824	11832
Mexico	8853	87.5	0.099	unsexed	3/-	11658	11678
Mexico	13738	93	0.113	unsexed	1/-	3090	3097
Mexico	10862	93.6	0.12	unsexed	-/-	11658	11679
Mexico	7296	82.1	0.135	unsexed	1/-	11658	11682
Mexico	10582	92.8	0.112	unsexed	1/-	11658	11680
Mexico	12681	98.5	0.171	unsexed	6/-	11658	11657
Mexico	10308	92	0.101	unsexed	6/-	11658	11659
USA	8651	79.9	0.179	unsexed	1/-	3090	3096
<i>Epinephelus multinotatus</i>							
Kuwait	5480	72.6	0.273	unsexed	1/f	3639	
<i>Epinephelus nigritus</i>							
USA	74300	163	0.137	unsexed	1/-	3090	
USA	245682	239	0.05	unsexed	1/-	11824	11834
<i>Epinephelus niveatus</i>							
USA	42817	126	0.074	unsexed	1/-	3094	
USA	40035	132	0.09	unsexed	1/-	3083	
<i>Epinephelus ongus</i>							
Papua New Guinea	2650	52.6	0.33	unsexed	-/f	1475	
<i>Epinephelus polylepis</i>							
Kuwait	3322	64.8	0.195	unsexed	1/f	3639	
<i>Epinephelus rivulatus</i>							
New Caledonia	691	32.9	0.49	unsexed	1/-	3111	2290
<i>Epinephelus sexfasciatus</i>							
Philippines	792	36.7	0.51	unsexed	6/e	1263	
<i>Epinephelus striatus</i>							
Cuba	12900	92.8	0.1	unsexed	-/-	8540	3249
Cuba	7630	76	0.12	unsexed	1/-	8540	8551
Cuba	16800	94	0.06	unsexed	1/-	8540	8551
Jamaica	12900	90	0.09	unsexed	5/f	29	716
Virgin Is. US	25704	113	0.183	unsexed	1/a	3098	
Virgin Is. US	22500	110	0.224	unsexed	5/c	312	716
<i>Epinephelus tauvina</i>							
Kuwait	17075	102	0.131	unsexed	1/f	3639	
Kuwait	16574	102	0.121	unsexed	1/f	3639	2010
Kuwait	12498	92	0.171	unsexed	1/f	3639	
Kuwait	14000	99.1	0.15	unsexed	6/-	6157	
Yemen	46931	150	0.09	unsexed	3/-	1498	
<i>Mycteroperca bonaci</i>							
USA	24800	120	0.16	unsexed	1/-	3090	
<i>Mycteroperca microlepis</i>							
USA	38532	129	0.122	unsexed	1/-	3090	3099
USA	24200	120	0.156	unsexed	1/-	3090	
USA	40226	130	0.155	unsexed	6/e	3111	3196
USA	26600	124	0.124	unsexed	1/d	312	1237

(continued)

Table 1 (continued)

	W_{∞} (g)	L_{∞} (TL, cm)	K (year ⁻¹)	Sex	Data type/ Method	References ^a
<i>Mycteroperca olfax</i>						
Galapagos Is.	11780	93	0.181	unsexed	1/a	6930
<i>Mycteroperca phenax</i>						
USA	13500	108	0.092	unsexed	1/-	3090
USA	2400	70.9	0.166	unsexed	1/-	3090
<i>Mycteroperca tigris</i>						
Cuba	6380	74	0.11	unsexed	1/-	8540
<i>Mycteroperca venenosa</i>						
Jamaica	10822	86	0.17	unsexed	1/b	29
Virgin Is. US	11300	89.5	0.086	unsexed	5/-	1475
<i>Paranthias furcifer</i>						
Puerto Rico	263	31.4	0.282	unsexed	6/e	11687
USA	722	43.8	0.22	unsexed	2/-	3090
<i>Plectropomus leopardus</i>						
Australia	2090	54.3	0.354	unsexed	1/d	7069
Australia	4150	79.5	0.25	unsexed	6/e	1912
Australia	2220	55.4	0.43	unsexed	1/d	1450
New Caledonia	3302	61.6	0.16	unsexed	1/-	3111
<i>Plectropomus maculatus</i>						
Australia	3880	67.5	0.206	unsexed	1/b	6985
<i>Variola louti</i>						
Papua New Guinea	4080	75.7	0.18	unsexed	-/f	1475
Family Lutjanidae						
Subfamily Apsilinae						
<i>Apsilus dentatus</i>						
Jamaica	2617	61.6	0.3	female	2/a	3093
Jamaica	2927	63.8	0.65	male	2/a	3093
Subfamily Etelinae						
<i>Aphareus rutilans</i>						
N. Marianas	23754	147	0.163	unsexed	1/d	2300
<i>Aprion virescens</i>						
New Caledonia	4875	82.1	0.31	unsexed	1/-	3090
Seychelles	13100	122	0.14	female	6/e	7194
Seychelles	5082	88.4	0.348	unsexed	-/-	7194
Seychelles	9010	108	0.29	male	6/e	7194
<i>Etells carbunculus</i>						
Hawaii	4470	72.5	0.36	unsexed	4/-	4560
Hawaii	6320	81.4	0.163	unsexed	4/b	2016
N. Marianas	2700	61.2	0.289	unsexed	4/b	2016
N. Marianas	1104	45.4	0.347	unsexed	1/d	2300
French Polynesia	5380	77.1	0.126	unsexed	4/b	2016
Vanuatu	14100	107	0.07	unsexed	1/-	160
<i>Etells coruscans</i>						
N. Marianas	18600	124	0.123	unsexed	1/d	2300
Vanuatu	7990	93.5	0.13	unsexed	1/-	160
<i>Etells oculatus</i>						
Saint Lucia	23300	102	0.29	unsexed	6/-	6914
Saint Lucia	23900	103	0.61	unsexed	6/e	6912
<i>Pristipomoides auricilla</i>						
N. Marianas	1050	43.7	0.357	unsexed	1/d	2300

(continued)

Table 1 (continued)

	W_{∞} (g)	L_{∞} (TL, cm)	K (year ⁻¹)	Sex	Data type/ Method	References ^a	
<i>Pristipomoides filamentosus</i>							
Hawaii	5137	89.7	0.146	unsexed	4/-	4560	4613
Hawaii	14300	118	0.31	unsexed	4/-	4560	
Hawaii	9284	92.6	0.164	unsexed	4/d	3124	
N. Marianas	3230	66.7	0.289	unsexed	1/d	2300	
Seychelles	12200	98.7	0.3	male	6/e	6441	
Seychelles	6790	89.2	0.275	female	6/e	6441	
Vanuatu	3140	69	0.29	unsexed	1/-	160	
<i>Pristipomoides flavipinnis</i>							
N. Marianas	1990	54.6	0.268	unsexed	1/d	2300	
Vanuatu	3210	64.7	0.36	unsexed	1/-	160	
<i>Pristipomoides multidens</i>							
Tunisia	97208.9	198	0.03	unsexed	-/-	5533	5545
Australia	4339	73	0.219	unsexed	2/-	3090	1451
<i>Pristipomoides sieboldii</i>							
N. Marianas	1560	49.9	0.351	unsexed	1/d	2300	
<i>Pristipomoides typus</i>							
Australia	2573	63.6	0.254	unsexed	2/-	3090	1451
<i>Pristipomoides zonatus</i>							
Hawaii	1660	51.8	1.09	unsexed	1/-	4560	4578
N. Marianas	1770	52.8	0.234	unsexed	1/d	2300	
Subfamily Lutjaninae							
<i>Lutjanus adetli</i>							
New Caledonia	308	36.7	0.34	unsexed	1/-	3111	2290
New Caledonia	476	41.9	0.26	unsexed	1/-	3111	2290
<i>Lutjanus analis</i>							
Cuba	21192	129	0.13	unsexed	1/-	3090	3103
Cuba	7947	88.2	0.132	unsexed	1/-	3090	3102
Cuba	7253	85.2	0.246	unsexed	1/-	3090	
Cuba	9840	89.5	0.2	unsexed	6/-	8540	8564
Cuba	21192	129	0.1	unsexed	1/-	3090	
Cuba	9913	96.1	0.152	unsexed	1/-	3090	3101
USA	7772	86	0.153	unsexed	1/-	3090	3104
Venezuela	15489	103	0.17	unsexed	3/-	11824	
<i>Lutjanus apodus</i>							
Virgin Is. US	803	36.6	0.35	unsexed	5/c	716	
<i>Lutjanus argentimaculatus</i>							
Malaysia	24400	105	0.187	unsexed	6/-	2299	
<i>Lutjanus bohar</i>							
Kenya	4875	66	0.27	unsexed	2/-	2316	
New Caledonia	4394	63.3	0.11	unsexed	1/-	2290	
Papua New Guinea	9232	87.5	0.27	unsexed	-/e	2315	
Seychelles	4923	66	0.33	unsexed	-/f	3111	1320
<i>Lutjanus buccanella</i>							
Cuba	4120	62.5	0.12	unsexed	-/3	8540	3252
Cuba	4140	62.6	0.1	unsexed	-/3	8540	8863
Jamaica	1441	47.8	0.35	female	6/b	3093	
Jamaica	2000	56.2	0.7	male	6/b	3093	
<i>Lutjanus campechanus</i>							
Mexico	12700	100	0.15	unsexed	6/f	11690	
Mexico	12200	98.7	0.12	unsexed	-/-	11690	11693
Mexico	11700	97.4	0.13	unsexed	-/-	11690	11692
USA	15730	95.4	0.225	unsexed	6/e	3111	3196

(continued)

Table 1 (continued)

	W _m (g)	L _m (TL, cm)	K (year ⁻¹)	Sex	Data type/ Method	References ^a
USA	13416	97	0.155	unsexed	Z/f	3112
USA	22572	126	0.18	unsexed	-/-	11824 2656
USA	12350	99.2	0.14	unsexed	-/-	11690 11689
USA	7567	60	0.35	unsexed	1/-	3111 3204
USA	13400	95	0.175	unsexed	Z/f	3112
USA	17144	97	0.165	unsexed	Z/f	3112
USA	12994	94.1	0.17	unsexed	Z/f	3112
<i>Lutjanus carponotatus</i>						
Papua New Guinea	3730	58.7	0.31	unsexed	-/f	1475
<i>Lutjanus cyanopterus</i>						
Cuba	5480	105	0.125	unsexed	-/-	8540 3249
<i>Lutjanus erythropterus</i>						
Australia	3400	62.5	0.41	male	1/f	5738
Australia	5350	75.6	0.21	unsexed	3/-	2318 2318
Australia	3400	62.5	0.44	female	1/f	5738
<i>Lutjanus fulviflamma</i>						
New Caledonia	506	30.3	0.3	unsexed	1/-	2290 2290
<i>Lutjanus gibbus</i>						
Palau	1300	43.3	0.4	unsexed	6/e	4895
Papua New Guinea	1790	48.1	0.31	unsexed	-/-	1475
<i>Lutjanus griseus</i>						
Cuba	1830	53.1	0.15	unsexed	1/-	8540 8568
Cuba	2450	58.1	0.228	unsexed	1/-	3090 3114
Cuba	3070	63.4	0.22	unsexed	6/-	8540 8564
Cuba	388	53.8	0.24	unsexed	1/-	3090 3113
USA	820	58.1	0.167	unsexed	-/d	312 1023
<i>Lutjanus jocu</i>						
Cuba	12900	90.2	0.1	unsexed	1/-	8540 8864
<i>Lutjanus johnii</i>						
India	16600	99.4	0.116	unsexed	Z/-	2320
Indonesia	6450	72.4	0.375	unsexed	-/d	11359
Philippines	5050	66.7	0.13	unsexed	6/e	3794
<i>Lutjanus kasmira</i>						
American Samoa	827	42.4	0.212	unsexed	1/-	2322
American Samoa	329	31.7	0.384	unsexed	1/-	2322
N. Marianas	1250	42.8	0.212	unsexed	1/d	2300
New Caledonia	299	25.9	0.38	unsexed	1/-	2290
<i>Lutjanus lutjanus</i>						
Malaysia	200	25.1	0.497	unsexed	6/-	2299
Philippines	271	25.6	0.75	unsexed	6/e	1449
<i>Lutjanus malabaricus</i>						
Australia	16700	98.7	0.18	male	1/f	5738
Australia	14500	94	0.126	unsexed	3/-	3090
Australia	15600	96.4	0.12	unsexed	3/-	2326
Australia	7373	83.8	0.168	unsexed	3/-	1451
Australia	11300	86.1	0.25	unsexed	3/-	5738 5739
Australia	12100	102	0.25	female	1/d	1450
Australia	10400	83.8	0.23	female	1/f	5738
Australia	15400	96	0.12	unsexed	3/-	3090 2326
Australia	10100	95.7	0.19	male	1/d	1450
China	14100	93	0.142	unsexed	3/-	3090
China	15900	97	0.148	unsexed	3/-	3090

(continued)

Table 1 (continued)

	W_{∞} (g)	L_{∞} (TL, cm)	K (year ⁻¹)	Sex	Data type/ Method	References ^a
Taiwan	15800	96.9	0.147	unsexed	-/-	2087
Vanuatu	4000	60	0.31	unsexed	1/-	160
<i>Lutjanus monostigma</i>						
Papua New Guinea	2980	58.4	0.22	unsexed	-/f	1475
<i>Lutjanus purpureus</i>						
Brazil	11665	96.7	0.096	unsexed	-/d	1139
Brazil	10800	92.9	0.103	unsexed	2/f	11684
Brazil	13800	97.7	0.117	unsexed	1/-	3090
Trinidad Tobago	8690	85.1	0.13	unsexed	1/-	3116
<i>Lutjanus quinquelineatus</i>						
New Caledonia	185	20.5	0.37	unsexed	1/-	2290
<i>Lutjanus rivulatus</i>						
Papua New Guinea	4310	80	0.22	unsexed	-/e	1475
<i>Lutjanus sanguineus</i>						
Djibouti	9590	89	0.236	unsexed	-/-	1488
<i>Lutjanus sebae</i>						
Australia	10300	94.7	0.18	female	1/f	5738
Australia	15900	106	0.14	male	1/d	1450
Australia	16100	109	0.15	male	1/f	5738
Australia	7540	84.2	0.21	female	1/d	1450
Australia	7950	87.2	0.13	unsexed	3/-	2329
Seychelles	12500	96.1	0.38	male	6/e	7194
Seychelles	15200	96	0.23	unsexed	6/c	1378
Seychelles	15500	105	0.22	unsexed	-/-	7194
Seychelles	10200	89.7	0.27	female	6/e	7194
Yemen	12900	90.8	0.16	unsexed	2/-	2328
<i>Lutjanus synagris</i>						
Brazil	1800	50.5	0.231	unsexed	1/-	1026
Cuba	723	37.3	0.28	unsexed	1/-	8540
Cuba	2012	96.9	0.113	unsexed	1/-	1475
Cuba	1530	48	0.26	unsexed	1/-	8540
Cuba	1830	51	0.2	unsexed	1/-	3090
Cuba	1500	47.7	0.25	unsexed	1/-	8540
Cuba	1120	43.2	0.35	unsexed	-/-	8540
Cuba	1030	42	0.15	unsexed	1/-	8540
Cuba	1360	46.1	0.29	unsexed	1/-	8540
Cuba	1070	42.6	0.16	unsexed	1/-	8540
Mexico	1195	45.4	0.28	unsexed	-/f	11824
Mexico	444	32.6	0.53	unsexed	-/-	11824
Mexico	1066	43.5	0.24	unsexed	-/f	11824
Puerto Rico	1209	47.8	0.23	unsexed	6/e	4834
Trinidad and Tobago	3040	60.3	0.2	female	1/a	3224
Trinidad and Tobago	3000	60	0.2	female	1/-	3090
Trinidad and Tobago	4960	71	0.22	male	1/-	3090
Trinidad and Tobago	4910	70.8	0.22	male	1/a	3224
USA	2310	50	0.134	unsexed	1/-	3090
<i>Lutjanus vitta</i>						
Australia	463	34.3	0.37	female	3/d	4840
Australia	1036	44.6	0.22	male	3/d	4840
Malaysia	1160	42.5	0.256	unsexed	6/-	2299
New Caledonia	384	30.2	0.3	female	1/-	2290
New Caledonia	672	35.2	0.32	male	1/-	2290
Philippines	1010	40.6	0.7	unsexed	6/e	1449

(continued)

Table 1 (continued)

	W _∞ (g)	L _∞ (TL, cm)	K (year ⁻¹)	Sex	Data type/ Method	References ^a	
<i>Lutjanus vivanus</i>							
Cuba	8200	81.2	0.1	unsexed	3/-	8540	5904
Cuba	7837	78.1	0.09	unsexed	3/-	11824	8866
<i>Ocyurus chrysurus</i>							
Cuba	7837	78.1	0.09	unsexed	3/-	11824	8866
Cuba	7837	78.1	0.09	unsexed	3/-	11824	8866
Cuba	1810	58.4	0.15	unsexed	3/-	3090	3121
Cuba	4757	79.4	0.159	unsexed	1/a	3122	
Cuba	3370	57.9	0.26	unsexed	3/-	8540	8565
Cuba	1030	47.8	0.29	unsexed	6/-	8540	8564
Cuba	4530	80.9	0.1	unsexed	1/-	8540	8548
Cuba	2980	70	0.103	unsexed	1/-	1475	1025
Cuba	1497	55.2	0.332	unsexed	1/a	3122	
Jamaica	3600	70	0.25	unsexed	6/b	3093	
Mexico	2952	61.8	0.1	unsexed	2/-	11824	11830
Mexico	1715	52.9	0.16	unsexed	2/-	11824	11831
Puerto Rico	1960	58.6	0.139	unsexed	1/d	5307	
USA	2240	52.5	0.279	unsexed	1/-	5307	3123
<i>Rhomboptilus aurorubens</i>							
USA	4169	63	0.198	unsexed	2/-	3090	3125
Subfamily Paradicichthyinae							
<i>Syphorus nematophorus</i>							
Papua New Guinea	16500	97.4	0.23	unsexed	-/f	1475	
Total:	250						

1 - otolith annuli; 2 - scale annuli; 3 - other annual rings; 4 - daily otolith rings; 5 - tagging/recaptures; 6 - length frequencies; a - Ford/Walford plot; b - v. Bertalanffy/Beverton plot; c - Gulland plot; d - non-linear regression; e - ELEFAN I; f - other methods.

* The first reference for growth is that from which the parameters were obtained. The second reference, if present, indicates the source of data.

Table 2. Estimates of natural mortality of groupers and snappers In FishBase. [Estimaciones de mortalidad natural de meros y pargos en FishBase.]

	M (1/y)	K (year ⁻¹)	L _∞ (TL, cm)	Sex	T (°C)	M	References ^a	Growth
Jamaica	1.95	34	0.63	unsexed	27	1784	29	784
<i>Epinephelus drummondhayi</i>								
USA	0.2	97	0.13	unsexed	21	3094	3094	
<i>Epinephelus guttatus</i>								
Jamaica	0.68	52	0.24	unsexed	27	29	29	
<i>Epinephelus marginatus</i>								
Tunisia	0.1	115	0.09	unsexed	17.6	5533	5533	5550
Tunisia	0.05	198	0.03	unsexed	17.6	5533	5533	5545
<i>Epinephelus niveatus</i>								
USA	0.18	132	0.09	unsexed	25	3083	3083	
<i>Epinephelus striatus</i>								
Jamaica	0.24	90	0.09	unsexed	27	1784	29	716
<i>Mycteroperca venenosa</i>								
Jamaica	0.42	86	0.17	unsexed	27	1784	29	1784

(continued)

Table 2 (continued)

	M (1/y)	K (year ⁻¹)	L _∞ (TL, cm)	Sex	T (°C)	M	References ^a	Growth
<i>Plectropomus leopardus</i>^b								
Australia	0.46	79.6	0.25	unsexed	24	2884	1912	2160
<i>Apsilus dentatus</i>								
Jamaica	1.9	63.8	0.65	male	27	1786	3093	
Jamaica	0.8	61.6	0.3	female	27	3093	3093	
<i>Etells carbunculus</i>								
Vanuatu	0.08	107	0.07	unsexed	27.8	3127	160	
<i>Etells coruscans</i>								
N. Marianas	0.36	124	0.123	unsexed	27.9	2300	2300	
Vanuatu	0.12	93.5	0.13	unsexed	27.8	3127	160	
<i>Lutjanus buccanella</i>								
Jamaica	2.2	56.2	0.7	male	27	3093	3093	
Jamaica	1.8	47.8	0.35	female	27	3093	3093	
<i>Lutjanus campechanus</i>								
USA	0.2	94.1	0.17	unsexed	22	4748	3112	
<i>Lutjanus malabaricus</i>								
Vanuatu	0.42	60	0.31	unsexed	26.7	3127	160	
<i>Lutjanus purpureus</i>								
Brazil	0.37	96.7	0.096	unsexed	27	1789	1139	1024
Brazil	0.35	98.9	0.09	unsexed	25	3127	1420	
<i>Ocyurus chrysurus</i>								
Jamaica	0.62	70	0.25	unsexed	27	3093	3093	
USA	0.45	52.5	0.279	unsexed	25.7	3123	5307	3123
<i>Pristipomoides auricilia</i>								
N. Marianas	0.62	43.7	0.357	unsexed	27.9	2300	2300	
<i>Pristipomoides filamentosus</i>								
Hawaii	0.25	89.7	0.146	unsexed	26	3127	4560	4613
N. Marianas	0.52	66.7	0.289	unsexed	27.9	2300	2300	
Vanuatu	0.53	69	0.29	unsexed	27.8	3127	160	
<i>Pristipomoides flavipinnis</i>								
Vanuatu	0.83	64.8	0.36	unsexed	27.8	3127	160	
<i>Pristipomoides zonatus</i>								
N. Marianas	0.48	52.8	0.234	unsexed	27.9	2300	2300	
<i>Rhomboptilus aurorubens</i>								
USA	0.2	63	0.198	unsexed	24.8	4748	3090	3125

^aThe first reference for growth is that from which the parameters were obtained. The second reference, if present, indicates the source of data.

^bM is the mean survival of 2-4 year olds in refs. 2884 and 3081.

the "growth space" occupied by that species.

Also, the overlap between ellipses representing different species (i.e., between the growth space they inhabit) can be computed, as can the distances between the centers of a number of ellipses. Finally, the latter can, in form of a dendrogram, express the similarity in growth between a number of species (Pauly et al. 1996).

Methods for predicting natural mortality

Beverton and Holt (1959) were the first to investigate the strong relationship, in fishes between growth parameters (especially K) and natural mortality (M), and to derive empirical relationships allowing the prediction of M from K in selected fish groups.

Their work was carried on by Pauly (1980) who extended both the database and the parameter set for prediction of M, and who proposed the widely used empirical model

$$\log_{10} M = -0.0066 - 0.279 \log_{10} L_{\infty} + 0.6543 \log_{10} K + 0.4634 \log_{10} T. \quad \dots 4)$$

based on 175 independent sets of M, L_{∞} (TL; cm), K and T ($^{\circ}\text{C}$) values (of which only 5 pertained to groupers, and 6 to snappers). We shall call this model "Pauly I".

Ralston (1987), based on a set of 19 estimates of M and K pertaining to groupers and snappers, showed that the linear regression

$$M = 0.0189 + 2.06 K \quad \dots 5)$$

(which we shall call "Ralston I"), led to better predictions of M than equation (4) for the data set in question.

We derived two improved models from the data in Table 2. The first of these is a version of equation (4) whose intercept was adjusted such as to provide a mean residual of zero when applied to the data of Table 2. We call the resulting model "Pauly II", and it has the form

$$\log_{10} M = -0.0636 - 0.279 \log_{10} L_{\infty} + 0.6543 \log_{10} K + 0.4634 \log_{10} T \quad \dots 6)$$

The second improved model is a linear regression of the M on the K values of Table 2, which we call "Ralston II", and which has the form

$$M = -0.1778 + 3.1687 \quad \dots 7)$$

The values of M predicted by these models were subtracted from the observed values, and the deviation squared and summed, providing residual sums of squares (RSS) that could be used to compare the fit of equations 4-7 to the data of Table 2.

Results and Discussion

Table 1 presents the growth parameters upon which much of this contribution is based, as extracted from FishBase 96. Observed asymptotic size range over one order of magnitude, from 20.5 cm TL in *Lutjanus quinquefasciatus* (Family Lutjanidae) to 201 cm TL in *Epinephelus itajara* (Family Serranidae). This is much less than for fishes as a whole, whose asymptotic lengths range over three orders of magnitude from 1.5 cm (in *Poecilia reticulata*) to well over 10 m (in *Cetorhinus maximus*).

Figs. 1 and 2 show some of the observed patterns between L_{∞} and K in fish in general (grey dots) and in groupers and snappers, respectively (black dots), based on the auximetric plot concept (from the Greek *metreos*, measure, and *auxein*, to grow).

As might be seen, groupers and snappers occupy, indeed, a small fraction of the growth space where fish occur, due to their relatively narrow range of sizes, and of growth patterns.

The narrowness of growth patterns is also expressed by the low standard error of the mean values of ϕ' for species in which enough L_{∞} , K data pairs were available (Table 3). This implies that estimates of K can be obtained from equation (3) when reasonable estimates of L_{∞} are available (e.g., from a Wetherall Plot, see Pauly 1986; Wetherall 1986; Wetherall et al. 1987; Gayanilo et al. 1996), along with a value of ϕ' with a low standard error.

This approach can also be used to select among various options for interpreting structure on otoliths and other hard parts.

Thus, microscopic rings on otoliths will produce estimates of K and ϕ' that will have certain values if the rings are assumed to be laid daily, different from those that would result if the rings are assumed to be laid, say only during high tides or subdaily.

Similarly, mean values of ϕ' can be used when using length-frequency data to select

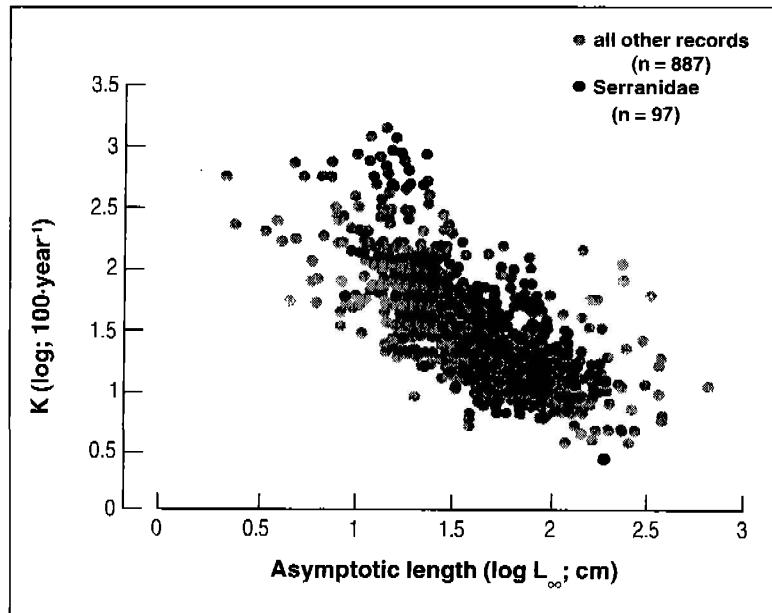


Fig. 1. Auximetric plot of the von Bertalanffy parameters K vs L_∞ for the fish of the world (grey dots, showing 20% of the records in FishBase 96), with emphasis on groupers (black dots). Based on a FishBase 96 graph (see text). [Rejilla auximétrica de los parámetros de von Bertalanffy K vs L_∞ para peces del mundo (puntos grises mostrando 20% de los registros en FishBase 96), con énfasis en meros (puntos negros). Basado en un gráfico de FishBase 96 (ver texto).]

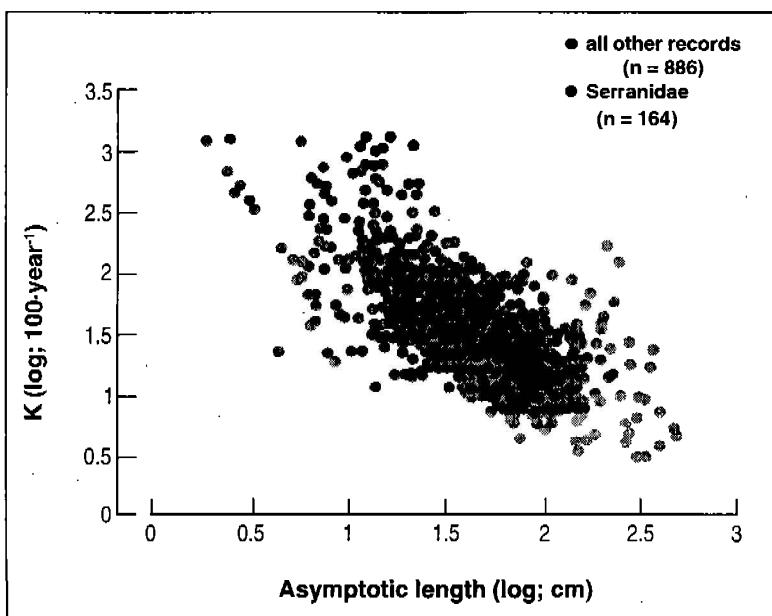


Fig. 2. Auximetric plot of the von Bertalanffy parameters K vs L_∞ for the fish of the world (grey dots, showing 20% of the records in FishBase 96), with emphasis on snappers (black dots). Based on a FishBase 96 graph (see text). [Rejilla auximétrica de los parámetros de von Bertalanffy K vs L_∞ para peces del mundo (puntos grises mostrando 20% de los registros en FishBase 96), con énfasis en pargos (puntos negros). Basado en un gráfico de FishBase 96 (ver texto).]

Table 3. Mean value of ϕ' (in ascending order) in 12 snappers with sufficient records ($n \geq 5$ in Table 1), documenting low standard errors and coefficients of variation. [Valor medio de ϕ' (en orden ascendente) de 12 pargos con suficientes registros ($n \geq 5$ en Tabla 1) documentando bajos valores para el error estándar y el coeficiente de variación.]

Species	n	mean ϕ'	SE	CV
<i>Lutjanus kasmira</i>	5	2.530	0.036	3.2
<i>Lutjanus vitta</i>	6	2.674	0.085	7.8
<i>Lutjanus synagris</i>	19	2.755	0.040	6.4
<i>Ocyurus chrysurus</i>	12	2.823	0.047	5.7
<i>Lutjanus griseus</i>	6	2.825	0.048	4.2
<i>Lutjanus purpureus</i>	5	2.974	0.019	1.4
<i>Etelis carbunculus</i>	7	3.058	0.082	7.1
<i>Lutjanus malabaricus</i>	15	3.167	0.029	3.5
<i>Lutjanus analis</i>	8	3.185	0.038	3.4
<i>Lutjanus campechanus</i>	11	3.188	0.033	3.5
<i>Lutjanus sebae</i>	10	3.254	0.048	4.7
<i>Pristipomoides filamentosus</i>	7	3.273	0.081	6.5

among competing solutions, corresponding to different (local) peaks of a score function (Pauly and Morgan 1987). The extent to which these procedures can be considered "validations" (*sensu* Beamish and McFarlane 1983) may be open for debate. However, we believe that an interpretation of growth patterns compatible with a previously computed value of ϕ' is more credible than one that is incompatible with such value.

Fig. 3 shows a detailed analysis of the growth patterns of snappers, using the auximetric plot concept and its implementation as a software (AUXIM, Pauly et al. 1996), applied to 12 species with an appropriate number of growth parameter sets. As might be seen, this approach enables:

- i) the definition, in quantitative terms, of the "growth space" covered by a single species (Fig. 3a);
- ii) the comparison of a pair of species, and the definition of the fishes' overlap in terms of growth (i.e., their niches?) (Fig. 3b);
- iii) the simultaneous plotting of ellipsoids representing a number of species (Fig. 3c); and thence
- iv) the identification of similarities of growth patterns, and their

quantification and display through cluster analysis (Fig. 3d).

Pauly et al. (1996) presented a similar analysis for tilapia (family Cichlidae), and related the position in growth space of various species (groups) to their ecology. We shall abstain from doing this here, but point out for interested readers that this tool will soon become widely available, through the incorporation of AUXIM as a subroutine of FishBase 97.

Fig. 4 shows a FishBase plot of $\log K$ vs $\log M$, showing the close relationships between these two parameters in fish in general, and in Lutjanidae.

Fig. 5, illustrating a FishBase plot of $\log M$ on $\log L_{\infty}$ shows, however, that K is not the only attribute of fish that is related to M . The plot confirms that both L_{∞} and water temperature also relate to M , as shown earlier by Pauly (1980).

However, because the values of M available for groupers and snappers stem from warm water (Fig. 5, Table 2), and because these fishes occupy a rather narrow range of asymptotic sizes (see above), relatively accurate predictions of M can be derived from K alone, as suggested by Ralston (1987). We recommend, however the use

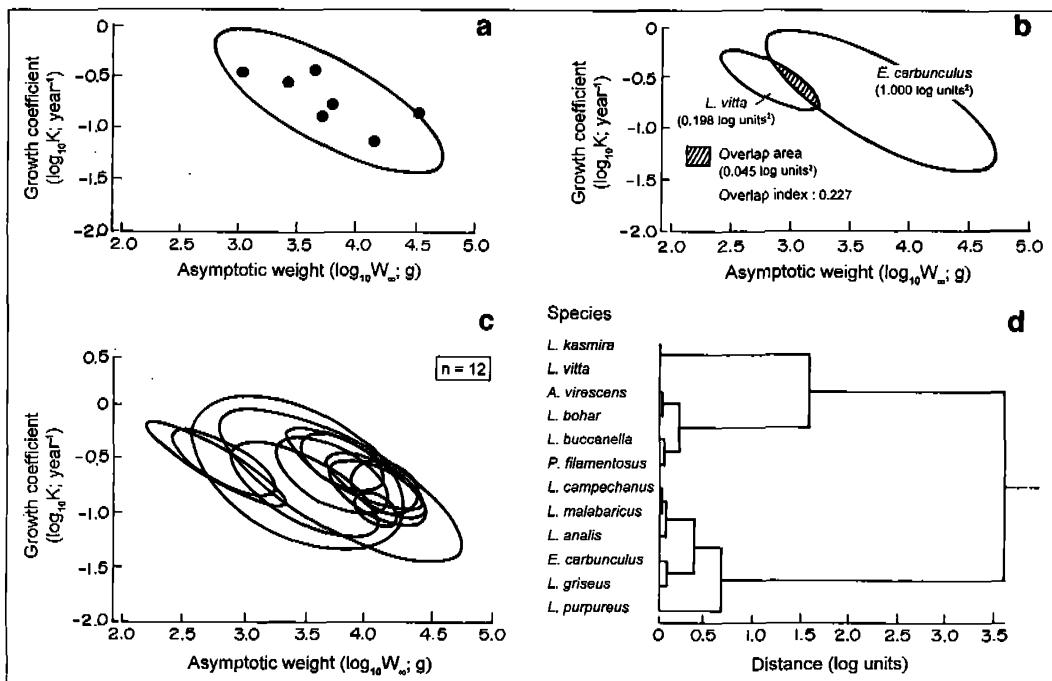


Fig. 3. Sequence of steps involved in a detailed analysis using AUXIM: a: An ellipse is defined by the growth parameters (W_∞ , K) of each species (here: *Etells carbunculus*; $n = 7$); b: The overlap (in growth space) between the ellipses of pairs of species can also be defined (here for *E. carbunculus* and *Lutjanus vitta*); c: The growth space occupied by a number of related species (here for 12 snapper species, each with a sufficient number of growth parameter pairs is then defined); and d: The dendrogram resulting from the distances among species in (c) is drawn; it shows the closeness in growth space of 12 species of Lutjanidae. [Secuencia de procesos involucrados en un análisis detallado usando AUXIM. a) Una ellipse es definida por los parámetros de crecimiento (K y W_∞) de cada especie (aquí *Etells carbunculus*; $n=7$); b) La superposición (espacio de crecimiento) entre las ellipses de pares de especies también pueden ser definidas (aquí para *E. carbunculus* y *Lutjanus vitta*); c) El espacio de crecimiento ocupado por varias especies asociadas (aquí 12 especies de pargos, cada una con un número suficiente de pares de parámetros de crecimiento); d) Se construye el dendrograma resultante de la distancia entre especies en (c), el cual muestra la cercanía de los espacios de crecimiento de 12 especies de Lutjanidos.]

of the "Ralston II" model, which gives a better fit to the data of Table 2 than the original version (Table 4).

It will be noted that the Pauly II model, due to its intercept having been adjusted to the data in Table 2, also provides improved predictions of M in groupers and snappers (Table 4).

Having illustrated the utility of FishBase (and of AUXIM) for analyzing the growth and mortality of fishes, we conclude this contribution with two graphs, simultaneously illustrating an aspect of the life his-

tory of snappers and anatomical feature of groupers, and the ease with which a relational database such as FishBase, can generate patterns from previously unconnected facts.

Fig. 6 shows a plot of reported longevity vs maximum reported length in fishes, and on 21 species of Lutjanidae. As might be seen, snappers are well within the scattergram.

Fig. 7 shows that groupers have average brain sizes relative to all other fishes (Froese 1996). However, they have below

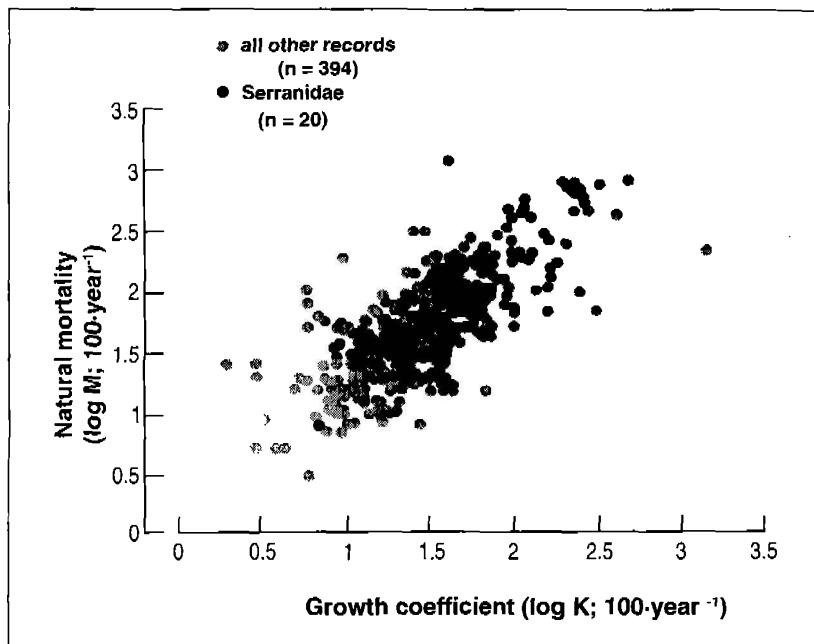


Fig. 4. FishBase plot of M vs K , illustrating the strong relationship between these two parameters for fish in general (grey dots), and Lutjanidae in particular (black dots). Based on a FishBase 96 graph (see text). [Gráfico de M vs K , obtenido de FishBase, ilustrando la fuerte relación entre estos dos parámetros para peces en general, y para Lutjánidos en particular.]

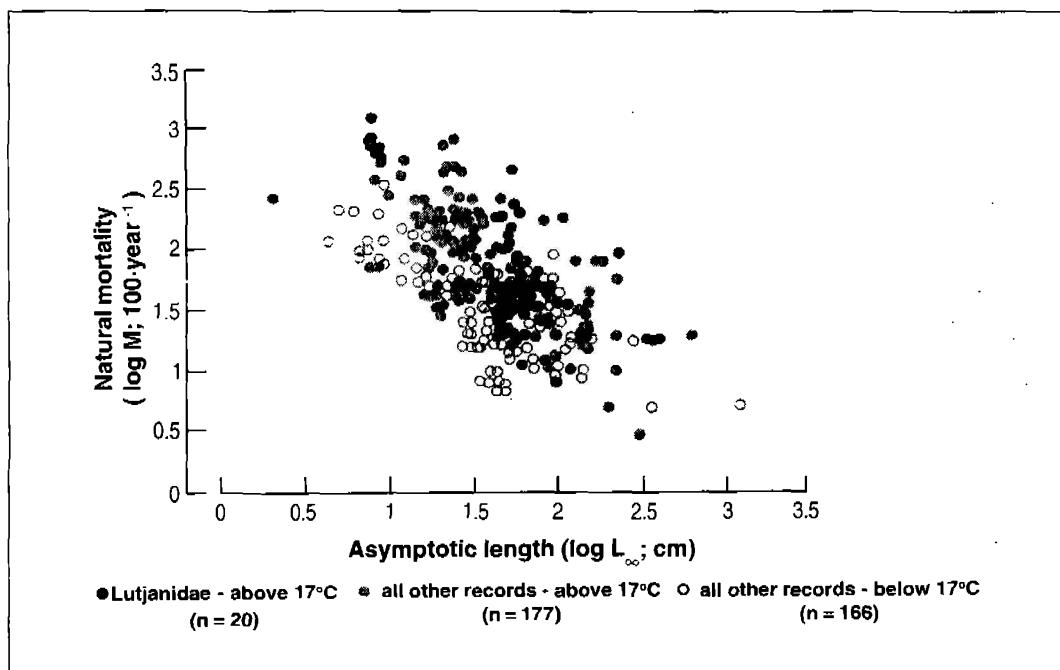


Fig. 5. FishBase plot of M vs L_{∞} , also showing the effect of low and high temperature on M for fish in general (open and grey dots). Note that the temperature effect is limited in lutjanids (black dots), owing to their being limited to warm waters. Based on a FishBase 96 graph (see text). [Gráfico de M vs K , obtenido de FishBase, mostrando también el efecto de temperaturas ligeramente bajas sobre M para peces en general (puntos blancos y puntos oscuros). Note que el efecto de la temperatura es limitado en Lutjánidos (puntos negros) debido a que ellos están confinados a aguas calientes.]

Table 4. Summary of results from comparisons of four models for predicting natural mortality in groupers and snappers ("S/G").
[Resumen de resultados de la comparación de cuatro modelos para predecir mortalidad natural en pargos y meros ("S/G").]

Model	S/G	non S/G res. ^a	Mean	SSR
Pauly I	11	164	-0.068	3.73
Pauly II	26	164	0	3.00
Ralston I	19	0	0.075	2.74
Ralston II	29	0	0	1.56

^a Mean residuals when values predicted by models were subtracted from observed values in Table 2.

average brain sizes relative to other reef fishes. We do not know how to interpret this finding, or whether we even should, since we may already have made our point about the utility of FishBase.

Acknowledgements

We thank our colleagues in the FishBase project, and those who contributed to this database, for making this contribution possible, and Felimon "Nonong" Gayanilo, Jr. for programming AUXIM.

References

- Allen, G.R. 1985. Snappers of the world: an annotated and illustrated catalogue of lutjanid species known to date. FAO Species Catalogue Vol. 6, 208 p. + 28 plates.
- Baranov, F.I. 1918. [On the question of the biological basis of fisheries.] Nauchni issledovatel'skii ikhtiologicheski. Institut Ivesti 1:18-128. [Originally published in Russian; available in translation along with his other work - in a 3-volume edition from Israel Program of Scientific Translation, Jerusalem.]
- Beamish, R.J. and G.A. McFarlane. 1983. Validation of age determination estimates:

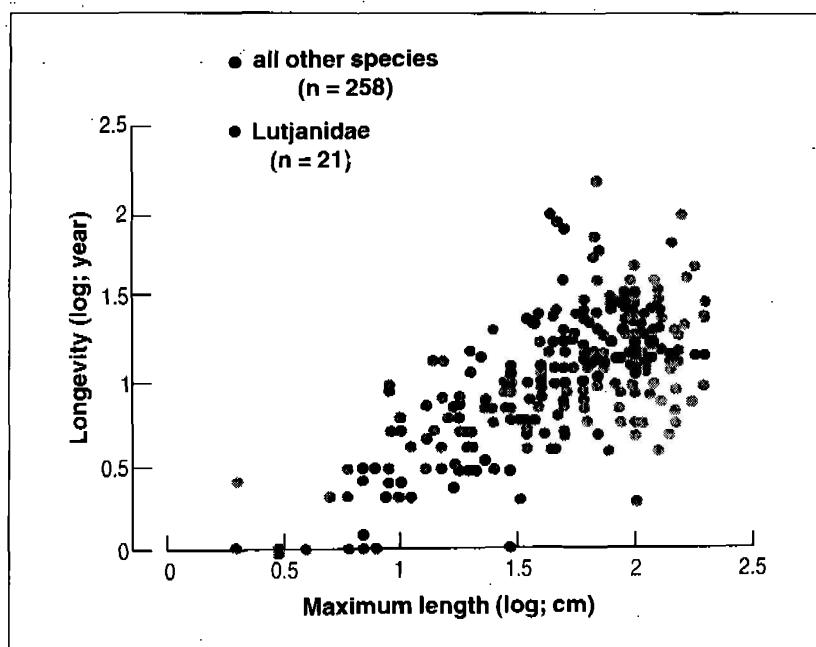


Fig. 6. FishBase plot of longevity vs length in fish (grey dots) and Lutjanidae in particular (black dots). [Gráficos de longevidad vs longitud obtenida de FishBase (puntos oscuros), y para Lutjanídos en particular(puntos negros).]

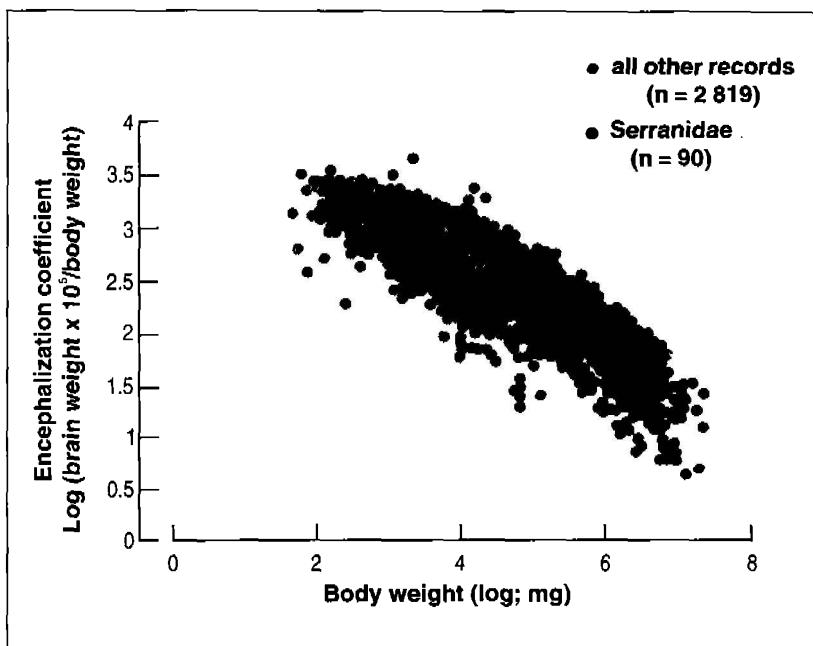


Fig. 7. FishBase plot of the relationship between relative brain size and the body weight of fish in general (grey dots), and Serranidae in particular (black dots), based on a FishBase 96 graph constructed using the data of R. Bauchot and colleagues at the University Paris VII (see Froese and Pauly 1996). [Gráfico de FishBase mostrando la relación entre tamaño relativo del cerebro y el peso del cuerpo para los peces en general (puntos grises), y los Serránidos en particular (puntos negros), basados en un gráfico general construido en FishBase 96, usando datos de R. Bauchot y colegas de la Universidad de París VII (ver Froese and Pauly 1996).]

the forgotten requirement, p. 26-34. In E.D. Prince and L.M. Pulos (eds.) Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes and Sharks, 15-18 February 1982, Miami, Florida. NOAA Tech. Rep. NMFS 8, 211 p.

Bertalanffy, L. von. 1938. A quantitative theory of organic growth (Inquiries on growth Laws II). Human Biol. 10(2):181-213.

Bevertton, R.J.H. and S.J. Holt. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics, p. 142-180. In G.E.W. Wolstenholme and M. O'Connor (eds.) CIBA Foundation Colloquia on Ageing. Vol. 5. The lifespan of animals. J. & A. Churchill, London.

Binohlan, C. and D. Pauly. 1996a. The POPGROWTH Table, p. 68-72. In R. Froese and D. Pauly (eds.) FishBase 96: concepts,

design and data sources. ICLARM, Manila.

Binohlan, C. and D. Pauly. 1996b. The LENGTHWEIGHT Table, p. 72-74. In R. Froese and D. Pauly (eds.) FishBase 96: concepts, design and data sources. ✓ ICLARM, Manila.

Froese, R. 1996. FishBase: a database with key information on coral reef fishes. Paper presented at the the 8th International Coral Reef Symposium, 23-28 June 1996, Panama City.

Froese, R. and D. Pauly, Editors. 1996. FishBase 96: concepts, design and data sources. ICLARM, Manila. 179 p.

Gayaniilo, F.C., Jr., P. Sparre and D. Pauly. 1996. The FAO-ICLARM Stock Assessment Tools (FiSAT) User's Guide. FAO Comp. Inf. Ser. Fish. 7, 126 p.

Heemstra, P.C. and J.E. Randall. 1993. Groupers of the world (Family Serranidae, subfamily

- Ephinephelinae). An annotated and illustrated catalogue of the grouper, rockcod, hind, coral grouper, and lyretail species known to date. FAO Species Catalogue Vol. 16, 382 p. +31 plates.
- Longhurst, A. and D. Pauly. 1987. Ecology of tropical oceans. Academic Press, San Diego. 407 p.
- Mohr, E. 1927. Bibliographie der Alters- und Wachstums-Bestimmung bei Fischen. J. Cons. CIEM 2(2):236-258.
- Mohr, E. 1930. Bibliographie der Alters- und Wachstums-Bestimmung bei Fischen. II Nachträge und Fortsetzung. J. Cons. CIEM 5(1):88-100.
- Mohr, E. 1943. Bibliographie der Alters- und Wachstums-Bestimmung bei Fischen. III Nachträge und Fortsetzung. J. Cons. CIEM 9(2):397-391.
- Mohr, E. 1994. Age determination in tropical fish. Naga, ICLARM Q. 17(2):27-30. [Translated by D. Pauly from original German version published in Zoologischer Anzeiger 53:87-95;29].
- Moreau, J., C. Bambino and D. Pauly. 1986. Indices of overall growth performance of 100 tilapia (Cichlidae) populations, 201-206. In J.L. Maclean, L.B. Dizon and L.V. Hosillos (eds.) The First Asian Fisheries Forum. Asian Fisheries Society, Manila, Philippines.
- Pauly, D. 1979. Gill size and temperature as governing factors in fish growth: a generalization of von Bertalanffy's growth formula. Berichte des Instituts für Meereskunde an der Universität Kiel. No. 63, xv+156 p. (Doctoral thesis).
- Pauly, D. 1986. On improving operation and use of the ELEFAN program. Part II: improving the estimation of L_{∞} . Fishbyte 4(1):18-20.
- Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. CIEM 39(3):175-192.
- Pauly, D. 1991. Growth performance of fishes: rigorous description of patterns as a basis for understanding causal mechanism. Aquabyte (ICLARM) 4(3):3-6. [Reprinted as Essay 7 in Pauly 1994].
- Pauly, D. 1994. On the sex of fish and the gender of scientists: a collection of essays in fisheries science. Chapman and Hall, London, 250 p.
- Pauly, D., J. Moreau and F. Gayanilo, Jr. 1996. A new method for comparing the growth performance of fishes, applied to wild and farmed tilapias, p. 433-441. In R.S.V. Pullin, J. Lazard, M. Legendre, J.B. Amon Kothias and D. Pauly (eds.) The Third International Symposium on Tilapia and Aquaculture. ICLARM Conf. Proc. 41. 575 p.
- Pauly, D. and G.R. Morgan, Editors. 1987. Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.
- Petersen, C.G.J. 1891. Eine Methode zur Bestimmung des Alters und Wuchses der Fische. Mitteilungen des Deutschen Fischerei-Vereins 11:226-235.
- Ralston, S. 1987. Mortality rates of snappers and groupers, p. 375-404. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Ocean Resour. Mar. Policy Ser. Westview Press, Boulder.
- Smith, T.D. 1994. Scaling fisheries: the science of measuring the effects of fishing, 1855-1955. Cambridge University Press, Cambridge. 392 p.
- Wetherall, J.A. 1986. A new method for estimating growth and mortality parameters from length-frequency data. Fishbyte 4(1):12-14.
- Wetherall, J.A., J.J. Polovina and S. Ralston. 1987. Estimating growth and mortality in steady-state fish stocks from length-frequency data, p. 53-74. In D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.
- Weatherley, A.H. and H.S. Gill. 1987. The biology of fish growth. Academic Press, London. 443 p.

Numbered References*

- 000029 Thompson, R. and J.L. Munro. 1983. The biology, ecology and bionomics of the hinds and groupers, Serranidae, p. 59-81. In J.L. Munro (ed.) Caribbean coral reef fishery resources. ICLARM Stud. Rev. 7, 276 p.
- 000160 Brouard, F. and R. Grandperrin. 1984. Les poissons profonds de la pente récifale

* As listed in Tables 1 and 2.

- externe. Notes Doc. Océanogr. Mission ORSTOM, Port-Villa 11. 131 p.
- 000312 Pauly, D. 1978. A preliminary compilation of fish length growth. Berichte des Instituts für Meereskunde an der Christian-Albrechts Universität Kiel (55), 200 p.
- 000716 Randall, J.E. 1962. Tagging reef fishes in the Virgin Islands. Proc. Gulf Caribb. Fish. Inst. 14:201-241.
- 000734 Gundermann, N. and D. Popper. 1975. Some aspects of recolonization of coral rocks. Mar. Biol. 33:109-117.
- 001023 Crocker, R.A. 1962. Growth and food of the gray snapper, *Lutjanus griseus*, in Everglades National Park. Trans. Am. Fish. Soc. 91:379-383.
- 001024 Fontelles-Filho, A.A. 1970. Estudio sobre a biología da pesca do parjo, *Lutjanus purpureus* Poey, no Nordeste Brasileiro, - Dado de 1969. Arq. Cién. Mar. 10(1):73-78.
- 001025 Rodriguez-Pino, Z. 1962. Estudios estadísticos y biológicos sobre la biaiba *Lutjanus synagris*. Centro de Investigaciones Pesqueras. Nota sobre Investigaciones (4), 99 p.
- 001026 Alegria, J. and M. Ferreira de. 1970. Edad y crecimiento del ariacó *Lutjanus synagris* en el Nordeste de Brasil. Arq. Cién. Mar. 10(1):65-68.
- 001139 Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. CIEM 39(2):175-192.
- 001232 Cadenat, J. 1935. Les Serranidés de la Côte occidentale d'Afrique (du Cap Spartel au Cap Vert.). Rev. Trav. Off. Scient. Tech. Pêch. Marit. 8(4):377-422.
- 001237 McErlan, A. 1963. A study of the age and growth of the gag *Mycteroperca microlepis* Goode and Bean (Pisces, Serranidae) on the West Coast of Florida. Fla. Board Conserv. Tech. Ser. 41:1-35.
- 001238 Rafail, S.Z. 1972. A statistical study of length-weight relationship of eight Egyptian fishes. Bull. Inst. Oceanogr. Fish. (Cairo) 2:136-156.
- 001239 Bortone, S.A. 1971. Studies on the biology of the sand perch, *Diplectum formosum* (Perciformes, Serranidae). Tech. Ser. Fla. Dep. Nat. Res. (65):1-27.
- 001242 Young, P. 1963. The kelp bass (*Paralabrax clathrus*) and its fishery 1947-1958. Calif. Fish Game, Fish. Bull. (122), 67 p.
- 001263 Ingles, J. and D. Pauly. 1984. An atlas of the growth, mortality and recruitment of Philippine fishes. ICLARM Tech. Rep. 13, 127 p.
- 001320 Wheeler, J. and F. Ommanney. 1953. Report on the Mauritius-Seychelles fisheries survey 1948-1949, part 4. Fish. Publ., Lond. 1(3):120-140.
- 001378 Lablache, G. and G. Carrara. 1988. Population dynamics of emperor red snapper *Lutjanus sebae* with notes on the demersal fishery of the Mahé Plateau, Seychelles, p. 171-192. In S.C. Venema, J.M. Christensen and D. Pauly (eds.) Contributions to tropical fisheries biology. FAO/DANIDA Follow-up Training Course on Fish Stock Assessment in the Tropics, Denmark, 1986 and Philippines, 1987. FAO Fish. Rep. (389).
- 001420 De Menezes, M.F. and T.C.V. Gesteira. 1974. Idade e crescimento do pargo, *Lutjanus purpureus* Poey, do norte e nordeste do Brasil. Arq. Cien. Mar. 14(2):81-85.
- 001449 Corpuz, A., J. Saeger and V. Sambilay. 1985. Population parameters of commercially important fishes in Philippine waters. Tech. Rep. Univ. Philipp. Visayas, Dept. Mar. Fish. (6), 99 p.
- 001450 McPherson, G.R. et al. 1985. Great Barrier Reef demersal fish research. South Pacific Commission, 17th Regional Technical Meeting on Fisheries, Noumea, New Caledonia, August 1985. SPC/Fisheries 17/WP 23.
- 001451 Edwards, R.R.C. 1985. Growth rates of Lutjanidae (snappers) in tropical Australian waters. J. Fish Biol. 26:1-4.
- 001475 Munro, J.L. and D. McB. Williams. 1985. Assessment and management of coral reef fisheries: biological, environmental and socio-economic aspects. p. 543-578. In Proceedings of the Fifth International Coral Reef Congress, Tahiti, 27 May-1 June 1985. Vol. 4. Antenne Museum-EPHE, Moorea, French Polynesia.
- 001488 Sanders, M.J. and G.R. Morgan. 1989. Review of the fisheries resources of the Red Sea and Gulf of Aden. FAO Fish. Tech. Rep. (304), 138 p.
- 001498 Edwards, R.R.C., A. Bakhader and S. Shaher. 1985. Growth, mortality, age composition and fishery yields of fish from the Gulf of Aden. J. Fish Biol. 27:13-21.
- 001501 Kedidi, S.M. and M. Bouhlel. 1985. Stock assessment for the blood snapper *Lutjanus sanguineus* from the Djiboutian waters Red Sea - Gulf of Aden. Project for the Development of Fisheries in the Red Sea areas of the Gulf of Aden, FAO/UNDP RAB/83/023/11. Cairo. 20 p. (mimeo).
- 001784 Thompson, R. and J.L. Munro. 1977. Aspects of the biology and ecology of

- Caribbean reef fishes: Serranidae (hinds and groupers). *J. Fish Biol.* 12:115-146.
- 001786 Munro, J.L. 1974. The biology, ecology, exploitation and management of Caribbean reef fishes. Scientific Report of the ODA/UWI Fisheries Research Project: 1969-1973. Part V.m. Summary of biological and ecological data pertaining to Caribbean reef fishes. *Res. Rep. Zool. Dep. Univ. West Indies* (3):24 p.
- 001789 Ivo, C.T.C. and T.C.V. Gestira. 1974. Estimacao preliminar das medida de mortalidad do pargo, *Lutjanus purpureus* Poey, no norte e norteeste brasiliense. *Arq. Ciént. Mar.* 14:123-127.
- 001912 Pauly, D. and J. Ingles. 1981. Aspects of the growth and natural mortality of exploited coral reef fishes. p. 89-98. In E. Gomez, C.E. Birkeland, R.W. Buddemeyer, R.E. Johannes, J.A. Marsh, Jr. and R.T. Tsuda (eds.) *Proceedings of the Fourth International Coral Reef Symposium*, Manila, Philippines. Vol. 1.
- 002010 Mathews, C.P. and M. Samuel. 1985. Stock assessment and management of newaiby, hamoor and hamra in Kuwait. p. 67-115. In C.P. Mathews (ed.) *Proceedings of the 1984 Shrimp and Fin Fisheries Management Workshop*. Kuwait Institute for Scientific Research, Kuwait.
- 002013 Cury, P. and J. Worms. 1982. Pêche, biologie et dynamique du thiof (*Epinephelus aeneus* E. Geoffroy Saint-Hilaire, 1817) sur les côtes sénégalaises. *Doc. Sci. Cent. Rech. Océanogr. Dakar-Tiaroye* (82), 88 p.
- 002016 Smith, M.K. and E. Kostlan. 1991. Estimates of age and growth of ehu *Etelis carbunculus* in four regions of the Pacific from density of daily increments in otoliths. *Fish. Bull.* 89:461-472.
- 002087 Han-lin, L. and L. Hsi-Chiang. 1974. Age determination and growth of *Lutjanus sanguineus* (C. & V.) in the South China Sea. *J. Fish. Soc. Taiwan* 3(1):39-57.
- 002160 Goeden, G.B. 1978. A monograph of the coral trout. *Plectropomus leopardus* (Lacepède). *Queensland Fish. Serv. Res. Bull.* 1:1-42.
- 002290 Loubens.,G. 1980. Biologie de quelques espèces de poissons du lagon Néo-Calédonien. III. Croissance. *Cah. Indo-Pac.* 2:101-153.
- 002299 Ambak, M.A., A.K.M. Mohsin and M.Z.M. Said. 1985. Growth characteristics of Lutjanidae off the east coast of Peninsular Malaysia. p. 165-174. In A.K.M. Mohsin, M.I.H. Mohamed and M.A. Ambak (eds.) *Ekspedisi Matahari '85: a study on the offshore waters of the Malaysian EEZ*. Occas. Publ. Fac. Fish. Mar. Sci. Univ. Pertanian Malays. No. 3.
- 002300 Ralston, S. and H.A. Williams. 1988. Depth distributions, growth, and mortality of deep slope fishes from the Mariana Archipelago. NOAA Technical Memorandum NMFS. NOAA-TM-NMFS-SWFC-113. 47 p.
- 002315 Wright, A., P.J. Dalzell and A.H. Richards. 1986. Some aspects of the biology of the red bass, *Lutjanus bohar* (Forsskål), from the Tigak Islands, Papua New Guinea. *J. Fish Biol.* 28:533-544.
- 002316 Talbot, F.H. 1957. The fishes of the genus *Lutjanus* of the east African coast. *Ann. Mag. Nat. Hist.* 12:241-267.
- 002318 Ju, D.R., S.Y. Yeh and H.C. Liu. 1988. Age and growth of *Lutjanus altifrontalis* in the waters off northwest Australia. *Acta. Oceanogr. Taiwanica* 20:1-12.
- 002320 Druzhinin, A.D. 1970. The range and biology of snapper (family Lutjanidae). *J. Ichthyol.* 10:715-735.
- 002322 Ralston, S. and H.A. Williams. 1988. Age and growth of *Lutjanus kasmira*, *Lethrinus rubrioperculatus*, *Acanthurus lineatus* and *Ctenochaetus striatus* in American Samoa. Adminstrative Report 11-18-18, Southwest Fisheries Center: NMFS (Honolulu Laboratory), 11 p.
- 002326 Lai, H.L. and H.C. Liu. 1979. Age and growth of *Lutjanus sanguineus* in the Arafura Sea and north west shelf. *Acta Oceanogr. Taiwanica* 10:164-175.
- 002328 Druzhinin, A.D. and N.A. Filatova. 1980. Some data on Lutjanidae from the Gulf of Aden area. *J. Ichthyol.* 20(1):8-14.
- 002329 Yeh, S.Y., C.Y. Chen and H.C. Liu. 1986. Age and growth of *Lutjanus sebae* in the waters off northwestern Australia. *Acta. Oceanogr. Taiwan. Sci. Rep.* 16:90-102.
- 002811 Sanchez-Gil, P., J.R. Miranda and D.F. Hernández. 1991. Avances en el atlas ecológico pesquero del sur del Golfo de México. *Jaina* 2(4):16.
- 003083 Moore, C.M. and R.F. Labisky. 1984. Population parameters of a relatively unexploited stock of snowy groupers in the lower Florida Keys. *Trans. Am. Fish. Soc.* 113:322-329.
- 003090 Manooch, C.S., III. 1987. Age and growth of snappers and groupers. p. 329-373. In J.J. Polovina and S. Ralston (eds.) *Tropical snappers and groupers: biology and fisheries management*. Ocean Resour. Mar. Policy Ser. Westview Press, Boulder.
- 003092 Nagelkerken, W.P. 1979. Biology of the graysby, *Epinephelus cruentatus*, of the coral reef of Curaçao. *Stud. Fauna Curacao Other Caribb. Isl.* 60:1-118.

- 003093 Thompson, R. and J.L. Munro. 1983. The biology, ecology and bionomics of the snappers, Lutjanidae, p. 94-109. In J.L. Munro (ed.) Caribbean coral reef fishery resources. ICLARM Stud. Rev 7, 276 p.
- 003094 Matheson, R.H., III, and G.R. Huntsman. 1984. Growth, mortality, and yield-per-recruit models for speckled hind and snowy grouper from the United states South Atlantic Bight. Trans. Am. Fish. Soc. 113: 607-616.
- 003095 Burnett-Herkes, J. 1975. Contribution to the biology of the red hind, *Epinephelus guttatus*, a commercially important serranid fish from the tropical western Atlantic. University of Miami, Coral Gables, Florida. 154 p. Ph.D. dissertation.
- 003096 Moe, M.A., Jr. 1969. Biology of the red grouper *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Fla. Dep. Nat. Resour., Mar. Res. Lab. Prof. Pap. Ser. 10:1-95.
- 003097 Melo, A.M. 1975. Aspectos biológicos pesqueros de *Epinephelus morio* (Val.). Univ. Nac. Autónoma Mexico, Mexico City, D.F., 68 p. M.S. thesis.
- 003098 Olsen, D.A. and J.A. LaPlace. 1979. A study of a Virgin Islands grouper fishery based on a breeding aggregation. p. 130-144. In Proc. 31st Gulf Caribb. Fish. Inst., Miami.
- 003099 Manooch, C.S., III, and M. Haimovici. 1978. Age and growth of the gag, *Mycteroperca microlepis*, and size-age composition of the recreational catch off the southeastern United States. Trans. Am. Fish. Soc. 107:234-240.
- 003101 Claro, R. 1981. Ecología y ciclo de vida del pargo criollo, *Lutjanus analis* (Cuvier), en la plataforma Cubana. Acad. Cienc. Cuba, Inf. Cient. Inst. Oceanol. (186):83 p.
- 003102 Pozo, E. 1979. Edad y crecimiento del pargo criollo (*Lutjanus analis* Cuvier 1928) en la plataforma nororiental de Cuba. Rev. Cubana Invest. Pesq. 4(2):1-24.
- 003103 Claro, R. 1976. Ecología y dinámica de algunos índices biológicos en los lutjanidos de Cuba. Cienc. URSS, Inst. Morfol. Evol. Ecol. Animal. Tesis. Acad.
- 003104 Mason, D.L. and C.S. Manooch III. 1985. Age and growth of mutton snapper along the east coast of Florida. Fish. Res. 3: 93-104.
- 003111 Munro, J.L. 1983. Epilogue: Progress in coral reef fisheries research, 1973-1982. p. 249-265. In J.L. Munro (ed.) Caribbean coral reef fishery resources. ICLARM Stud. Rev. 7, 276 p.
- 003112 Nelson, R.S. and C.S. Manooch III. 1982. Growth and mortality of red snappers, *Lutjanus campechanus*, in the west central Atlantic Ocean and northern Gulf of Mexico. Trans. Am. Fish. Soc. 111: 465-475.
- 003113 Baez Hidalgo, M., L. Alvarez-Lajonchere and B. Pedrosa Tabio. 1980. Edad y crecimiento del caballero *Lutjanus griseus* (Linné), en tunas de Zaza, Cuba. Rev. Invest. Mar. 1(3-5):135-150.
- 003114 Claro, R. 1983. Ecología y ciclo de vida del caballero, *Lutjanus griseus* (Linnaeus), en la plataforma Cubana II. Edad y crecimiento, estructura de las poblaciones y pesquerías. Rep. Invest. Inst. Oceanol. Acad. Cienc. Cuba 8, 26 p.
- 003115 Manooch, C.S., III and R.H. Matheson III. 1981. Age, growth and mortality of gray snapper collected from Florida waters. Proc. Anñ. Conf. Southeastern Assoc. Fish Wildl. Agencies 35:331-344.
- 003116 Lima, F.R. 1965. Crescimento do 'pargo' (*Lutjanus aya*, Bloch, 1795): aspectos quantitativos. Bol. Estud. Pesca 5:33-42.
- 003119 Claro, R. and Y.S. Reshetnikov. 1981. Ecología y ciclo de vida de la biajiba, *Lutjanus synagris* (Linnaeus), en la plataforma Cubana. 1. Formación marcas de crecimiento en sus estructuras. Inf. Cient. Tec. Inst. Oceanol. Acad. Cienc. Cuba Oceanol. 174, 28 p.
- 003120 Manooch, C.S., III and D.L. Mason. 1984. Age, growth and mortality of lane snapper from Southern Florida. Northeast Gulf Sci. 7:109-115.
- 003121 Piedra, G. 1969. Materials on the biology of the yellow-tail snapper (*Ocyurus chrysurus* Bloch). p. 251-296. In A.S. Bogdanov (ed.), Soviet-Cuban fishery research. Isr. Progr. Sci. Trans. Jerusalem, Israel.
- 003122 Claro, R. 1983. Ecología y ciclo de vida de la rabirubia, *Ocyurus chrysurus* (Bloch), en la plataforma Cubana II. Edad y crecimiento, estructura de poblaciones, y pesquerías. Rep. Invest. Inst. Oceanol. Acad. Cienc. Cuba 19, 33 p.
- 003123 Johnson, A.G. 1983. Age and growth of yellowtail snapper from South Florida. Trans. Am. Fish. Soc. 112:173-177.
- 003124 Ralston, S. 1980. An analysis of the Hawaiian offshore handline fishery: a progress report. p. 204-215. In R. Grigg and R. Pfund (eds.) Proc. Symp. on Status of Resource Investigation in the N.W. Hawaiian Islands. Univ. Hawaii Seagrant Misc. Rept. UNIHI-SEAGRANT-MR-8004.

- 003125 Grimes, C.B. 1978. Age, growth and length-weight relationships of vermilion snapper, *Rhombopterus aurorubens* from North Carolina and South Carolina waters. Trans. Am. Fish. Soc. 107:454-456.
- 003127 Ralston, S. 1987. Mortality rates of snappers and groupers. p. 375-404. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Ocean Resour. Mar. Policy Ser. Westview Press, Boulder.
- 003196 Saloman, C.H. and W.A. Fable, Jr. 1981. Length-frequency distribution of recreationally caught fishes from Panama City, Florida in 1978 and 1979. NOAA Tech. Memo. NMFS-SEFC-61.
- 003204 Futch, R.B. and G.E. Bruger. 1976. Age, growth and reproduction of red snapper in Florida waters. p. 165-184. In H.R. Bullis and A.C. Jones (eds.) Proc. Colloquium on Snapper-Grouper Fishery Resources of the Western Central Atlantic Ocean. Florida Sea Grant Program Report 17.
- 003224 Manickchand-Dass, S. 1987. Reproduction, age and growth of the lane snapper, *Lutjanus synagris* (Linnaeus), in Trinidad, West Indies. Bull. Mar. Sci. 40(1): 22-28.
- 003249 Baisre, J.A. and J. Paez. 1981. Los recursos pesqueros del archipielago Cubano. WECAF Stud. 8:79.
- 003252 Espinosa, L. and E. Pozo. 1982. Edad y crecimiento del sesi (*Lutjanus buccanella* Cuvier, 1928) en la plataforma suroriental de Cuba. Rev. Cuba. Invest. Pesq., 7(1): 80-100.
- 003626 Edwards, R.R.C. and S. Shaher. 1991. The biometrics of marine fishes from the Gulf of Aden. Fishbyte 9(2):27-29.
- 003627 Mathews, C.P. and M. Samuel. 1991. Growth, mortality and length-weight parameters for some Kuwaiti fish and shrimp. Fishbyte 9(2):30-33.
- 003639 Mathews, C.P. and M. Samuel. 1987. Growth, mortality and assessment for groupers from Kuwait. Kuwait Bull. Mar. Sci. 9:173-191.
- 003794 Pinto, L. 1986. Use of ELEFAN programs for emigrating species. Fishbyte 4(1):14-15.
- 004560 Uchida, R.N. 1986. Berycidae. p. 78-79. In R.N. Uchida and J.H. Uchiyama (eds.) Fishery Atlas of the Northwestern Hawaiian Islands. NOAA Tech. Rep. NMFS 38.
- 004578 Uchiyama, J.H. and D.T. Tagami. 1984. Life history, distribution, and abundance of bottomfishes in the Northwestern Hawaiian Islands. p. 229-247. In R.W. Grigg and K.Y. Tanoue (eds.) Proceedings of the Second Symposium on Resource Investigations in the Northwestern Hawaiian Islands.
- 004613 Ralston, S. and G.T. Miyamoto. 1983. Analyzing the width of daily otolith increments to age the Hawaiian snapper, *Pristipomoides filamentosus*. Fish. Bull., US 81:523-535.
- 004748 Sherman, K., L.M. Alexander and B.D. Gold. 1991. Food chains, yields, models, and management of large marine ecosystems. Westview Press, Inc., Boulder, Colorado. 320 p.
- 004834 Acosta, A. and R.S. Appeldoorn. 1992. Estimation of growth, mortality and yield per recruit for *Lutjanus synagris* (Linnaeus) in Puerto Rico. Bull. Mar. Sci. 50(2):282-291.
- 004840 Davis, T.L.O. and G.J. West. 1992. Growth and mortality of *Lutjanus vittus* (Quoy and Gaimard) from the North West Shelf of Australia. Fish. Bull. 90:395-404.
- 004841 Bullock, L.H., M.D. Murphy, M.F. Godcharles and M.E. Mitchell. 1992. Age, growth, and reproduction of jewfish *Epinephelus itajara* in the eastern Gulf of Mexico. Fish. Bull. 90:243-249.
- 004895 Kitalong, A.H. and P. Dalzell. 1994. A preliminary assessment of the status of inshore coral reef fish stocks in Palau. Inshore Fish. Res. Tech. Doc. No. 6, South Pacific Commission, Noumea, New Caledonia.
- 005307 Manooch, C.S., III and C.L. Drennon. 1987. Age and growth of yellowtail snapper and queen triggerfish collected from the U.S. Virgin Islands and Puerto Rico. Fish. Res. 6:53-68.
- 005533 Djabali, F., A. Mehalia, M. Koudil and B. Brahmi. 1993. Empirical equations for the estimation of natural mortality in Mediterranean teleosts. Naga, ICLARM Q. 16(1):35-37.
- 005545 Bouain, A. 1985. Croissance linéaire des mérous du Golfe de Gabès (Tunisie). Rapp. P.-v. Réun. CIEM 29(8):99-100.
- 005550 Chauvet, C. 1988. Etude de la croissance du mérou *Epinephelus guaza* (Linné 1758) des côtes Tunisiennes. Aquat. Living Resour. 1:277-288.
- 005738 McPherson, G.R. and L. Squire. 1990. Age and growth of three dominant *Lutjanus* species of the Great Barrier Reef inter-reef fishery. Asian Fish. Sci. 5(1):25-36.
- 005739 Chen, C.Y., S.Y. Yeh and H.C. Liu. 1984. Age and growth of *Lutjanus malabaricus* in the northwestern shelf off Australia. Acta Oceanogr. Taiwan 15:154-164.

- 005760 Erzini, K. 1991. A compilation of data on variability in length-age in marine fishes. Working paper 77. Fisheries Stock Assessment, Title XII, Collaborative Research Support Program, University of Rhode Island. (unpaged).
- 005777 Briggs, P.T. 1978. Black sea bass in New York waters. N.Y. Fish Game J. 25:45-58.
- 005793 Ezzat, A.A., W.F. Wadie, M.Y. Mikail and M.T. Hashem. 1981. Age and growth of *Epinephelus aeneus* in the Egyptian Mediterranean waters. Bull. Inst. Oceanogr. (ARE) 7:395-406.
- 005808 Hastings, P.A. and S.A. Bortone. 1980. Observations on the life history of the belted sandfish *Serranus subligarius* (Serranidae). Env. Biol. Fish. 5:365-374.
- 005847 Morales-Nin, B. 1989. Growth determination of tropical marine fishes by means of otolith interpretation and length analysis. Aquat. Living Resour. 22:241-253.
- 005877 Wadie, W.F., M.T. Hashem, M.Y. Mikail and A.A. Ezzat. 1981. Age and growth of *Epinephelus alexandrinus* in the Egyptian Mediterranean waters. Bull. Inst. Oceanogr. ARE 7:559-574.
- 005904 Pozo, E. and L. Espinosa. 1982. Estudios de la edad el crecimiento del pargo del alto (*Lutjanus vivanus* Cuvier, 1828) en la plataforma surooriental de Cuba. Rev. Cub. Inv. Pesq. 7:1-23.
- 006157 Lee, J.U. and A.F. Al-Baz. 1989. Assessment of fish stocks exploited by fish traps in the Arabian Gulf area. Asian Fish. Sci. 2:213-231.
- 006441 Mees, C.C. 1993. Population biology and stock assessment of *Pristipomoides filamentosus* on the Mahé Plateau, Seychelles. J. Fish Biol. 43:695-708.
- 006486 Hostetter, E.B. and T.A. Monroe. 1993. Age, growth, and reproduction of tautog, *Tautoga onitis* (Labridae: Perciformes) from coastal waters of Virginia. Fish. Bull. US 91:45-64.
- 006844 Wenner, C.A., W.A. Roumillat and C.W. Waltz. 1986. Contributions to the life history of black sea bass, *Centropristes striata*, off the southeastern United States. Fish. Bull. 89:723-741.
- 006846 Matheson, R.H., III, G.R. Huntsman and C.S. Manooch III. 1986. Age, growth, mortality, food and reproduction of scamp, *Myctoperca phenax*, collected off North Carolina and South Carolina. Bull. Mar. Sci. 38:300-312.
- 006912 Murray, P.A., L.E. Chinnery and E.A. Moore. 1992. The recruitment of the queen snapper, *Etelis oculatus* Val., into the St. Lucian fishery: recruitment of fish and recruitment of fishermen. Proc. Gulf Caribb. Fish. Inst. 41:297-303.
- 006914 Murray, P.A. and E.A. Moore. 1992. Recruitment and exploitation rate of *Etelis oculatus* Val. in the St. Lucian fishery. Proc. Gulf Caribb. Fish. Inst. 42:262. (abstract).
- 006930 Rodriguez, W.T. 1984. Estudio preliminar para evaluar las características biológicas pesqueras de *Mycteroperca olfax* en las islas Galápagos (Ecuador). Bol. Cient. Téc., Inst. Nac. de Pesca, Guayaquil-Ecuador 6(3):3-66.
- 006975 Sanders, M.J., G. Carrara and G. Lablache. 1988. Preliminary assessment for the brownspotted grouper *Epinephelus chlorostigma* occurring on the Mahé Plateau (Seychelles). p. 268-277. In M.J. Sanders, P. Sparre and S.C. Venema (eds.) Proceedings of the workshop on the assessment of the fishery resources in the Southwest Indian Ocean. FAO/UNDP: RAF/79/065/WP/41/88/E.
- 006985 Ferreira, B.P. and G.R. Russ. 1992. Age, growth and mortality of the inshore coral trout *Plectropomus maculatus* (Pisces: Serranidae) from the central Great Barrier Reef, Australia. Aust. J. Mar. Freshwat. Res. 43:1301-1312.
- 007046 Abdel-Aziz, S.H. 1991. Sexual differences in growth of the painted comber, *Serranus sciba* (Linnaeus, 1758) (Teleostei, Serranidae) from the southeastern Mediterranean. Cybium 15(3):221-228.
- 007069 Ferreira, B.P. and G.R. Russ. 1993. Age validation and estimation of growth rate of the coral trout, *Plectropomus leopardus* (Lacepède 1802) from Lizard Island, northern Great Barrier Reef. Fish. Bull. 92:46-57.
- 007185 Romero, M.C., E.E. Barr and A.G. Boa. 1987. Algunos aspectos biológicos-pesqueros de la cabrilla *Epinephelus labriformis* (Jenyns, 1840). Acta Científica Potosina 9(2):165-176.
- 007194 Mees, C. 1992. Seychelles demersal fishery: an analysis of data relating to four key demersal species. Seychelles Fishing Authority, SFA/R&D/019. 142 p.
- 007196 Moussac, G. de. 1988. Synthèse des données sur la pêche artisanale aux Seychelles, biologie-resources-exploitation. SFA/R&D/006. 64 p.
- 007198 Van der Knapp, M., Z. Waheed, H. Shareef and M. Rasheed. 1991. Reef fish resources survey in the Maldives. Bay of Bengal Program/WP/64/MDV/88/007. 61 p.
- 008540 Valle, S.V. and J.P. Garcia-Arteaga. Growth parameters of marine fishes in Cuban waters. (MS)

- 008542 Artiles, M. 1985. Estudios sobre los efectos de los otolitos, la edad y el crecimiento de la biajaiba, (*Lutjanus synagris*, 1758). Trab. Dipl. Cent. Inv. Mar., Univ., Hab. 29 p.
- 008548 Carrillo de Albornoz, C. and M.E. Ramiro. 1988. Estudio biológico de la rabirrubia (*Ocyurus chrysurus*) en el W. de la plataforma SE de Cuba. I. Edad y crecimiento. Rev. Invest. Mar. 9(1):9-24.
- 008551 Claro, R., A. Garcia-Cagide, L.M. Sierra and J.P. Garcia-Arteaga. 1991. Características biológicas-pesqueras de la cherna criolla *Epinephelus striatus* (Bloch) (Pisces:Serranidae) en la plataforma Cubana. Cienc. Biol. 23:23-43.
- 008559 Garcia-Arteaga, J.P., A. Garcia-Cagide, L.M. Sierra and R. Claro. Características biológicas del bonaci gato, *Mycteroperca tigris* (Pisces: Serranidae) en la plataforma suroccidental de Cuba. Scientia Marina. (In press).
- 008561 Olaechea, A. and M. Quintana. 1970. Preevaluación sobre la determinación de la edad en la biajaiba, *Lutjanus synagris* (Linné). II. Reun. Balance Trabajo. Cent. Invest. Pesq. La Habana, Cuba.
- 008564 Perez, A. and R. Rubio. 1986. Análisis electrónico de frecuencias de largo en poblaciones de peces cubanos. Sto. Foro Cient. Cip., Cent. Invest. Pesq. Cuba. En. 1986.
- 008565 Piedra, G. 1965. Materiales sobre la biología de la rabirrubia, *Ocyurus chrysurus* (Bloch), p. 267-283. In A.S. Bogdanov (ed.) Invest. Pesq. Soviet-Cubanas Pischevaia Promishlenost, Moscú, Vol. 1.
- 008568 Salahange, P. 1984. Edad y crecimiento del caballero (*Lutjanus griseus*, Linné 1758) en la plataforma suroccidental de Cuba. Resum. Biol. IV Conf. Cient. Cienc. Nat. Exactas., II. Congr. Cienc. Biol. 82 p.
- 008863 Espinosa, L., E. Pozo and R. Quevedo. 1984. Edad y crecimiento del sesi (*Lutjanus bucanella* Cuvier, 1828) en la plataforma nororiental de Cuba. Rev. Cub. Inv. Pesq. 9(1):9-20.
- 008864 Claro, R., J. Baisre and J.P. Garcia-Arteaga. 1994. Pesquerías. In R. Claro (ed.) Ecología de los peces marinos de Cuba. Inst. Oceanol. Acad. Cienc. Cuba and Cen. Invest. Quintana Roo (CIQRO) México.
- 008866 Pozo, E., L. Espinosa and M. Guardiola. 1984. Características biológicas de los especies pelágico-oceánicas en la plataforma SW de Cuba. Resum. I Jor. Cient. BTJ., Cent. Inv. Pesq. La Habana. 8 p.
- 008867 Rubio, R., P. Salahange and M. Betancourt. 1985. Relaciones de la edad con el largo, el peso y la fecundidad de la biajaiba (*Lutjanus synagris*) de la plataforma suroccidental de Cuba. Rev. Cub. Invest. Pesq. 10(3-4):77-90.
- 008868 Rubio, R. 1986. Estudio sobre la edad y el crecimiento de la biajaiba (*Lutjanus synagris* Linnaeus 1758) (Pisces: Lutjanidae), en la plataforma noroccidental de Cuba. Sto. Foro Cient. Cip., Centr. Invest. Pesq., La Habana.
- 008869 Algunas consideraciones sobre la formación e interpretación del patrón de marcas de crecimiento de los otolitos de la biajaiba (*Lutjanus synagris*, Linnaeus 1758) y su uso en los estudios de edad y crecimiento. Sto. Foro Cient. Cip., Centr. Invest. Pesq., La Habana.
- 008870 Salahange, P. 1981. Edad y crecimiento de la biajaiba (*Lutjanus synagris*, Linnaeus). Resum. I. Congr. Nac. Cienc. Biol., La Habana.
- 008871 Buesa, R.J. and A. Olaechea. 1970. Estudios sobre la biajaiba: zona B y área de Diego Pérez. Cent. Inv. Pesq., Archivo (0120). 9 p.
- 011359 Badrudin, M. 1985. Untitled. Manuscript, Res. Inst. Mar. Fish., Jakarta.
- 011657 Arreguin-Sánchez, F. 1987. Estado actual de la explotación del mero (*Epinephelus morio*) del Banco de Campeche. 25 Aniv. Inst. Nat. Pesca. CRIP, Yucalpeten, INP, México.
- 011658 Arreguin-Sánchez, F., M. Contreras, V. Moreno, R. Burgos and R. Valdes. 1996. Population dynamics and stock assessment of red grouper (*Epinephelus morio*) fishery on Campeche Bank, México, p. 202-217. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.
- 011659 Arreguin-Sánchez, F. 1992. An approach to the study of the catchability coefficient with application to the red grouper (*Epinephelus morio*) fishery from the continental shelf of Yucatan, Mexico. Centro de Invest. Estudios Avanzados del IPN, México. 222 p. Doctoral thesis.
- 011676 Doi, T., D. Mendizabal and M. Contreras. 1981. Análisis preliminar de la población de mero *Epinephelus morio* (Valenciennes) en el Banco de Campeche. Cienc. Pesq., México (1):1-16.
- 011678 González, P.D., S. Zupanovic and H.E. Ramis. 1974. Biología pesquera de la cherna americana del Banco de Campeche. INP/CIP Cuba. Res. Invest. 1:107-111.
- 011679 Guzmán, E. 1986. Contribución al conocimiento de la pesquería de mero (*Epinephelus morio*, Valenciennes) de las costas de Yucatán. ENEP-Iztacala, UNAM, México. Tesis profesional.

- 011680 Muhlia, A. 1976. Aspectos biológico-pesqueros de *Epinephelus morio* (Val.): mero. Mem. Primer Simp. al. Rec. Pesq. Mar. México. Inst. Natl. Pesca, México. 2:223-265.
- 011681 Rodríguez, H. 1986. Estudio comparativo de dos estructuras rígidas (otolito y hueso mesopterigoide) para la estimación de edad crecimiento del mero (*Epinephelus morio*) del Banco de Campeche. Univ. Autón., Nuevo León, México. Tesis profesional.
- 011682 Salazar, A.R. 1988. Contribución al conocimiento de la pesquería de mero (*Epinephelus morio*) de la flota menor de las costas de Yucatán. ENEP-Iztacala, UNAM, México. Tesis profesional.
- 011683 Valdés, E. and G. Padrón. 1980. Pesquerías de palangre. Rev. Cub. Invest. Pesq. 5(2):38-52.
- 011684 Manickchand-Heileman, S.C. and D.A.T. Phillip. 1996. Reproduction, age and growth of the Caribbean red snapper *Lutjanus purpureus* in waters off Trinidad and Tobago, p. 137-149. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.
- 011686 Ximenes, M.O.C. and A.A. Fonteles-Filho. 1988. Estudo da idade e crescimento do pargo, *Lutjanus purpureus* Poey (Pisces: Lutjanidae), no norte e nordeste do Brasil. Arq. Cienc. Mar. 27:69-81.
- 011687 Posada, J.M. and R.S. Appeldoorn. 1996. The validity of length-based methods for estimating growth and mortality of groupers, as illustrated by comparative assessment of the creole fish, *Paranthias furcifer* (Pisces, Serranidae), p 163-173. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.
- 011689 Nelson, R.S., C.S. Manooch III and D.L. Mason. 1986. Ecological effects of energy development on reef fish of the Flower Garden Banks: reef fish bioprofiles. Final Report. Southeast Fish. Cent. Beaufort Lab., Natl. Mar. Fish. Serv., NOAA, Beaufort, North Carolina. 251 p.
- 011690 Leonce-Valencia, C.O. and C. Monroy. 1993. Growth parameter estimation based on length frequency data of red snapper (*Lutjanus campechanus*) on Campeche Bank. Paper presented at the International Workshop on Tropical Groupers and Snappers, 28-29 October 1993, Campeche, Mexico
- 011692 Gonzalez, M.E. 1988. Estudio de la pesquería de huachinango (*Lutjanus campechanus* Poey) del Banco de Campeche. CINVESTAV Unidad Mérida. Tesis maestría.
- 011693 Rodriguez Castro, J. 1992. Contribución al conocimiento de la biología pesquería del huachinango *Lutjanus campechanus* (Poey 1860) en las costas del sur de Tamaulipas, México. Tec. de Ciudad Victoria, Tamaulipas, México. Tesis de licenciatura.
- 011824 Claro, R. and J.P. García-Arteaga. 1994. Crecimiento. p. 321-402. In R. Claro (ed.) Ecología de los peces marinos de Cuba. Inst. Oceanol. Acad. Cienc. Cuba, and Cen. Invest. Quintana Roo (CIQRO) México.
- 011827 Ayala, D.L. 1984. Determinación de algunos parámetros poblacionales y de la biología pesquera de la biajaiba *Lutjanus synagris* (Linneo), 1758 (Pisces: Lutjanidae). E.N.E.P.I., UNAM, México. Tesis de licenciatura.
- 011828 Torres-Lara, R. and E. Chávez. 1987. Evaluación y diagnóstico de la pesquería de rubia (*Lutjanus synagris*) en el estado de Yucatán. Cienc. Mar. 13(1):7-29.
- 011829 Mexicano-Cintora, G. and F. Arreguin-Sánchez. 1989. Dinámica de las poblaciones de rubia (*Lutjanus synagris*) y canané (*Ocyurus chrysurus*) de las costas de Yucatán, México. Centro de Investigación y Estudios Avanzados del Instituto Politécnico Nacional, Unida Mérida, México. 12 p., 3 tabs, 1 fig.
- 011830 Cantarell, E. 1982. Determinación de la edad y el ritmo de crecimiento del pargo canané (*Ocyurus chrysurus*, Bloch 1871), en el estado de Yucatán. E.N.E.P.I., UNAM, México. Tesis de licenciatura.
- 011831 Mexicano-Cintora, G. and F. Arreguin-Sánchez. 1989. Estimación de edad y crecimiento del pargo canané (*Ocyurus chrysurus*) del litoral de Yucatán, México. Centro de Investigación y Estudios Avanzados del Instituto Politécnico Nacional, Unida Mérida, México. 12 p., 3 tabs, 1 fig.
- 011832 Valdés-Alonso, R. and D. Fuentes-Castellanos. 1987. Informe anual del programá de cruceros de investigaciones sobre el mero, *Epinephelus morio* (Valenciennes) en el Banco de Campeche. Centro de Investigaciones Pesqueras, La Habana, Cuba. (manuscript), 10 p.
- 011834 Manooch, C.S., III and D.L. Mason. 1987. Age and growth of Warsaw grouper from the southeast region of the United States. Northeast Gulf Sci. 9(2):65-75.

ENTERED IN NAGA

PART IV: FISHERIES ASSESSMENTS

APR 14 1998

**Effect of Gas Bladder Deflation
on Mortality of Hook-and-Line Caught and Released
Red Snappers: Implications for Management**

J.H. RENDER^a
C.A. WILSON

*Coastal Fisheries Institute
Center for Coastal, Energy, and Environmental Resources
Louisiana State University, Baton Rouge
Louisiana 70803-7503, USA*

RENDER, J.H. and C.A. WILSON. 1996. The effect of gas bladder deflation on mortality of hook-and-line caught and released red snappers: implications for management [*Efecto de la vejiga gaseosa deflacionada sobre la mortalidad de pargos del golfo capturados con palangre y liberados: implicaciones para el manejo*], p. 244-253. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) *Biology and culture of tropical groupers and snappers*. ICLARM Conf. Proc. 48, 449 p.

Abstract

Size and bag limits are commonly used to protect certain species from overexploitation. However, the effectiveness of these practices is poorly understood particularly for released deep-water physoclistous fish like the red snapper, *Lutjanus campechanus*. The purpose of this study was to determine the short- and long-term effects of gas bladder deflation on mortality of hook-and-line caught and released red snappers. The study was conducted initially at a single depth (21 m) from a gas platform owned by Mobil Corporation. Red snappers (n=250) were caught using typical recreational fishing gear, brought to the surface and treated according to one of the following groups: 1) control; 2) gas bladder deflated; 3) tagged; and 4) deflated and tagged. Snappers were then released into a holding net that extended 10 m into the water column. After 24-48 hours, mortality was tallied by treatment group. Long-term mortality effects, by treatment, were estimated by monitoring the mortality of 345 red snappers held in aquaria for 30-40 days. In the second phase of the study, mortality was estimated at various depths (n=345). Results indicated that mortality rate of red snappers caught at 21 m averaged 19.7%. There was no significant difference in mortality in the treatment groups compared for the short- or long-term experiments. For fish caught at depths greater than 21 m, the results were more variable and mortality ranged from 0 to 30%. Based on histological evidence, actual mortality of fish caught at depths greater than 21 m may have been greater than observed due to delayed physiological response. Based on our results, gas bladder deflation is not an effective tool for enhancing survival of red snappers which are released after capture on hook-and-line.

Resumen

Límites en la talla y en el tamaño del bolso son herramientas comúnmente usadas para proteger ciertas especies de la sobre-explotación. La efectividad de estas prácticas, sin embargo, es pobremente entendida, particularmente para peces fisoclistos de aguas profundas como el pargo del Golfo. El propósito

^a Deceased; please address correspondence to coauthor.

de este estudio fué determinar los efectos a corto y largo plazo de la deflación de la vejiga gaseosa sobre la mortalidad de pargos del Golfo capturados y liberados utilizando palangres. El estudio se efectuó inicialmente a solo un nivel de profundidad (21 m) desde una plataforma de gas perteneciente a Mobil Corporation. Los pargos del Golfo ($n=250$) fueron capturados usando artes para pesca deportiva, traído a la superficie y colocado de acuerdo a alguno de los siguientes grupos: (1) control, (2) vejiga gaseosa desinflada, (3) marcados, y (4) marcados/deflacionados. Los pargos fueron entonces liberados en una red colgante que se extendió 10 m en la columna de agua. Despues de 24 a 48 horas, la mortalidad fué registrada para cada grupo/tratamiento. El efecto a largo plazo, por tratamiento, fué estimado por monitoreo de la mortalidad de 345 pargos mantenidos en acuarios por 30-40 días. En la segunda etapa del estudio, la mortalidad fué estimada a varias profundidades ($n=345$). Los resultados indican que la tasa de mortalidad del pargo del Golfo capturado a 21 m promedió 19.7%. No hubo diferencias significativas en mortalidad entre grupos de tratamiento comparando cada experimento, a corto y largo plazo. Los resultados de los peces capturados a profundidades mayores a 21 m fueron más variables y las mortalidades observadas fluctuaron de 0% a 30%. Con base en evidencias histológicas, la mortalidad actual de peces capturados a profundidades mayores de 21 m pudieron haber sido más altas que las observadas debido a un retraso en la respuesta fisiológica. Los resultados aquí obtenidos sugieren que la deflación de la vejiga gaseosa no es una herramienta efectiva para obtener estimados de supervivencia en el pargo del Golfo capturado con palangre y posteriormente liberado.

Introduction

The red snapper (*Lutjanus campechanus*) is an important commercial and recreational species in the northern Gulf of Mexico (GOM) (see Cuellar et al.; Ehrhardt and Legault; Monroy-Garcia et al., this vol.). Off Louisiana, red snappers comprise a significant portion of the communities that are associated with offshore oil and gas production platforms. These platforms serve as 'de facto' reefs since natural hard substrate is limited and far from shore.

The red snapper population in the northern GOM was recently characterized by the Gulf of Mexico Fisheries Management Council's (GMFMC) Reef Fish Assessment Panel as being in a state of "severe overfishing" (Muller 1990). Much of the current problem has been attributed to high mortality rates in young fish. Highest fishing mortality is on age 1 (juvenile) snappers taken in the shrimp fishery bycatch, followed by age 3 fish from the commercial and recreational fisheries (Muller 1990). Age 1 and 2 fish are also common in commercial and recreational catches (Wilson et al. 1993). Undersized fish caught in the directed commercial and recreational fisheries are returned to the water, presumably to recover and grow larger. Although the question of survival of released red snapper has been raised, it has not been adequately addressed particularly

off Louisiana where extremely large numbers of undersized fish are caught and released (Capt. Steve Tomeny, pers. comm.). Little is known about the success of release practices since contact with an individual fish is lost at time of release and return rates in most tagging studies have been low.

There has been considerable debate and interest on the question of whether gas bladders in certain fishes should be deflated by recreational anglers to increase a fish's ability to descend rapidly (Sport Fishing Institute 1991). The question has merit since vertical movements of physoclistous species are limited in either upward or downward directions due to positive or negative buoyancy effects as explained by Boyle's Law (Alexander 1967). A central question exists, however, as to whether deflation techniques increase the survival of released fish or simply enable the fish to submerge where they experience delayed mortality. Gotshall (1964) studied the effect of deflating gas bladders on the survival of tagged rockfish (Genus *Sebastodes*). He concluded that deflated rockfish may have suffered greater mortality than non-deflated ones and suggested that more detailed studies were needed on the survival of deflated and non-deflated rockfish.

The goal of this study was to estimate mortality rates of red snapper which have been caught on hook-and-line and released in order to determine whether gas bladder deflation techniques could be used to increase survival. Specific objectives were to: a) determine short-term effects of air bladder deflation on mortality rates and b) determine long-term effects of gas bladder deflation on mortality rates.

Materials and Methods

Initially, the study was conducted on a gas production platform (Mobil West Cameron 352) approximately 90 km south of Cameron, Louisiana, from October 1990 to September 1991, with water depth of 21 m. Red snappers ($n=250$) were caught near the bottom by hook-and-line with typical bottom fishing gear (Penn 309 reels, 6 ft medium action rods, 5° stainless hooks). Bait was usually cut blue runner (*Caranx cryos*), bluefish (*Pomatomus saltatrix*) or little tunny (*Euthynnus alletteratus*). Following hooking, the fish were brought quickly to the surface, treated, and released into a holding net. Out-of-water handling time was usually less than 1 min and never more than 2 min, otherwise the specimen was rejected from testing due to excessive handling time. The holding net consisted of a modified commercial hoop net (#15 twine, 2.5 cm square mesh) (Fig. 1) that was extended to 11 m length with a 1.8 m diameter hoop at the mouth. The nets were moored vertically within the platform structure by pulling a rope attached to the bottom of the net through a shackle that was attached to the platform 8.5 m below the surface. After their release into the net, the fish were held from 24 to 48 hours. Mortality was tallied at the end of each experiment for each treatment group.

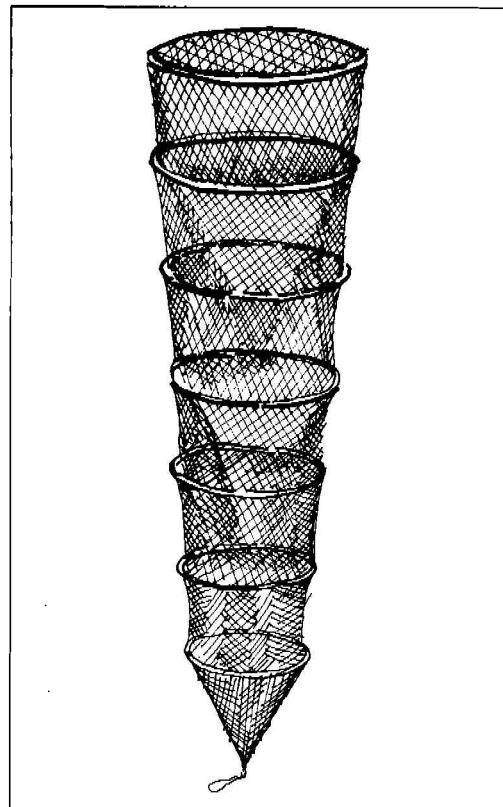


Fig. 1. Modified hoop net design used for holding hook-and-line caught and released red snappers. [Diseño modificado de la red de aro usada para contener pargos del Golfo capturados y liberados con palangre.]

Experimental design included the following treatments: a) control; b) air bladder deflation; c) tagging; and d) air bladder deflation and tagging. Control here refers to the release of fish into a net with no treatment. Air bladders were deflated by inserting a sterile disposable needle tip (Becton Dickinson & Co., Precision Glide #20, 4 cm) through the side of the fish under the fourth dorsal spine and directly behind the opercular spine. This site was preselected based on our determination that no other organs would be damaged

by insertion at this site. Tags (Hallprint dart tags) were inserted below the first dorsal fin to hook between the pterygiophores of that fin. Treatments were designed to test the effects of tagging and air bladder deflation relative to a control through the following comparisons: a) tagging versus not tagging; b) air bladder deflation versus no deflation; and c) tagging with air bladder deflation versus tagging without deflation.

The effects of tagging and tagging with deflation were investigated since all of the specimens in the long-term studies would be tagged as described below.

Long-term effects of catch on survival were tracked by transferring specimens to the Aquarium of the Americas in New Orleans, Louisiana. The aquarium specimens were transported via ship in an oxygenated tank to Cameron, Louisiana, where they were received by Aquarium personnel for final transport via truck to New Orleans. The fish were held for 30-40 days in a 6.25 m diameter tank with a volume of approximately 34 m³ water capacity. Salinity and temperature were maintained at 32 ppt and 25°C. All fish were tagged for identification. Thirty-five of the red snappers had deflated air bladders, while 72 were tagged without gas bladder deflation. Mortality rates between the treatment groups (tagged, and tagged and deflated) were monitored by Aquarium personnel.

The effects of treatment on mortality rates were investigated using analysis of variance (ANOVA). Type III sums of squares were used for the analysis due to the unequal number of observations in each subclass.

In the second phase of the study, mortality effects were tested at variable depths by modifying the net system. From our work during the first phase of the study, we observed that most of the fish released into the closed net system were unable to submerge more than several feet, or for more than a few minutes, and then floated to

the surface. We hypothesized, therefore, that a conservative estimate of mortality could be obtained by releasing red snappers into an open net system and tallying the number of red snappers that were unsuccessful in submerging. Further, this estimate of submergence rate would allow us to evaluate the necessity of air bladder deflation (i.e., at what depth red snappers were unable to compensate for positive buoyancy).

To test whether the open net system could be used, we deployed closed and open net systems at 21 m water depth. Twenty red snappers were caught and released into each net. There was no significant difference in our mortality estimates ($p < 0.05$) between the two systems.

Six cruises were conducted aboard the *F/V Southerner* from September 1992 to March 1993. The original net design was modified by placing floats at the mouth of the net and opening the bottom of the net to allow the fish to swim out. The net was deployed from the rear of the vessel and the tail was weighted with two 4.5 kg mushroom anchors to keep the net suspended vertically. As in the first phase, fish were caught near the bottom, brought to the surface, and released after one of the following treatments: control or air bladder deflation. Red snappers were tested at five depth intervals (Table 1).

The effect of depth interval on mortality was investigated using ANOVA. Type III sums of squares were used for analysis due to unequal number of observations in each subclass.

A subsample of six fish collected at two depths (28 and 44 m, three from each) during the 4 March 1993 cruise were taken to compare physiological damage by depth. The specimens were preserved on ice, and transported back to the laboratory for gross necropsy analysis. Internal organs were examined, and condition or damage of organs and tissues were noted.

Table 1. Numbers of red snapper tested at various depth intervals during variable depth mortality experiments. [Número de pargos rojos a varios Intervalos de profundidad durante los experimentos de mortalidad a profundidades variables.]

Depth Interval (m)	FALL		SPRING	
	Control	Treatment Deflated	Control	Deflated
25 - 30	20	20	22	19
31 - 39	50	49	--	--
40 - 47	6	--	20	20
48 - 55	4	--	31	30
>55	--	--	10	7

Results

The length-frequency distribution of red snappers tested during this study is shown in Fig. 2. The minimum size limit for red snapper legally retained by the commercial and recreational fisheries is indicated on the chart. Overall mortality during the study averaged 19.7%. We observed no

significant differences among treatments (Table 2).

Red snappers that were transferred to the Aquarium of the Americas allowed us to examine long-term mortality. Twenty of the 107 specimens died within 2 to 37 days (average 11.4 days) from the time of transfer. Sixty percent of deaths occurred within the first week of captivity. Mortality rates between the tagged (18.0%), and tagged and

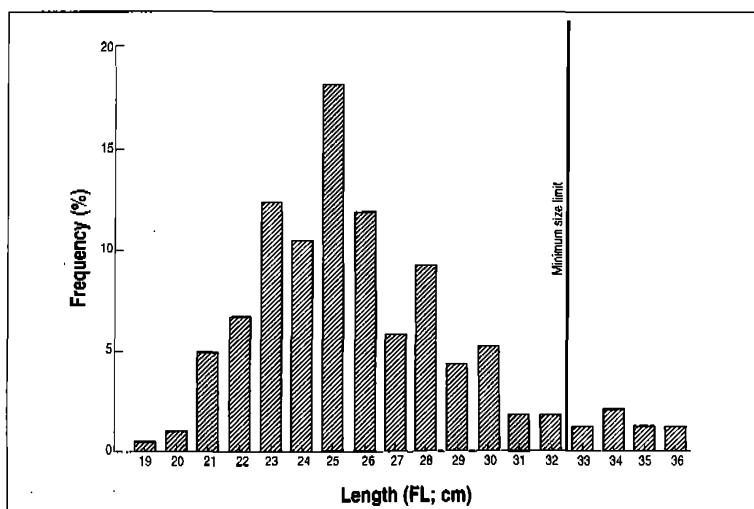


Fig. 2. Length-frequency distribution of red snappers used in mortality tests at 21 m depth. The minimum size limit for the commercial and recreational fisheries is indicated. [Distribución de frecuencia de longitudes del pargo del Golfo usados en las pruebas de mortalidad a 21 m de profundidad. Los límites mínimos de tamaño para la pesca comercial y deportiva son señalados.]

Table 2. Analysis of variance table testing the effects of treatment on mortality rates of hook-and-line caught and released red snapper. [Tabla del análisis de varianza probando los efectos de tratamiento sobre las tasas de mortalidad de pargos del Golfo capturados y liberados utilizando palangres.]

Source	df	ss	Model F-ratio	p>F
Model	3	0.0221	0.49	0.6952
Error	13	0.1950	--	--

Table 3. Mortality rate (%) of red snapper by treatment and season during variable depth mortality experiments. [Tasas de mortalidad (%) de pargo del Golfo por tratamiento y estación durante los experimentos de mortalidad a profundidad variable.]

Depth Interval (m)	FALL		SPRING	
	Control	Treatment	Control	Deflated
25 - 30	5.0	5.0	4.6	10.5
31 - 39	6.0	4.4	--	--
40 - 47	17.0	--	10.0	0.0
48 - 55	25.0	--	7.0	7.0
>55	25.0	--	20.0	0.0

deflated (20.1%) treatment groups were not significantly different ($p>0.05$).

Results from the depth tests are summarized in Table 3 by treatment, season and depth interval. A total of 345 red snappers were tested. Results from the fall cruises suggested increasing mortality with depth for the control group (Fig. 3); however, the numbers of fish tested at the two greatest depths tested were low, 6 and 4, respectively, and the relationship was not significant at $p=0.05$ (Table 4). Sample size was low in the deeper stations owing to our inability to catch sufficient numbers of

red snappers at a particular station, or because of current conditions that were sufficiently strong to prohibit deployment of the net system. During the spring cruises there was again a general trend of increasing mortality with depth for the control treatment (Fig. 3), but it was not significant at $p<0.05$.

Data from the deflated treatment group in the variable depth experiments exhibited considerably more variation for both the fall and spring cruises. Mortality was not significantly related to depth for either seasonal period. Greatest mortality in

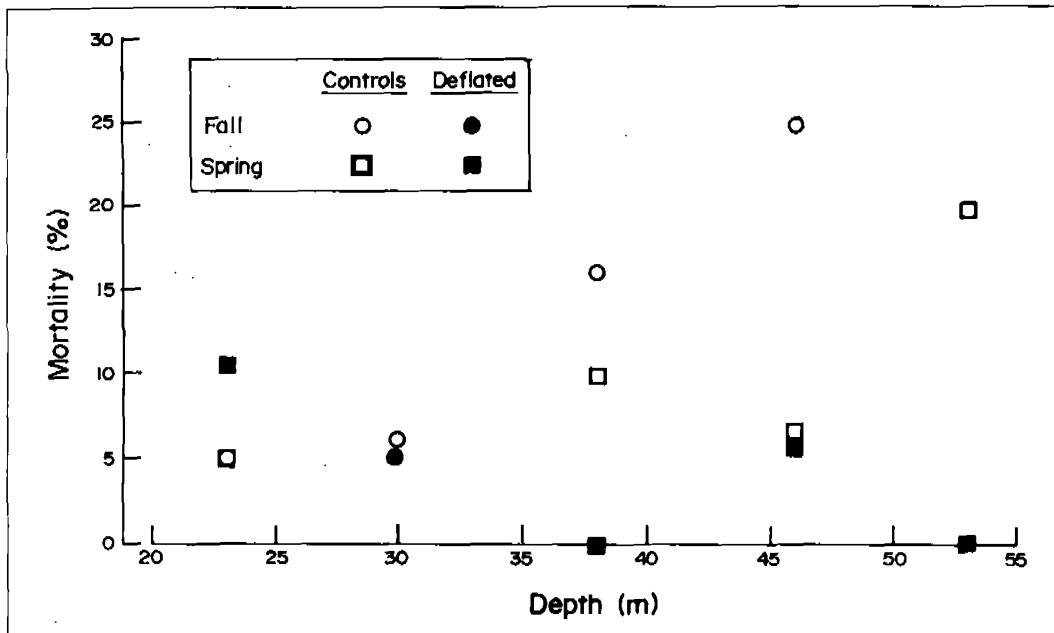


Fig. 3. Mortality rate, by treatment, of red snapper tested in the variable depth experiments during Fall 1992. [Tasa de mortalidad, por tratamiento, de las pruebas con pargo del Golfo en los experimentos con profundidad variable durante la época de lluvias en 1992.]

Table 4. Analysis of variance table testing the effects of depth, treatment, and the interaction between treatment and depth on mortality rates of hook-and-line caught and released red snapper. [Tabla de análisis de varianza probando los efectos de profundidad, tratamiento, y la Interacción entre tratamiento y profundidad sobre las tasas de mortalidad del pargo del Golfo capturado y liberado usando palangres.]

Source	df	Model		
		ss	F-ratio	p>F
Model	26	0.2056	0.74	0.7283
Error	5	0.0537		
Type III				
Variable	df	ss	F-ratio	p>F
Depth	15	0.1193	0.74	0.7035
Treatment	1	0.0126	1.17	0.3290
Depth*Trt	10	0.0698	0.65	0.7378

this group was 20% at >55 m during the spring cruises.

During the necropsy analyses we examined each specimen and noted whether: a) the gas bladder had ruptured; b) the stomach was everted; c) there was hemorrhaging of muscle tissue; d) there was hemorrhaging of the liver; and e) whether there was an

intussception (i.e., blockage) of the gut caused by the stomach eversion. For the three specimens examined from 28 m, there were no cases in which the stomach was everted and therefore no intussception of the gut. One of the three specimens had a ruptured gas bladder. Liver hemorrhage was noted in two specimens, and light muscle

hemorrhage noted for one. Of the fish examined from 44 m, two of the three specimens had everted stomachs and intussusception of the gut. The gas bladder was ruptured in two of the three specimens. Muscle hemorrhage was noted in all three specimens, and liver hemorrhage in two.

Discussion

We observed a mean mortality of 19.7% for fish caught and released at 21 m, and a general trend toward increasing mortality with depth of the control group during the variable depth tests. There was no significant difference in hook-and-line induced mortality among treatments (control, tagging, gas bladder deflation, tagging/gas bladder deflation) during the closed net experiments at 21 m.

Estimates of mortality at various depths were highly variable. We feel that the estimates obtained from these experiments are low given our results at 21 m with the closed net system. Mean mortality rate by depth is presented in Fig. 3. Our estimates of mortality at 50-56 m (18%) appear lower than our estimates obtained at 21 m (20.1%). Therefore, mortality in the open net test system may have been underestimated. It is possible, indeed likely, that some of the released fish that apparently survived based on our criteria (i.e., that the fish successfully submerged) probably died after they submerged through the net, particularly those caught at depths great enough to cause rupture of the air bladder.

Results indicated that gas bladder rupture and other types of physiological damage occur due to rapid change in hydrostatic pressure, and these conditions vary with depth. The consequence of these conditions on survival, however, are not known. When a gas bladder ruptures, the gas is released into the gut. The volume of the

expanded gas is great enough at some depth displacements to force the stomach to evert through the mouth. Intussusception of the gut caused by the eversion could potentially cause delayed mortality if the blockage is not reversed (A. Camus, pers. comm.). The effect of tissue hemorrhage on survival is also unknown. Although the effect of hemorrhage in muscle tissue is likely to be of minor significance, severe hemorrhage of the liver and other vital organs may be of greater consequence (A. Camus, pers. comm.).

Alexander (1967) estimated that on average a fish without a functional gas bladder is 5% denser than sea water. One adaptive advantage to having a gas bladder is that by achieving neutral buoyancy, an organism does not have to compensate for the force of gravity (Aleev 1969). Although some fin movement is required to maintain a particular vertical position since equilibrium is unstable, the energy cost for neutrally buoyant fish is thought to be minor (Alexander 1967). Fishes that do not have gas bladders generally have to compensate by generating an upward hydrodynamic force as they swim to prevent them from sinking (Alexander 1972), or have structural or chemical adaptations for buoyancy compensation (Denton 1963; Childress and Nygaard 1973; Lee et al. 1975; Horn et al. 1978). The added energetic cost to a released fish that has lost its ability to maintain neutral buoyancy due to gas bladder rupture is likely to be high, and may ultimately cause mortality through exhaustion. Denton (1961) stated that although a few percent of body weight may seem insignificant in terms of the load that the organism must bear, we must remember that a weight easily supported on land can only be sustained in water through continuous movement. He likened the effort to a 60 kg man having to hold up to 3 kg of weight while continuously treading water throughout his life. Further, disruption of normal swimming

behavior may increase the risk of mortality since odd or conspicuous individuals are often targeted by predators (Curio 1976).

Air bladder deflation did not significantly affect survival of red snappers caught at 21 m depth for either the short- or long-term comparisons. Several factors should be considered when interpreting these results, particularly for fish that were transferred to the aquarium for the long- term experiments. These fish were held in the net at 9 m for at least 24 hours. This acclimation period allowed some adjustment in buoyancy prior to transfer to the tank for transport. Steen (1970) modeled the rate at which fish could maintain neutral buoyancy with vertical displacement. Although his model calculated a rate of 5 hours for a vertical displacement of 150 m, he concluded that direct observations of gas deposition rates (Fange 1953) indicate that appreciably longer time would be needed for an adjustment of this magnitude. Second, the tank was highly oxygenated and was without current, therefore the necessity of neutral buoyancy for position maintenance was removed. There is evidence based on observation of the fish transferred to the aquarium and ancillary data, that small puncture holes (#20 hyperdermic needle tips) in the gas bladder apparently reseal or repair rapidly. The tissue composition of the gas bladder as described by Fange (1958) indicate elastic properties.

Although deflation techniques may have some significance in enhancing our ability to obtain physoclistous species for aquaria and experimental collections, the fate of deflated specimens released *in situ* is less certain given the harsher environmental conditions that the fish is released into and the fact that return to capture depth would imply negative buoyancy. It is predictable based on Boyle's law that if only a partial amount of the total gas in the bladder is vented (as was usually the case), that a released fish could find neutral buoyancy

at some depth between surface and initial capture depth assuming that the gas bladder reseals effectively. The effect of a "compensatory return depth" is unknown. We suspect that for red snappers caught and released around an oil or gas platform, the effect would be less significant than for snappers caught and released around submerged natural or artificial substrate. Platform structure extends through the entire water column and red snappers at various depths from near surface to bottom were observed when in association with these structures. The effect on red snapper caught near-bottom around submerged natural or artificial hard substrate is less predictable since the structure provided by the substrate may be important for predation shelter (Parrish 1987), and the "compensatory return depth" may not be sufficient to adequately protect these fish from predation.

Results from the variable depth tests did not show evident differences in apparent survival due to deflation until depths of approximately 30-40 m were reached. Based on these results it does not appear that air bladder deflation is an effective tool for enhancing survival of released red snapper. For fish caught at depths not great enough to rupture the gas bladder (approx. >30 m), most of the fish (93%) were able to submerge. Since the gas in the bladder compresses as the fish descends, neutral buoyancy can be reached by the fish as it returns to capture depth. Negative buoyancy resulting from the venting of gas as previously described or "compensatory return depth" may adversely affect survival. When capture depth is great enough to cause air bladder rupture, survival of the released individual becomes increasingly unlikely, for reasons previously described.

A further argument for not encouraging deflation techniques is that deflation techniques need to be rather precise and the tools used should be sterile. One of the authors has observed a well meaning angler

venting gas from an everted stomach (a common misconception exists that this is the gas bladder) by knife puncture. As stated earlier in the discussion, stomach eversion generally occurs as a result of gas bladder rupture. Although venting gas through the stomach may increase a fish's ability to submerge, our results indicate that long-term survival of these fish is unlikely. Further the effect of stomach puncture on survival is not known, particularly given the stress already present from hydrostatic pressure damage. Although all deflation efforts by anglers are not as crude as those described above, it demonstrates that significant angler education would be necessary for proper utilization of these techniques, if it is found that deflation techniques enhance survival for a given species.

References

- Aleev, Y.G. 1969. Adaptations toward neutralizing the force of gravity, p. 31-89. In V.A. Vodyanitskii (ed.) Function and gross morphology in fish. Keter Press, Jerusalem.
- Alexander, R.McN. 1967. Functional design in fishes. Hutchinson University Library, London.
- Alexander, R.McN. 1972. The energetics of vertical migration by fishes. Symp. Soc. Exp. Biol. 26:273-294.
- Childress, J.J. and M.H. Nygaard. 1973. The chemical composition of midwater fishes as a function of depth of occupancy off southern California. Deep-Sea Res. 20:1093-1109.
- Curio, E. 1976. The ethology of predation. Springer-Verlag, Berlin. 250 p.
- Denton, E.J. 1961. The buoyancy of fish and cephalopods. Progr. Biophys. 11:117-234.
- Denton E.J. 1963. Buoyancy mechanisms of sea creatures. Endeavor 22:3-8.
- Fange, R. 1953. The mechanism of gas transport in the euphysoctist swimbladder. Acta Physiol. Scand. 23, Suppl. 110, 1-133.
- Fange, R. 1958. The structure and function of the gas bladder in *Argentina silus*. Q. J. Microscope Sci. 99:95-102.
- Gotshall, D.W. 1964. Increasing tagged rockfish (Genus *Sebastodes*) survival by deflating the swimbladder. California Fish and Game 50(4):253-260.
- Horn, M.H., P.W. Grimes, C.F. Phleger and H. McElhanan. 1978. Buoyancy function of the enlarged fluid-filled cranium in the deep sea ophidiid fish *Acanthus armatus*. Mar. Biol. 46:335-339.
- Lee, R.F., C.F. Phleger and M.W. Horn. 1975. Composition of oil in fish bones: possible function in neutral buoyancy. Comp. Biophys. Physiol. 50B:13-16.
- Muller, R. 1990. Report of the reef fish assessment panel, March 1990. Miami Laboratory, Southeast Fisheries Center, National Marine Fisheries Service, Miami, Florida. 15 p.
- Parrish, J.D. 1987. The trophic biology of snappers and groupers, p. 405-439. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Sport Fishing Institute. 1991. Puncturing air bladders: successful release method? Sport Fishing Inst. Bull. 426:3.
- Steen, J.B. 1970. The swim bladder as a hydrostatic organ, p. 413-443. In W.S. Hoar and D.J. Randall (eds.) Fish physiology, vol. IV. Academic Press, New York.
- Wilson, C.A., J.H. Render and D.L. Nieland. 1993. Life history gaps in red snapper (*Lutjanus campechanus*), swordfish (*Xiphias gladius*) and red drum (*Sciaenops ocellatus*) in the northern Gulf of Mexico; age determination, growth, and some reproductive biology. Interim report. U.S. Department of Commerce, MARFIN., 44 p.

ENTERED IN NAGA

APR 14 1998

Demersal Fish Stock Assessment in Seychelles: An Analysis of a Mothership/Catcher Boat Fishery

C.C. MEES

Marine Resources Assessment Group

47 Prince's Gate

London SW7 2QA, UK

MEES, C.C. 1996. Demersal fish stock assessment in Seychelles: An analysis of a mothership/catcher boat fishery [*Evaluacion de peces demersales en Seychelles: Un análisis de una pesquería basada en un bote nodrizo*], p. 254-265. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Stock assessments for certain important tropical demersal species are presented, based on the analysis of commercial line fishing data collected from a mothership/catcher boat operation targeting snappers, groupers and emperors in Seychelles waters. Six fishing trips were conducted over the period March 1991 - March 1993 at a number of unexploited or lightly fished banks and sea mounts of varying sizes far from the main centers of population.

Depletion estimates of initial population size (biomass, B_0) are derived from daily information within single fishing voyages at specific locations. An attempt to determine production is presented using biomass estimates from subsequent voyages to the same locations. The limited time spent at any one fishing location and variability in catch rates resulting from changes in fishing depths and target species restrict the number of comparisons of site-specific analyses from the present data, but the method will be of increasing value as more information becomes available. The implications for management purposes are great: inferences may be made regarding the rate of recovery of depleted areas, which is useful in what is essentially a 'hit and run' fishery.

It is suggested that if adequate care is taken to account for variability in catch rates not directly attributable to fishing pressure, the application of this type of analysis to commercial data offers a cheap alternative to intensive fishing experiments during research cruises.

Resumen

La evaluación de recursos de ciertas especies demersales tropicales importantes son presentadas en base al análisis de datos de la pesca comercial con línea colectados de la operación de un bote nodrizo orientado a la pesca de pargos, meros, y emperadores en aguas de Seychelles. Seis viajes de pesca fueron efectuados en el período comprendido entre Marzo de 1991 y Marzo de 1993, hacia varios bancos no explotados o ligeramente explotados y varias montañas marinas de tamaño variable, alejadas de los principales centros de población.

Las estimaciones de descuento en el tamaño inicial de la población (biomasa, B_0) fueron derivadas de información diaria dentro de viajes de pesca sencillos a localidades específicas. Se presenta un intento para determinar la producción usando estimaciones de biomasa de viajes subsecuentes a las mismas localidades. La limitada duración de las operaciones de pesca en cualquiera de las localidades, y la variabilidad en las tasas de captura resultantes de los cambios en las profundidades de pesca (especies objetivo) limitaron el número de comparaciones para el análisis de sitios específicos del presente conjunto de datos, pero el método tendrá mayor valor conforme mas cantidad de información vaya

siendo disponible. Las implicaciones para propósitos de manejo son grandes: algunas inferencias pueden ser hechas sobre la tasa de recuperación de las áreas que mostraron decrementos, aspecto que es esencial en una pesquería basada en el éxito de cada operación de pesca.

Se sugiere que si se toma cuidadosamente en cuenta la variabilidad en las tasas de captura que no son atribuibles directamente a la intensidad de pesca, la aplicación de este tipo de análisis de datos comerciales puede ofrecer una alternativa de bajo costo para intensificar experimentos de pesca durante los cruceros de investigación.

Introduction

The large number of fish species and information-intensive requirements of most multi-species stock assessment models (for reviews, see Gulland and Garcia 1984; Kerr and Ryder 1989; Polovina 1992) means that data-collection requirements for adequate stock assessment are beyond the means of many small fishery departments in tropical countries. Depletion methods of stock assessment, however, can be substantially cheaper and more effective than others (Hilborn and Walters 1992). Polovina (1986) applied this approach to data collected during an intensive fishing experiment in the Marianas. Where commercial data can be utilized, substantial cost savings may be gained over the application of experimental fishing during planned research cruises, although at the expense of experimental design.

In this paper stock assessments are based on the analysis of commercial line fishing data collected from a mothership/catcher boat operation targeting snappers, groupers and emperors in Seychelles waters. Mees (1993) estimated the biomass of *Pristipomoides filamentosus* (Valenciennes 1830) from data collected during a single voyage of this vessel. Here, subsequent voyages to a number of locations are presented, and enable estimates of stock production.

The study area

Seychelles consists of four island groups in the western Indian Ocean between 5° and 10°S and 45° and 56°E (Fig. 1). The

majority of the population live on the granitic islands Mahé, Praslin and La Digue within the Mahé Plateau, whilst the coralline Amirantes, Providence/Farquhar and Aldabra/Cosmoledo groups are sparsely inhabited.

Demersal fishing effort by the artisanal fleet (mostly wooden vessels, 12 m length or smaller) is largely confined to the Mahé Plateau and its periphery, but in periods of good weather a few vessels may venture to the Amirantes group. The Providence/Farquhar and Aldabra/Cosmoledo groups may be regarded as unfished excepting some exploitation during the 1970s by mothership/catcher boat ventures at the former group. Fishing activity at these locations and at lightly fished banks and sea mounts south of the Mahé Plateau is examined.

Climatic conditions during the southeast trade winds, which average 12 knots, frequently limit fishing activity from the end of May to October. It may also be affected by the northwest monsoon between mid-November and mid-March. During the two inter-monsoon periods light variable winds and frequent calms occur.

Materials and Methods

Between March 1991 and March 1993 an 88.4 m refrigerated cargo ship deployed up to twelve 7 m fiberglass catcher boats during six fishing voyages to remote banks and island groups in the Seychelles. Each voyage lasted between 46 and 71 fishing days (Table 1).

Catcher boats were equipped with echo sounder and compass and usually fished within 10 miles of the mothership. Handlines were used during the first voyage. Electric fishing reels were fitted subsequently although

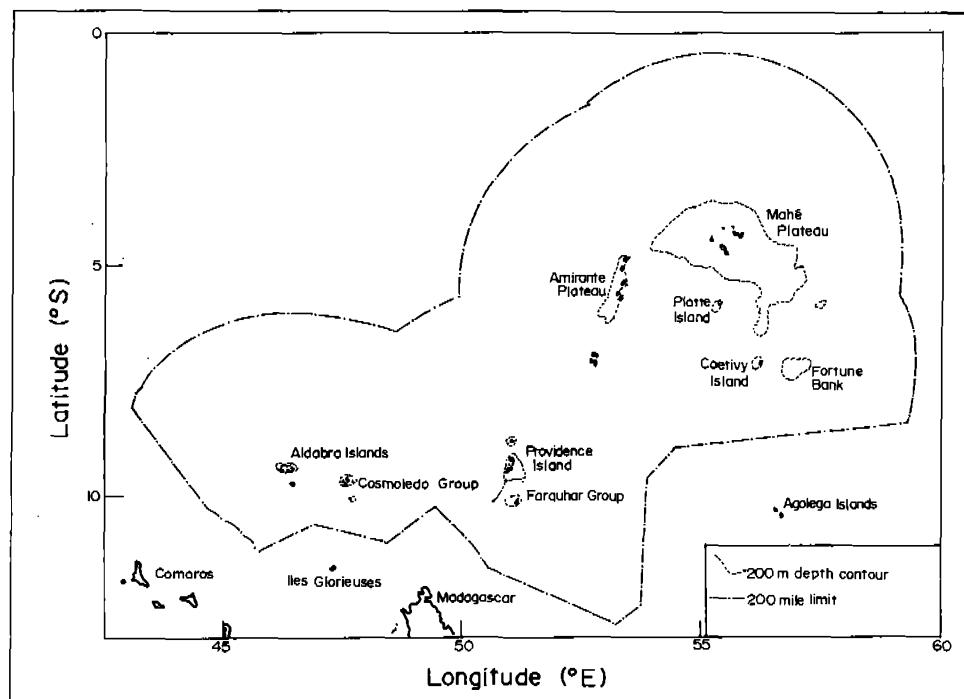


Fig. 1. Seychelles EEZ indicating the fishing locations visited by the mothership catcher vessel: Mahé Plateau, and Banks South of the Plateau, the Amirantes group, Providence/Farquhar group, and Aldabra/Cosmoledo group. [ZEE de Seychelles Indicando las localidades de pesca visitadas por el barco nodriza: Planicie de Mahe, y Bancos del Sur de la Planicie, el grupo Amirantes; el grupo Providence/Farquhar y el grupo Aldabra/Cosmoledo.]

Table 1. Details of the fishing voyages undertaken between March 1991 and March 1993. [Detalle de los viajes de pesca efectuados entre Marzo de 1991 y Marzo de 1993.]

Voyage	Fishing dates	Days	Fishing locations	Boat-days
1	03/03/91-02/05/91	70	Mahé Plateau (MP) Banks south of MP	169 547
2	23/10/91-16/12/91	54	Mahé Plateau Banks south of MP Platte Plateau Amirantes group Providence/Farquhar	297 142 4 58 137
3	08/01/92-12/03/92	64	Mahé Plateau Banks south of MP Amirantes group	73 252 325
4	11/04/92-27/05/92	46	Providencia/Farquhar	501
5	26/10/92-20/12/92	55	Amirantes group Providencia/Farquhar Aldabra/Cosmoledo	13 443 79
6	10/01/93-22/03/93	71	Mahé Plateau Banks south of MP Platte Plateau Saya de Mahla bank	12 60 12 591

frequently a combination of electric reels and hand-lines were used by the crew of three. One trip per boat per day was usual, although occasionally two trips were made.

Detailed catch and effort data were recorded for each catcher boat trip by an observer from the Seychelles Fishing Authority. Factors which could potentially affect catch rates and/or species composition were also recorded on the catch and effort log: depth fished, bait type, climatic conditions. These latter data are not available for all voyages and reported details for voyage 4 were considered unreliable. This information is utilized tentatively in interpretation of the results.

Total daily catch and effort data were generated by gear type (lines, reels or both) and location. In order to enable intra-voyage comparisons, relative fishing power was determined for gear type, month and fishing location by application of the following model to standardize fishing effort:

$$U_{tik} = U_{111} \alpha_t \beta_i \gamma_k \varepsilon_{tik} \quad \dots 1$$

where U is the catch rate, subscript t refers to time, i to gear type and k to fishing location. U_{111} is the catch rate obtained by the first gear type in the first time period at the first location, α_t is a factor that is the abundance in month t relative to month 1, β_i is the efficiency of gear type i relative to gear type 1, γ_k is the average abundance differential in area k relative to location 1, and ε_{tik} is a factor explaining the deviation between the observed U_{tik} and the expected value for t , i and k (Hilborn and Walters 1992).

Taking the logarithms of both sides of equation 1, a linear statistical model is derived:

$$\log(U_{tik}) = \log(U_{111}) + \log(\alpha_t) + \log(\beta_i) + \log(\gamma_k) + \log(\varepsilon_{tik}) \quad \dots 2$$

from which the parameters α , β and γ may be estimated by multiple linear regression.

Fishing effort of the original catcher-boat data was standardized relative to hand-lines and to the month of January. Total daily catch and effort data were recalculated by location. These data were employed in a modification of the Leslie depletion model (Leslie and Davis 1939) in order to determine original biomass at the start of subsequent fishing occasions (B_{01} and B_{02}), as follows:

Since each fishing occasion lasts only a few days, natural mortality, growth, recruitment and immigration will be negligible and may be disregarded. B_{ti} , the biomass remaining on day t of voyage i may be expressed as:

$$B_{ti} = B_{0i} - \sum_{s < t} C_{si} \\ = B_{0i} - D_{ti} \quad \dots 3$$

where C_{si} is the catch taken during day s of voyage i , and D_{ti} is the total catch taken on that voyage before day t .

The catch rate U_{ti} on day t of voyage i will be related to the biomass, B_{ti} by:

$$U_{ti} = qB_{ti} + \omega_{ti} \\ = qB_{0i} - qD_{ti} + \omega_{ti} \quad \dots 4$$

where q is the catchability, and ω_{ti} explains random variability.

Whilst biomass (B_0) changes between fishing voyages due to mortality, recruitment, growth and immigration, catchability (q) is expected to remain constant. To ensure the same estimate of q for all voyages, and to reduce estimation 'noise' due to short data series, equation (4) may be rewritten enabling simultaneous estimation of q and the B_{0i} 's by multiple regression. First, indicator variables I_{2ti} I_{3ti} are defined

for all voyages except the first, so that $I_{2t1} = 1$ for all data from Voyage 2 and 0 for all other data, $I_{3t1} = 1$ for all data from Voyage 3 and 0 for all other data, and so on.

Consider the example of three voyages to one location. Using equation (4) we set for Voyage 1:

$$\begin{aligned} U_{t1} &= qB_{01} - qD_{t1} + \omega_{t1} \\ &= qB_{01} + I_{2t1}(qB_{02} - qB_{01}) + \\ &\quad I_{3t1}(qB_{03} - qB_{01}) - qD_{t1} + \omega_{t1} \end{aligned} \quad \dots 5)$$

noting that for all observations in Voyage 1, $I_{2t1} = I_{3t1} = 0$.

For Voyage 2, ($I_{2t2} = 1$, $I_{3t2} = 0$):

$$\begin{aligned} U_{t2} &= qB_{02} - qD_{t2} + \omega_{t2} \\ &= qB_{01} + I_{2t2}(qB_{02} - qB_{01}) + \\ &\quad I_{3t2}(qB_{03} - qB_{01}) - qD_{t2} + \omega_{t2} \end{aligned} \quad \dots 6)$$

and Voyage 3 ($I_{2t3} = 0$, $I_{3t3} = 1$):

$$\begin{aligned} U_{t3} &= qB_{03} - qD_{t3} + \omega_{t3} \\ &= qB_{01} + I_{2t3}(qB_{02} - qB_{01}) + \\ &\quad I_{3t3}(qB_{03} - qB_{01}) - qD_{t3} + \omega_{t3} \end{aligned} \quad \dots 7)$$

This may be written in general form as:

$$U_{ti} = \alpha + \sum_{j=1}^v I_{jti} B_j - qD_{ti} + \omega_{ti} \quad \dots 8)$$

where v is the total number of voyages undertaken,

$$\alpha = qB_{01} \quad \dots 9)$$

$$\beta_j = (qB_{0j} - \alpha) \quad \dots 10)$$

for $j = 1$ to v . The variables q , α and β_j may be estimated by multiple linear regression. The biomass at the start of the first voyage may then be estimated from equation (9):

$$\hat{B}_{01} = \frac{\alpha}{q} \quad \dots 11)$$

and subsequent voyages for $j = 1$ to v from equation (10)

$$\hat{B}_{0j} = \frac{(\alpha + \beta_j)}{q} \quad \dots 12)$$

Production (P) between voyages i and $(i+1)$ to the same location can be estimated from:

$$\hat{P}_{i \rightarrow (i+1)} = \frac{\hat{B}_{0,i+1} - (\hat{B}_{0i} - C_i)}{d_{i \rightarrow (i+1)}} \quad \dots 13)$$

where C_i is the total catch removed at the end of voyage i , and $d_{i \rightarrow (i+1)}$ is the time interval, in days, between fishing occasions. Production is equivalent to all gains due to growth, recruitment and immigration, less losses due to natural mortality.

Results

Factors applied to standardize the original data by month and gear type are indicated in Table 2. Throughout the six voyages, fishing took place at a total of 31 different banks, sea mounts or islands. At any one location fishing duration varied between 1 and 8 days and the prevalent pattern observed was that of decreasing daily catch rates. Results relate to those locations fished during two or more voyages for greater than one day (Table 3 and Figs. 2a and 2b).

In general, mean catch rates were observed to decrease from one voyage to the next. This was true for small banks and sea mounts, but not for the large banks (Constant Bank). Daily catch rates at Fortune Bank, like Constant Bank, indicated no evidence of depletion between voyages (Fig. 2c). For small banks, exceptions were Bulldog Bank and Sea Mount '25' in the Providence/Farquhar group. During Voyage 4, strong currents depressed catch rates but this was not the case during Voyage 5 to these locations.

Table 2. Parameters derived by multiple linear regression for standardization of fishing effort relative to hand-lines, January and the south-east edge of the Mahé Plateau (MP). [Parámetros obtenidos de la regresión lineal múltiple para la estandarización del esfuerzo de pesca relativo a líneas de mano, Enero y el borde suroriental de la Planicie Mahe (MP).]

Parameter	Detail	Value
α_2	February	1.0697
α_3	March	1.5664
α_4	April	1.7115
α_5	May	1.1500
α_6	October	1.9031
α_7	November	1.6164
α_8	December	1.7403
β_2	unknown (gear)	0.0291
β_3	lines and reels	1.0009
β_4	reels only	1.2479
γ_2	Junon Bank	0.9871
γ_3	South Edge MP	1.1702
γ_4	Banks south of MP	1.2525
γ_5	Platte Plateau	0.9407
γ_6	Amirantes	1.5601
γ_7	Providence/Farquhar	2.2391
γ_8	Aldabra/Cosmoledo	1.1974
γ_9	Saya de Mahla Bank	2.4658

After eliminating those locations at which changes in depth and target species were significant (Sea Mount '20', Wizard Reef), only three locations of the original 31 were considered suitable for the present depletion study; namely, Correira Bank, Small Constant Bank and Farquhar (Table 4 and Figs. 2d-2f, respectively). However, Small Constant Bank was also eliminated from the analysis because of inconsistent results which were considered unreliable (only two data points for each of Voyages 2 and 3). This bank was also subject to fishing by other vessels between voyages, so the total catch removed was unknown. Correira Bank was unlikely to have been fished by other vessels and Farquhar had not.

At Correira Bank, no consistently decreasing trend with time occurred for the combined catch rate of all demersal species, but was observed for the target species, *P. filamentosus*. At Farquhar, no trend occurred for individual species but was observed for the combined demersal catch. The biomass preceding each voyage was estimated by regression of standardized catch rate on adjusted cumulative catch for *P. filamentosus* at Correira Bank (Fig. 3, Table 5) and all demersal species at Farquhar

Table 3. Locations visited on two or more voyages for more than one day, and the fishing areas in shallow and intermediate depth strata where available. [Localidades visitadas en dos o más viajes por más de un día y las áreas de pesca en aguas de profundidad baja e intermedia donde los estratos estuvieron disponibles.]

Fishing location	Area (km ²) 0-75 m	Length of 100 m contour (km)	Area (km ²) 75-150 m
BANKS SOUTH OF THE MAHE PLATEAU			
Constant Bank	590.0	114.8	28.7
Correira Bank	17.4	33.3	8.3
Fortune Bank	600.0	120.4	30.1
Sea Mount '20'	6.6	11.1	2.7
Small Constant Bank	170.0	55.6	13.8
PROVIDENCE/FARQUHAR			
Bulldog Bank	--	--	--
Farquhar	172.0 ^a	--	--
Sea Mount '25'	--	--	--
Wizard Reef	--	--	--

^aTotal area of Farquhar Atoll (UNEP/IUCN 1988) - actual fishing area will be less than this.

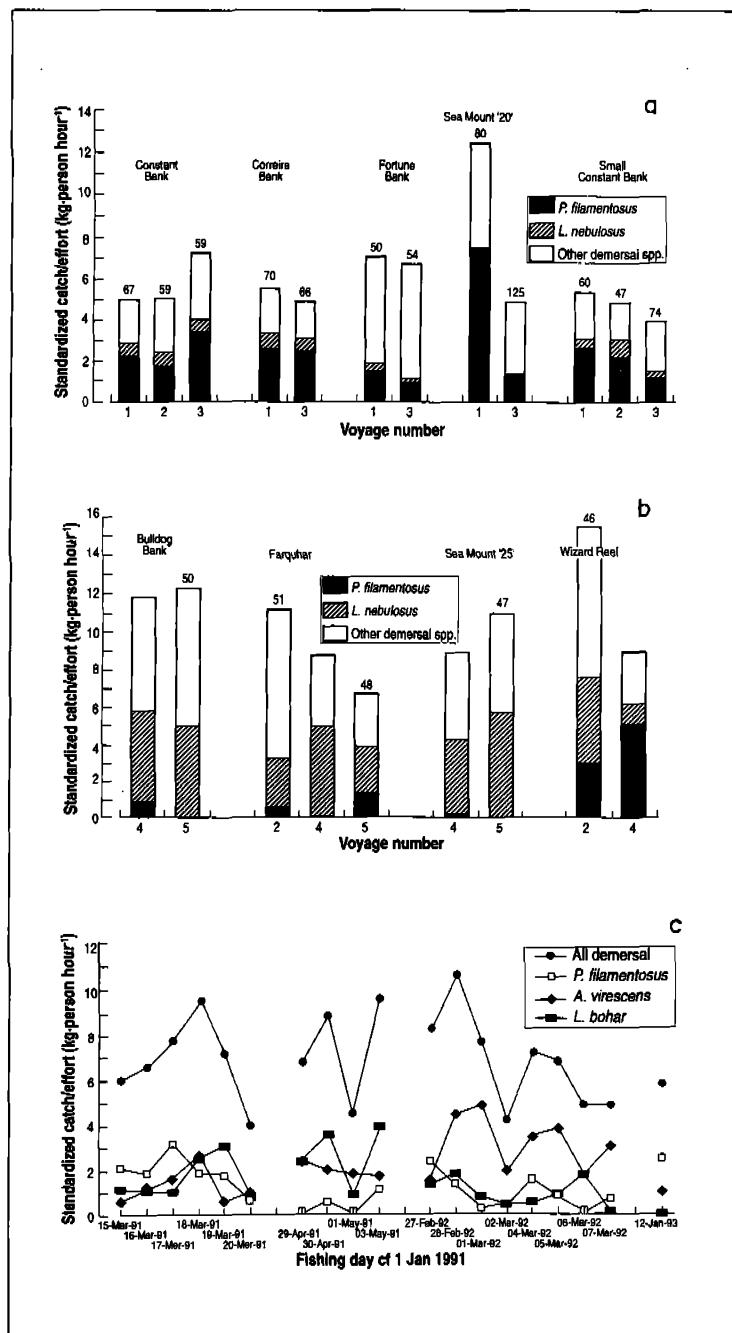


Fig. 2. Mean standardized CPUE (kg/person per hour) by voyage to: a) south of the Mahé Plateau; b) Providence/Farquhar group; c) standardized daily catch rates at Fortune Bank [CPUE media estandarizada (kg/persona por hora) por viaje en: a) sur de la Plataforma Mahé; b) grupo Providence/Farquhar; c) tasas de captura diaria estandarizadas en el Banco Fortuna] (continued)

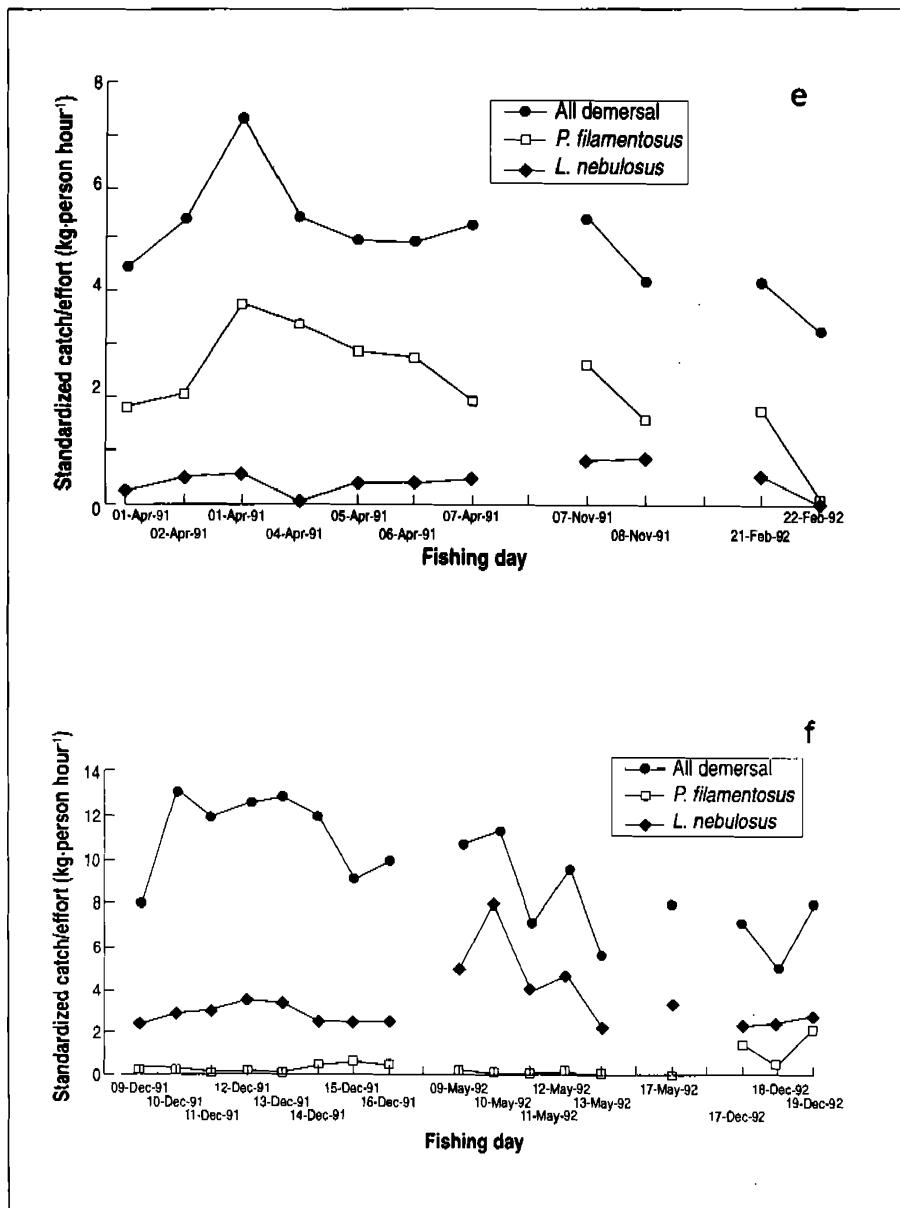


Fig. 2. (continued) d) Correlra Bank; e) Small Constant Bank; and f) Farquhar. For Figs. c-f, the x-axis does not represent a linear scale. A break in the line indicates that the mothership moved location (within any voyage) or that the data relate to different voyages. [d) Banco Correlra; e) Banco Small Constant; y f) Farquhar. Para las figuras c-f, el eje-X no representa una escala lineal. Un corte en la línea indica que el bote nodriza se movió de lugar (dentro de un viaje) o que los datos se refieren a diferentes viajes.]

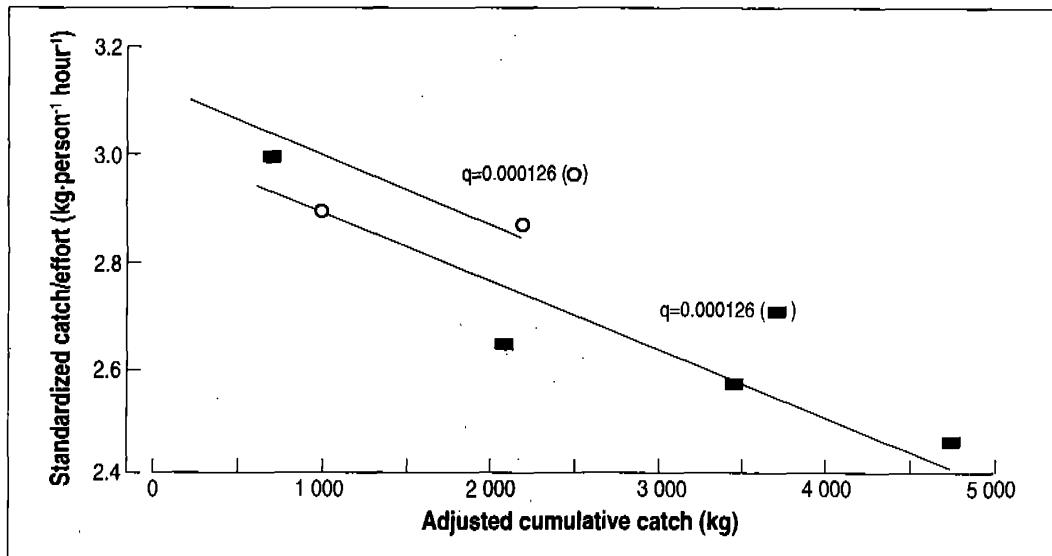


Fig. 3. Depletion of *Pristipomoides filamentosus* at Correira Bank during Voyages 1 and 3. Data for 26 February 1992 were excluded from the analysis since the reported depth was significantly less than on the previous three days and the position had changed. [Decreimiento de *Pristipomoides filamentosus* en el Banco Correira durante los viajes 1 y 3. Febrero 26 de 1992 fué excluido del análisis porque la profundidad reportada fué significativamente menor que la de los tres días previos y la posición ha cambiado.]

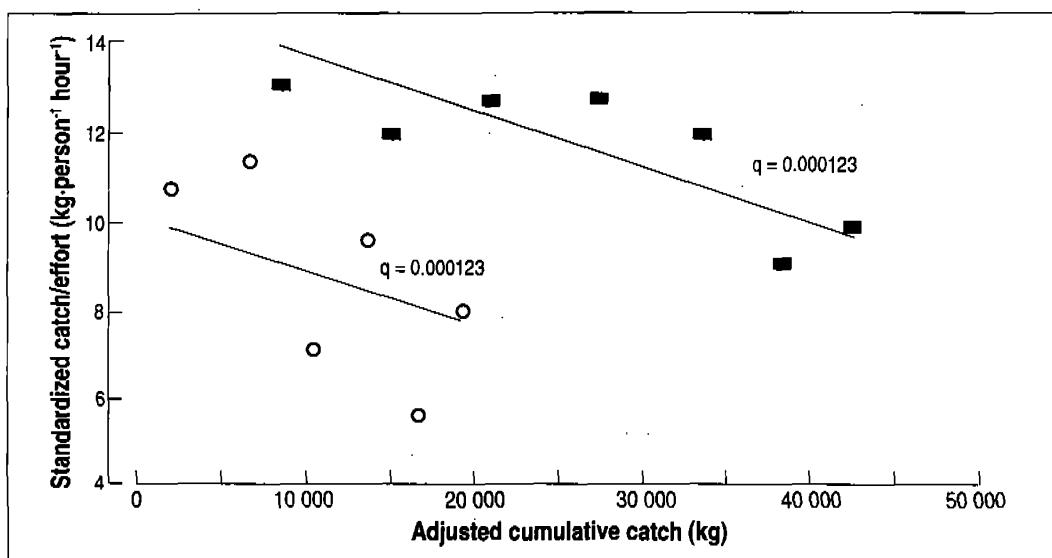


Fig. 4. Depletion of the total demersal species catch at Farquhar during Voyages 3, 4 and 5. Excluded from the analysis were 9 December 1991 and Voyage 5. [Decreimiento de la captura total de especies demersales de Farquhar durante los viajes 3, 4 y 5. Diciembre 9 de 1991 fué excluido del análisis.]

Table 4. Anchoring position of the mothership each day at each of the locations studied showing (*) the days used in the analyses. [Posición geográfica del barco nodriza cada día de cada una de las localidades estudiadas mostrando los días usados en el análisis (*).]

Location	Voyage	Dates	Position
Correira Bank	1	24/04/91	06° 29' S 57° 10' E *
Correira Bank	1	25-27/04/91	06° 22' S 57° 05' E *
Correira Bank	1	10/05/91	06° 22' S 57° 05' E
Correira Bank	3	23-25/02/92	06° 21' S 57° 06' E *
Correira Bank	3	26/02/92	06° 30' S 57° 16' E
Small Constant	1	01-07/04/91	06° 03' S 56° 18' E *
Small Constant	2	07-08/11/91	06° 04' S 56° 18' E *
Small Constant	3	21-22/02/92	06° 03' S 56° 17' E *
Farquhar	2	09-16/12/91	10° 08' S 51° 09' E *
Farquhar	4	09-13/05/92	10° 08' S 51° 01' E *
Farquhar	4	17/05/91	10° 05' S 51° 10' E
Farquhar	5	17-18/12/92	10° 08' S 51° 59' E
Farquhar	5	19/12/92	10° 11' S 51° 11' E

Table 5. Regression parameters derived for *Pristipomoides filamentosus* at Correira Bank, and estimates of catchability, biomass, and production between Voyages 1 and 3; all demersal species at Farquhar, and estimated values between Voyages 2 and 4. [Parámetros de regresión obtenidos para: *Pristipomoides filamentosus* en el Banco de Correira, y estimaciones de capturabilidad, biomasa y producción entre viajes 1 y 3; todas las especies demersales en Farquhar, y valores estimados entre los viajes 2 y 4.]

Parameter	Correira Bank	Farquhar
No. obs	7	13
R ²	0.9066	0.6724
α	3.017958	14.90345
β ₂	0.108966	-4.73422
q	0.000126	0.000123
C ₁ (kg)	5426	44788
B ₀₁ (kg)	23903	121177
B ₀₂ (kg)	24766	82684
d _{1→2}	302	145
P _{1→2} (kg·day ⁻¹)	20.8	43.4
P _{1→2} (kg·day ⁻¹ km ⁻²)	2.5	0.25

(Fig. 4, Table 5). No attempt was made to partition effort directed at *P. filamentosus* in the case of Correira Bank. This species formed approximately 50% of the catch and at the depth range fished (>70 m) it was the target species. Thus the total effort was assumed to be directed at this species.

In Seychelles, *P. filamentosus* is caught in the depth range 75-150 m (Mees 1993). The net rate of production for *P. filamentosus* at Correira Bank was 2.5 kg day⁻¹ km⁻² of the intermediate depth range (Table 5) or 0.6 kg day⁻¹ km⁻¹ of the 100 m isobath. For all demersal species at Farquhar, where fishing occurred in the shallow stratum, it was 0.25 kg day⁻¹ km⁻².

Discussion

Mothership/catcher boat operations exert significant fishing pressure at localized areas over a short time period. At large banks, local depletion may occur during any one voyage (as appeared to be the case during Voyage 3 at Fortune Bank, Fig. 2c) but differences in precise fishing location and the relatively larger standing stock at these locations mean depressed catch rates are not observed between voyages. However,

it is apparent that depletion of small isolated areas can be significant, and that catch rates remain depressed from one fishing occasion to the next indicating that insufficient time has elapsed to allow complete recovery.

The rate of recovery, or production, was estimated. At Correira Bank the stock of *P. filamentosus* had fully recovered between Voyages 1 and 3. The production estimate of $2.5 \text{ kg km}^{-2} \text{ day}^{-1}$ equates to $914.6 \text{ kg km}^{-2} \text{ year}^{-1}$ (228.0 kg km^{-1} of the 100 m isobath). Mees (1993) estimated the sustainable yield of this species to be $717 \text{ kg km}^{-2} \text{ year}^{-1}$. Polovina and Ralston (1986) estimated the total yield of all snappers and groupers within the 200-m isobath in the Marianas to be $300 \text{ kg km}^{-2} \text{ year}^{-1}$ whilst Polovina et al. (1990) gave mean estimates of 380 kg km^{-1} of the 200 m isobath on reefs and $1\,460 \text{ kg km}^{-1}$ of the 200 m isobath at sea mounts for all species. Given the differences in depth, and the fact that *P. filamentosus* represented approximately 50% of the catch, the estimate of production is of the right order and sufficient to generate the estimated yield for this resource.

Incomplete recovery had occurred at Farquhar between Voyages 2 and 4. Production was estimated to be $0.25 \text{ kg day}^{-1} \text{ km}^{-2}$ in the shallow stratum, which is a rather low value. However, the total area of Farquhar Atoll is an inappropriate value to apply because it is unlikely that fishing actually took place inside the lagoon: this is not permitted, and the maximum depth of the lagoon is 14.6 m, whilst the mean fishing depth was around 50 m. It is most likely that localized depletion of a smaller area occurred. At Farquhar the anchoring positions for Voyages 2 and 4 were 8 nautical miles (nmi) apart. However, the catcher boats fish within a radius of approximately 10 nmi of the mothership and so the same area would have been exploited. Assuming a fished reef area of 10-20 nmi by 0.5-1 nmi ($17-69 \text{ km}^2$) the production estimate becomes $2.5-0.62 \text{ kg day}^{-1} \text{ km}^{-2}$.

Polovina (1986) indicated that the catchability of subordinate species in a multispecies assemblage is inversely related to the abundance of a more dominant species, although this change in catchability may have a time lag associated with it. He also showed that the pooled estimate of abundance for three species representing 90% of the exploitable population was 71% of the estimate derived for these species individually. From this we may conclude the biomass derived for all species at Farquhar may be underestimated on each voyage, but not necessarily the production. At Correira, *P. filamentosus* was dominant in the catch.

Whilst the results presented for *P. filamentosus* are of the correct order and support previous estimates of yield, there are potential sources of bias and error. During each period of fishing the model assumed a 'closed' study population, due to the short time frame involved. Between fishing it was 'open'. Hilborn and Walters (1992) discuss sources of error in estimates based on closed population depletion assessments and suggest that over a short time frame catchability may decline with the removal of the more stupid and/or aggressive fish, increasing q and depressing estimates of B_0 . Catchability was assumed to be constant for each fishing occasion although its real value may change within each fishing period in this manner. The time interval between fishing occasions (145 days at Farquhar; 302 at Correira Bank) was considered sufficiently long to negate such a change by the start of the second fishing period. In contrast to this potential bias, q may be underestimated and B_0 overestimated if errors occur in the measurement of the cumulative catch or effort. These are considered to be reliable.

It has been demonstrated that commercial data may be used for depletion estimates of stock size and production. The possible analyses were constrained by lack of replicates which under research

conditions would have been contained in the experimental design: particularly depth fished, duplicate fishing trials at certain locations despite low catch rates, longer time series at each location. Nevertheless, for single voyages depletion estimates of stock size were frequently possible (see Mees 1993, for *P. filamentosus* and Mees 1992, for *P. filamentosus* and *L. nebulosus*). For estimating production between voyages it was seen that the number of site specific comparisons was limited. Additionally, depletion estimates of abundance are subject to the bias discussed. Nevertheless, it is argued that despite these limitations, valuable information has been gained at minimal cost, and that this method will be of increasing value as more data become available from future voyages.

Acknowledgements

The author is grateful to Mahé Pêche Ltd. and Seychelles Fishing Authority (SFA) for permission to publish these data, collected and compiled by SFA observers and computer staff under an SFA-funded demersal fisheries project. The author was financed through the British Overseas Development Administration Fish Management Science Programme. Mark Bravington of MRAG Ltd. helped significantly with the statistical treatment of data and development of the biomass model. Professor John Beddington and Julie Rossouw critically reviewed the text.

References

- Gulland, J.A. and S. Garcia. 1984. Observed patterns in multispecies fisheries, p. 155-190. In R.M. May (ed.) Exploitation of marine communities: report of the Dahlem workshop on exploitation of marine communities, 1-6 April 1984 Berlin. Life Sci. Res. Rep. 32. Springer-Verlag, Berlin.
- Hillborn, R.Y. and C.J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York and London. 570 p.
- Kerr, S.R. and R.A. Ryder. 1989. Current approaches to multispecies analyses of marine fisheries. Can. J. Fish. Aquat. Sci. 46:528-534.
- Leslie, P.H. and D.H.S. Davis. 1939. An attempt to determine the absolute number of rats on a given area. J. Anim. Ecol. 8:94-113.
- Mees, C.C. 1992. Pêcheur Breton: an analysis of data relating to a mothership-dory fishing operation in Seychelles waters from March 1991-June 1992. Seychelles Fishing Authority, SFA/R&D/023, October 1992.
- Mees, C.C. 1993. Population biology and stock assessment of *Pristipomoides filamentosus* on the Mahé Plateau, Seychelles. J. Fish Biol. 43(5):695-708.
- Polovina, J.J. 1986. A variable catchability version of the Leslie model with application to an intensive fishing experiment on a multispecies stock. Fish. Bull. 84(2):423-428.
- Polovina, J.J. 1992. Modeling fish stocks: applicability, problems and requirements for multispecies and multigear fisheries in the tropics, p. 28-54. In Proceedings of the Sixth Session of the Standing Committee on Resources Research and Development, 18-21 May 1990, Colombo, Sri Lanka. FAO Fish. Rep. (Suppl.) 463.
- Polovina, J.J. and S. Ralston. 1986. An approach to yield assessment for unexploited resources with application to the deep slope fishes of the Marianas. Fish. Bull. 84(4):759-770.
- Polovina, J.J., R. Benco, A. Carlot, E. Cillauren, P. Dalzell, N. Howard, D. Kobayashi, T. Latu, P. Lokani, G. Nath, H. Pili, A. Sesewa, R. Shomura, T. Sua, G. Tiroba and S. Tulua. 1990. Summary of the methods and results from the tropical stock assessment workshop, p. 1-6. In J.J. Polovina and R.S. Shomura (eds.) United States Agency for International Development and National Marine Fisheries Service Workshop on Tropical Fish Stock Assessment. Honolulu, Hawaii.
- UNEP/IUCN. 1988. Coral reefs of the world. Volume 2: Indian Ocean, Red Sea and Gulf. UNEP regional seas directories and bibliographies. IUCN, Gland.

ENTERED IN NAGA

APR 14 1998

Abundance and Distribution of Snappers and Groupers Targeted by the Artisanal Medium Range Fishery off Northeastern Venezuela (1981-1992)

J.J. MENDOZA

*Dpto. de Biología Pesquera, Instituto Oceanográfico
Universidad de Oriente, Apdo. 245, Cumaná, Venezuela*

A. LÁREZ

*Estación Nueva Esparta, CIAPES-FONAIAP
Isla de Margarita, Venezuela*

MENDOZA, J.J. and A. LÁREZ. 1996. Abundance and distribution of snappers and groupers targeted by the artisanal medium range fishery off northeastern Venezuela (1981 to 1992) [*Abundancia y distribución, pargos y meros por la pesquería artesanal de media altura del noreste de Venezuela de 1981 a 1992*], p. 266-276. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauty (eds.) *Biology, fisheries and culture of tropical groupers and snappers*. ICLARM Conf. Proc. 48, 449 p.

Abstract

Changes in catch-per-unit effort (CPUE) for the main species (red snapper [*Lutjanus purpureus*], yellowedge grouper [*Epinephelus flavolimbatus*], and vermillion snapper [*Rhomboplites aurorubens*]) exploited by the medium-range artisanal fishery in northeastern Venezuela are analyzed for 1981 to 1992. The study is based on data obtained from interviews and landing controls. Vessels operate within the area between 7°N 58°W and 12°N 67°W, in the waters of Venezuela and Guyana and those of neighboring island countries. Fishing gears used are manually operated hooks-and-lines and longlines. The analysis is presented for the aforementioned area and three subareas: the Atlantic (east of Trinidad and Orinoco Delta), eastern Margarita (including northern Trinidad) and western Margarita. Handline effort is directed mainly to red snapper (45% of total handline catches) while longline effort is directed to grouper (59% of total longline catches). Species abundance varies from one subarea to another: red snappers are dominant in the Atlantic subarea, groupers in the east and west of Margarita Island and vermillion snappers are present mainly East of Margarita. For the general area, red snapper handline CPUE (kg/handline per fishing day) shows a 40% reduction for the study period. However, this decrease is particularly pronounced in the Atlantic subarea (approx. 60%). Grouper longline CPUE (kg/hook per fishing day) shows a stronger reduction (50%) for the whole area, the decline in abundance being stronger east of Margarita. Vermilion snapper handline CPUE shows the strongest reduction East of Margarita. Finally the strong seasonality of CPUE is discussed, as well as possible implications of overall results regarding stock structure in the study area.

Resumen

En este trabajo se analizan los cambios en la CPUE para las principales especies: pargo colorado (*Lutjanus purpureus*), mero fraile (*Epinephelus flavolimbatus*) y el pargo cunaro (*Rhomboplites aurorubens*), explotadas por la pesquería artesanal de media altura del noreste de Venezuela para el periodo 1981 a 1992. El estudio está basado en datos obtenidos de entrevistas y controles de descargas. Los botes operan dentro de un área entre 7°N 58°W y 12°N 67°W, comprendiendo aguas territoriales de Venezuela y Esequibo (Guyana) y aquellas en las islas de los países vecinos. Las artes de pesca usadas son líneas de mano y palangres operados manualmente. El análisis es efectuado para el área arriba mencionada y 3 subáreas: Atlántico (este de Trinidad y Delta del Orinoco), este de Margarita (incluyendo el norte de Trinidad) y el oeste de Margarita. El esfuerzo de líneas de mano es dirigido principalmente al pargo colorado (45% de las capturas totales de línea de mano), mientras que el esfuerzo con palangres es dirigido al mero (59% de las capturas totales con palangre). La abundancia de especies varía de una subárea a otra: el pargo colorado es dominante en la subárea del Atlántico, el mero al este y oeste de Isla Margarita y el pargo cunaro está presente principalmente al este de Margarita. Para el área general, la CPUE de las líneas de mano (kg/línea/días de pesca) mostró un 40% de reducción para el periodo de estudio, sin embargo este decremento es particularmente pronunciado en la subárea del Atlántico (aprox. 60%). La CPUE del mero con palangre (kg/no. de anzuelos/días de pesca) mostró una fuerte reducción (50%) para toda el área, siendo la declinación de la abundancia más fuerte al este de Margarita. Finalmente una fuerte estacionalidad de la CPUE es discutida así como las posibles implicaciones de los resultados globales en relación a la estructura de la población en el área de estudio.

Introduction

The northeastern Venezuela artisanal snapper-grouper fishery is an important regional socioeconomic activity. The fleet is traditionally divided into two components: the long range fishery operating in waters of the Guianas Plateau (Guyana, Surinam, French Guiana and, to a lesser degree, Brazil) and the medium-range fishery operating in Venezuelan waters and those of neighboring island countries (Trinidad & Tobago and Grenada). Fishing gear consists of manually operated hook-and-line and longlines. These multispecies fisheries are directed mainly toward red snappers (*Lutjanus purpureus*), yellowedge groupers (*Epinephelus flavolimbatus*) and, to a lesser degree, vermillion snappers (*Rhomboplites aurorubens*) (see Cuellar et al., this vol.).

Despite their importance, the analysis of these fisheries has received limited attention. Statistics of catch and effort for the long-range fleet and medium-range fleet have been analyzed for 1983-1984 (Celaya and González 1988; Gonzalez 1990). Furthermore, Anon. (1990) presented estimates of catch and number of boats for

1983-1989 for both fleets. Other studies have been directed towards biological aspects of red snapper, such as growth (González 1990) and reproduction (Lugo 1986) in northeastern Venezuela. Previously, exploratory fishing results in the late sixties and early seventies were reported by Kawaguchi (1974).

In this study we present an analysis of available data on changes in apparent abundance for the medium-range fleet for 1981-1992.

Materials and Methods

The basic data consist of information obtained from interviews and landing controls on a per trip basis. Each trip provides observations on days at sea, days fishing, area fished, fishing gear, number of hooks (longlines) or number of handlines, average depth in area fished, catch per species and value of catch. Over 12 000 fishing trips were analyzed for the study period with an average of about 90 trips per month.

The area considered (Fig. 1) is included within 7°N 58°W at the mouths of the

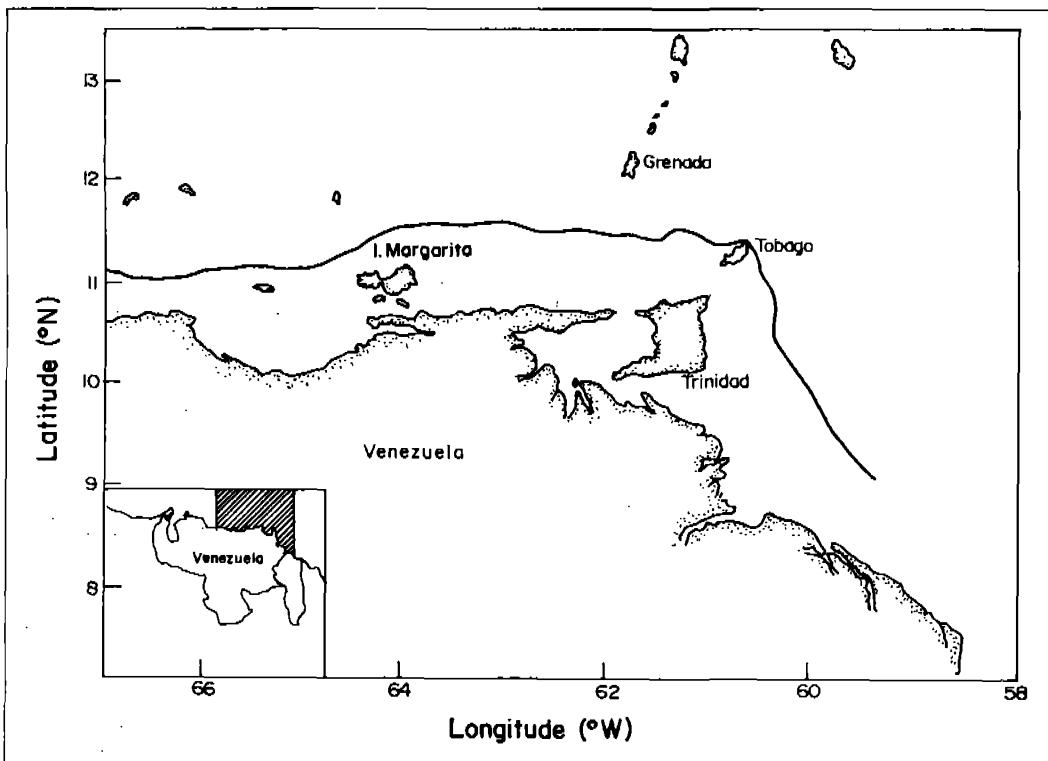


Fig. 1. Fishing area of the northeastern Venezuelan medium-range snapper-grouper artisanal fishery. [Área de pesca de la pesquería artesanal de media altura de meros y pargos del Noreste de Venezuela.]

Essequibo river and 12°N 67°W, north of the Los Roques archipelago in the Venezuelan central marine province. This area was further subdivided into three subareas with distinct hydrological regimes: Atlantic (7°N 58°W; 12°N 61°W), eastern Margarita (10°N 61°W; 12°N 64°W) and western Margarita (10°N 64°W; 12°N 67°W). The Atlantic subarea is dominated by the influence of the Orinoco and other important rivers including the Esequibo and the Demerara. The eastern Margarita subarea has a mixed regime of wind-induced upwelling (November through May) and riverine influence (mainly from the Orinoco). In the western subarea upwelling events and riverine input are of relatively minor importance.

Catch per species and fishing effort were used to compute monthly CPUE values per

fishng gear and four geographical strata (total area and three subareas). The fishing effort units retained were number of hooks x fishing days for longliners and number of lines x fishing days for handliners.

For any month j , two different CPUE were estimated per gear:

- 1) $\text{CPUE}_j = \sum C_i / \sum f_i$ for i individual fishing trips, referred to as CPUE1.
- 2) $\text{CPUE}_j = 1/n \sum (C_i/f_i)$ for i individual fishing trips and n total trips sampled, referred to as CPUE2.

The ratio $\text{CPUE1}/\text{CPUE2}$ is considered to be an index of effort concentration on a per trip basis.

Annual CPUE per species and gear for both indices was estimated as the average of monthly values for each year. Additionally, the seasonal component was

determined from the average CPUE for each month over the 12-year study period for red snappers and yellowedge groupers for both gears.

Results

The analysis of relative catch composition per gear allowed us to establish that handline fishing effort is mainly directed towards red snapper (45% of total catches sampled) and that yellowedge grouper is the target species in the longline fishery (approximately 59% of total catches sampled). Vermilion snapper is also caught by both gears but in a higher proportion by handlines (about 17% of total catches sampled).

Figs. 2-4 show the yearly trend for handline CPUEs per species in the total area. It is clear that red snapper CPUE is significantly higher than for other species. All species show a marked decline in abundance during the period, especially red snapper and yellowedge grouper. Vermilion snapper CPUE has apparently stabilized at about 2.5 kg/hook per fishing day in recent years. Both indices (CPUE1 and CPUE2) show similar trends for all species.

Figs. 2 and 3 show, for the whole area, yearly changes in longline CPUE for red snappers and yellowedge groupers. CPUE values are significantly higher in the case of yellowedge groupers. The decreasing trend over the period is especially marked in the case of this species. Red snappers show a strong reduction in apparent abundance between 1981 and 1982, but afterwards the declining trend is relatively moderate. Curiously, CPUE2 values for groupers are almost always higher than CPUE1 estimates, as opposed to red snappers, which do not present any significant difference regarding both indices. It would thus appear that longline effort is not well concentrated on yellowedge grouper.

The analysis of red snapper handline CPUE per subarea (Fig. 5) indicates that overall abundance is much higher in the Atlantic subarea, despite a continuously decreasing trend in apparent abundance. The subareas east and west of Margarita island show relative stability at similar levels of CPUE for this species between 1985 and 1992. Yellowedge grouper handline abundance is higher in the subareas east and, especially, west of Margarita (Fig. 6). Notwithstanding large interannual fluctuations in the western sector, it would appear that trends in abundance differ between the Atlantic subarea and the subareas east and west of Margarita. Vermilion snapper (Fig. 4) abundance is higher in the eastern Margarita sector, though this subarea shows a strong reduction in CPUE from 1983 onwards. Although strong variations occur, the other subareas show relative stability of CPUE over the study period.

Longline red snapper CPUE (Fig. 5) shows a marked decrease in the Atlantic sector and to a lesser degree west of Margarita, while apparent abundance east of Margarita has remained stable over the last six years of the series. Overall abundance was much higher in the Atlantic subarea at the beginning of the period, though present levels are similar for the three subareas considered. If we exempt the last four years of the study period in the subarea east of Margarita, yellowedge grouper longline CPUE (Fig. 6) does not show a sharp declining trend over the study period for the different sectors.

Figs. 2 and 3 show average monthly handline CPUE per subarea for red snappers and groupers from 1981 through 1992. Apparent abundance of red snapper tends to be low at the beginning and end of the average year, especially in the Atlantic and eastern Margarita subareas. On the other hand, yellowedge grouper shows a clear trend towards higher CPUE values in the first and last months. Average monthly longline red snapper CPUE (Fig. 2) differs from handline observations, except for the

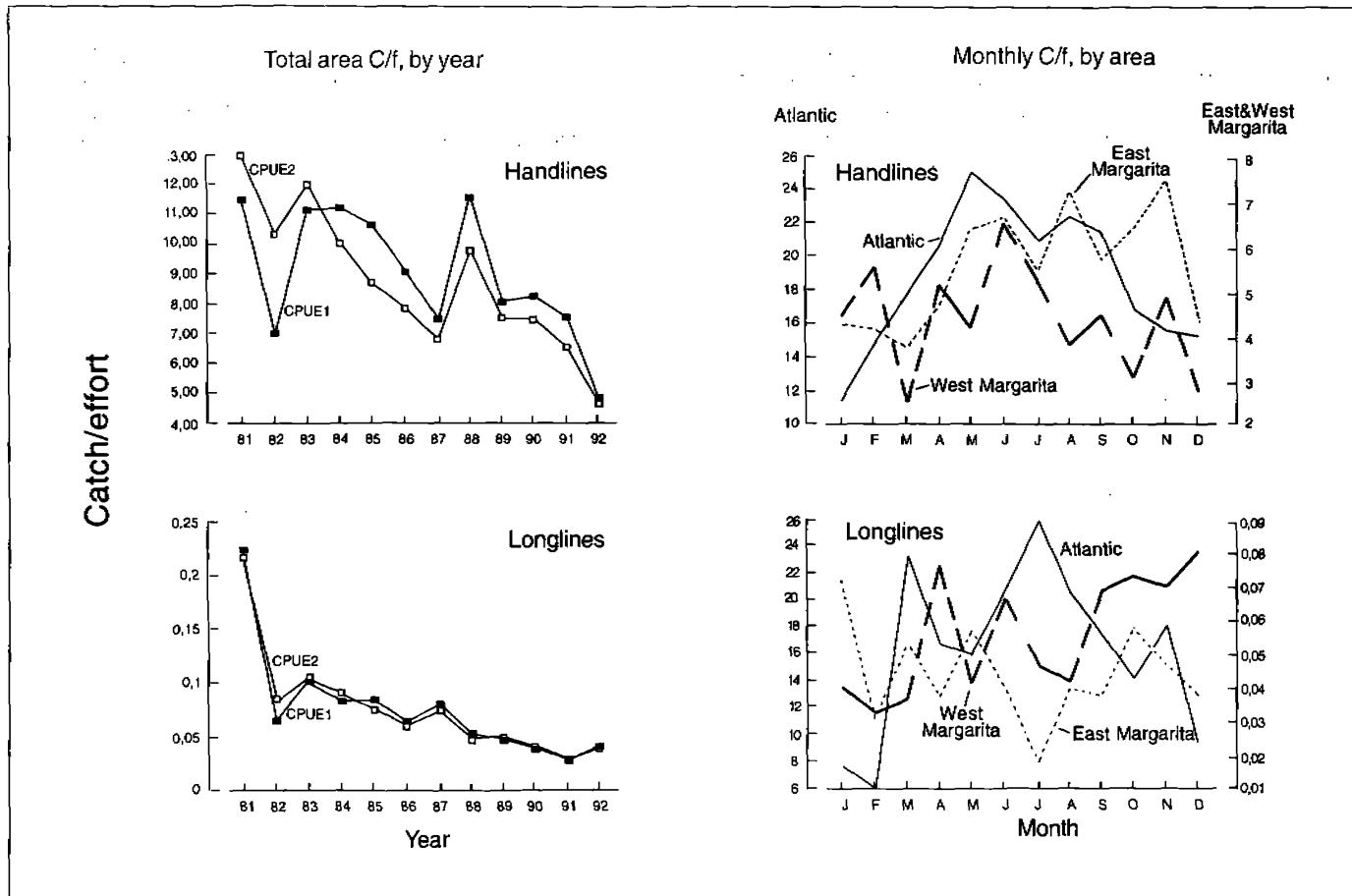


Fig. 2. Average annual red snapper (*Lutjanus purpureus*) CPUE (CPUE1 = $\Sigma C_i / \Sigma f_i$, and CPUE2 = $1/n \sum (C_i/f_i)$ for i individual fishing trips and n total trips sampled) by handlines (kg/line per day) and longlines (kg/hook per day) in all areas, and average monthly (1981-1992) red snapper CPUE by subarea. [Promedio anual de la CPUE (CPUE1 = $\Sigma C_i / \Sigma f_i$, and CPUE2 = $1/n \sum (C_i/f_i)$ para i viajes de pesca y n número total de viajes) del pargo colorado (*Lutjanus purpureus*) por líneas de mano (kg/línea por día) y palangres (kg/anzuelo por día) en todo el área y promedio mensual (1981-1992) de la CPUE del pargo colorado por subáreas.]

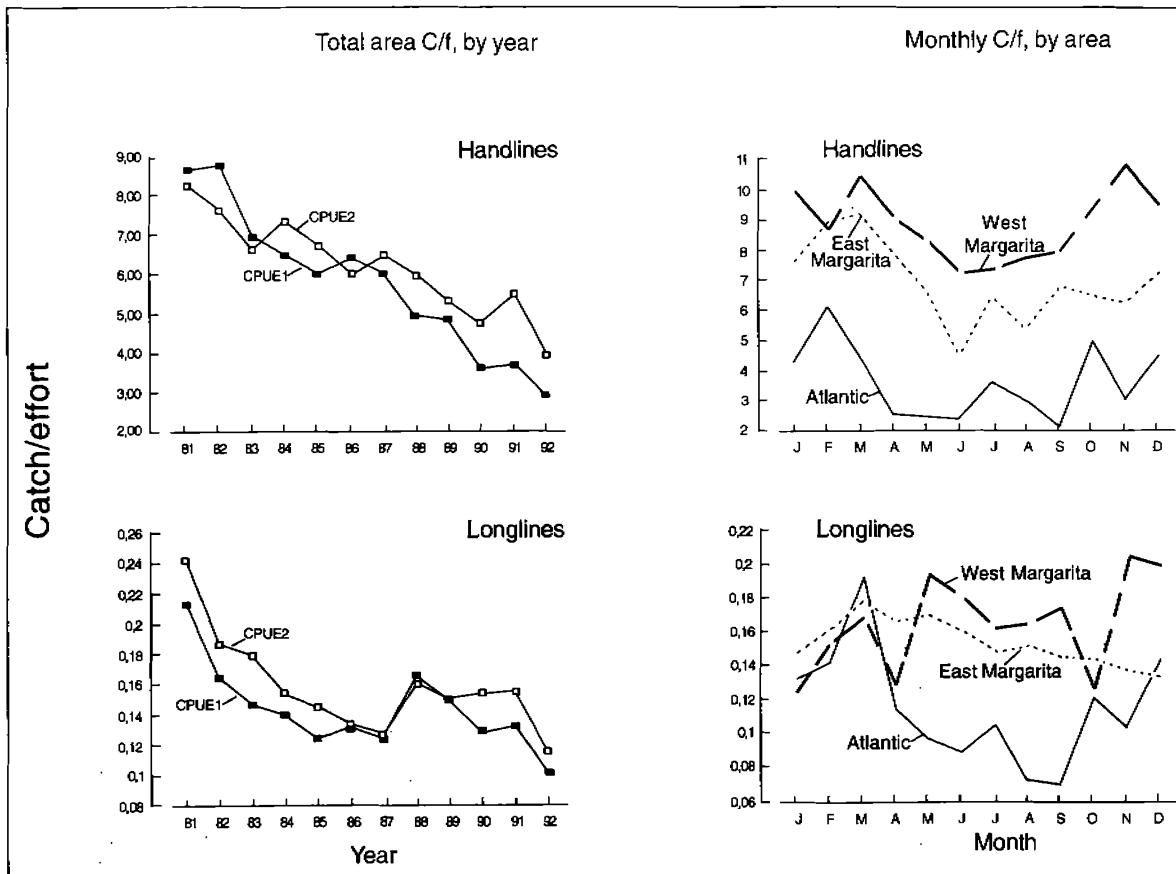


Fig. 3. Average annual yellowedge grouper (*Epinephelus flavolimbatus*) CPUE (CPUE1 = $\sum C_i / \sum f_i$ and CPUE2 = $1/n \sum (C_i/f_i)$ for i individual fishing trips and n total trips sampled) by handlines (kg/line per day) and longlines (kg/hook per day) in all areas, and average monthly (1981-1992) yellowedge grouper CPUE by subarea. [Promedio anual de la CPUE (CPUE1= $\sum C_i / \sum f_i$ y CPUE2= $1/n \sum (C_i/f_i)$ para i viajes de pesca y n número total de viajes) del mero fraile (*Epinephelus flavolimbatus*) por líneas de mano (kg/línea por día) y palangres (kg/anzuelo por día) en todo el área y promedio mensual (1981-1992) de la CPUE del mero fraile colorado por subáreas.]

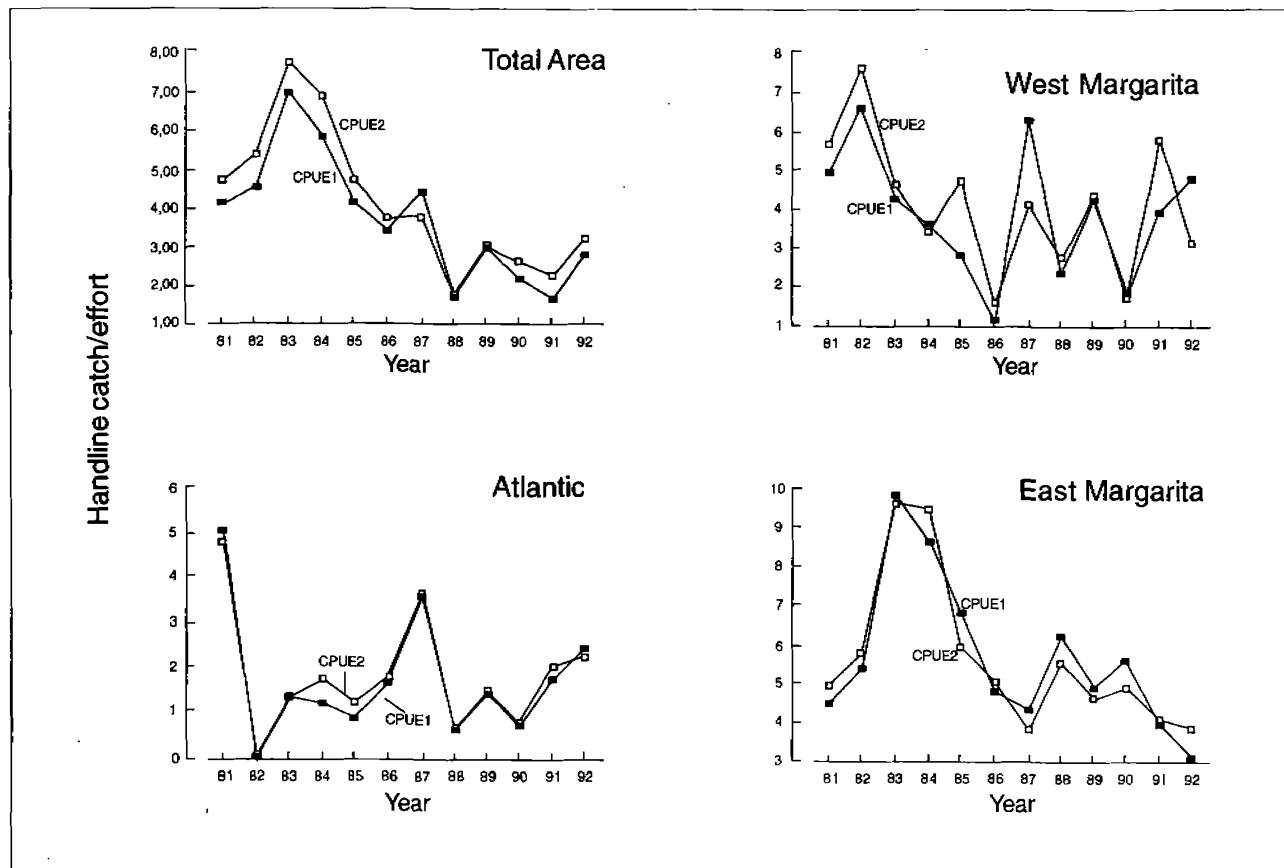


Fig. 4. Average annual vermilion snapper (*Rhomboplites aurorubens*) CPUE (CPUE1 = $\Sigma C_i / \Sigma f_i$, and CPUE2 = $1/n \sum (C_i/f_i)$ for 1 individual fishing trips and n total trips sampled) by handline (kg/line per day) in all areas. [Promedio anual de la CPUE (CPUE1 = $\Sigma C_i / \Sigma f_i$ y CPUE2 = $1/n \sum (C_i/f_i)$ para 1 viajes de pesca y n número total de viajes) del cunaro (*Rhomboplites aurorubens*) por líneas de mano (kg/línea por día) en todas las áreas.]

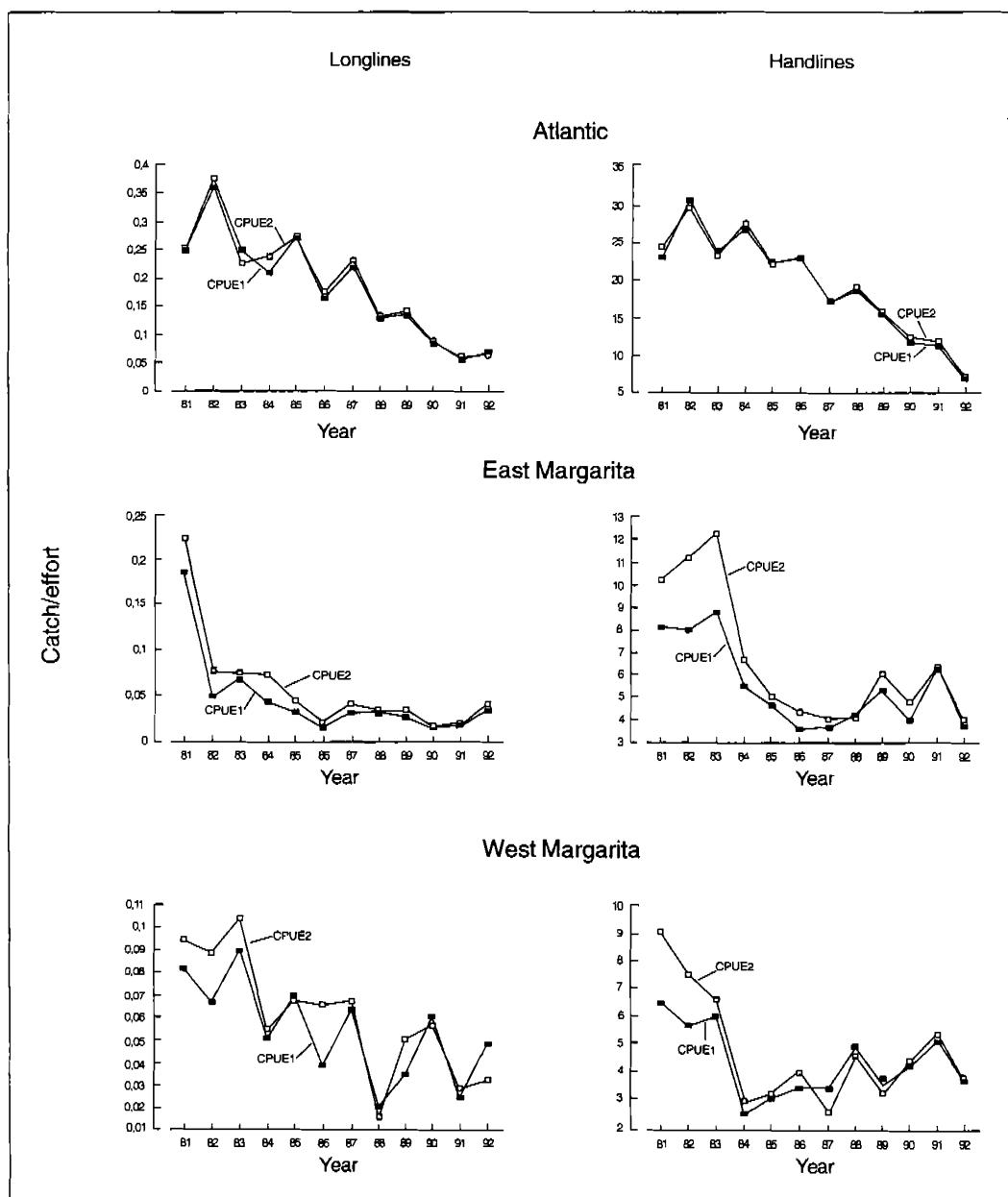


Fig. 5. Average annual red snapper (*Lutjanus purpureus*) CPUE by handlines (kg/line per day) and longlines (kg/hook per day) by subarea (CPUE1 = $\Sigma C_i / \Sigma f_i$ and CPUE2 = $1/n \sum (C_i/f_i)$ for 1 individual fishing trips and n total trips sampled). [Promedio anual de la CPUE del pargo colorado (*Lutjanus purpureus*) por líneas de mano (kg/línea por día) y palangres (kg/anzuelo por día) por subáreas (CPUE1=SCI/Sfi y CPUE2= 1/n (S CI/fi) para 1 viajes de pesca y n número total de viajes).]

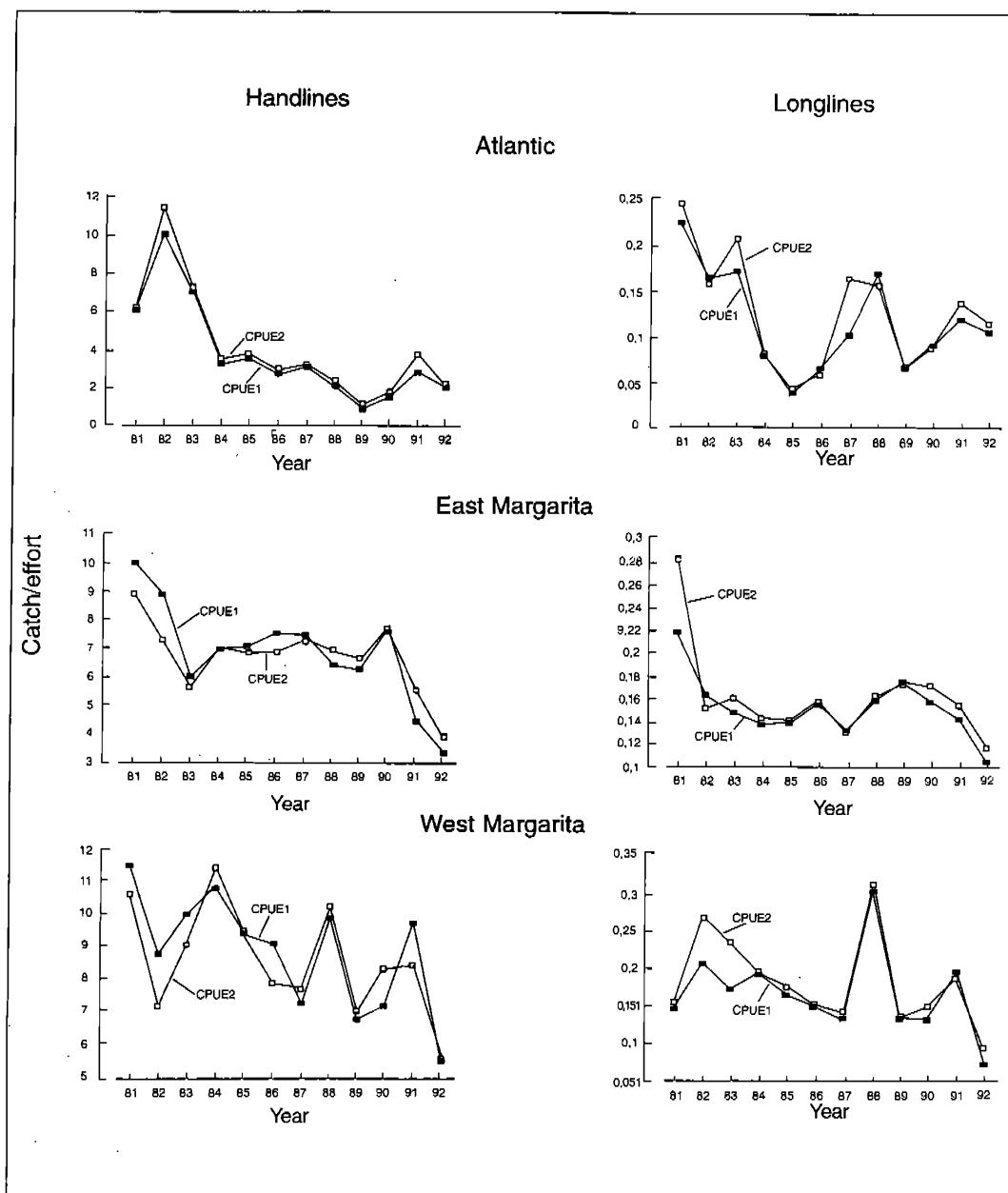


Fig. 6. Average annual yellowedge grouper (*Epinephelus flavolimbatus*) CPUE by handlines (kg/line per day) and longlines (kg/hook per day) by subarea (CPUE1 = $\sum C_i / \sum f_i$, and CPUE2 = $1/n \sum (C_i/f_i)$ for i individual fishing trips and n total trips sampled). [Promedio anual de la CPUE del mero fraile (*Epinephelus flavolimbatus*) por líneas de mano (kg/línea por día) y palangres (kg/anzuelo por día) por subáreas CPUE1= $\sum C_i / \sum f_i$ y CPUE2= $1/n \sum (C_i/f_i)$ para i viajes de pesca y n número total de viajes].

Atlantic sector. In east and west Margarita, higher values are observed in the first and second semesters, respectively. For yellowedge grouper longline CPUE (Fig. 3) only the Atlantic subarea presents monthly variations similar to the ones observed for handlines, and monthly fluctuations east and west of Margarita are much less pronounced.

Discussion

Economic policies developed by the Venezuelan government during the period 1983-1988 favored a large increase in number of boats and consequently fishing effort in several national fisheries. The northeastern Venezuelan snapper-grouper fleet increased from an estimated 341 boats in 1983 to 961 boats in 1989, of which approximately 50% participated in the medium range fishery (Anon. 1990).

Estimates of total catch for the latter fishery were only available for the years 1988 and 1989, in which a reduction from 6 331 t to 3 659 t was observed (Anon. 1990). Current work will try to reconstruct longer catch series in order to obtain a more precise picture of the response of these resources to exploitation. In any case, the analysis of CPUE data for the period 1981-1992 indicates that overall apparent abundance has decreased markedly for the main exploited species. This is particularly evident in the case of red snapper, yellowedge grouper and vermillion snapper handline CPUE for the total area, in which relative declines over the study period have been greater than 50%. Longline yellowedge grouper CPUE and, to a lesser degree, red snapper longline CPUE, present a similar trend. The image obtained from this analysis suggests that these resources are heavily exploited and that measures should be adopted to reduce fishing effort.

However, the additional information obtained from the geographical stratification of catch and effort data may imply that

more than one unit stock exists for each species in the fishing area. Red snappers are more abundant in the Atlantic subarea where reduction of CPUE for both gears shows a pronounced and continuous trend, as opposed to the western subareas where abundance is lower and CPUE estimates have remained relatively stable in the last seven years of the series. In this case we may be dealing with at least two separate stocks; an Atlantic stock associated with the Guianas Plateau and what may be called a southeastern Caribbean stock (northeastern Venezuela and northern Trinidad). A similar situation may exist for yellowedge grouper: the species is more abundant in the western subareas and its CPUE series resemble each other more than those from the Atlantic subarea. Following the same line of thought, trends in abundance of vermillion snapper would indicate that three different unit stocks may be present (Fig. 4). However, this species is a secondary target in the handline fishery and trends in CPUE may not adequately reflect changes in population abundance.

The relation between the two CPUE estimates indicates that handline effort is somewhat concentrated on red snapper, relative to longline effort, which is more dispersed. Snappers and groupers are generally more abundant on "hard bottoms" and rocky outcrops over the continental shelf and slope edge (Kawaguchi 1974). Experienced medium-range artisanal fishers use visual reference points to locate hard bottom grounds and, once within them, they employ a leaded wire or a fishfinder to determine the nature of the substrate. A preliminary assessment of our data showed that fishing occurs mainly in 60-240 m depth with higher red snapper catches obtained in less than 160 m, while yellowedge groupers were more abundant in deeper waters. This difference in depth distribution and higher mobility to avoid ground where "strikes" are not satisfactory, may explain why handliners are able to concentrate fishing effort on red snappers.

Seasonal changes in apparent abundance are not easily interpreted in this fishery. Red snapper handline CPUE peaks during the months from April to September, which corresponds with low apparent abundance for yellowedge grouper. This pattern is present in longline CPUE only in the Atlantic sector. Longline CPUE in other subareas does not present a well-defined seasonal pattern. Numerous factors related to fish behavior, environment, recruitment and fishing strategy and tactics may determine the observed changes in the handline fishery. We think, however, that changes in local densities associated with reproductive behavior may be a major determinant factor. Snappers (Thompson and Munro 1983a) and groupers (Thompson and Munro 1983b; Robertson 1991) have been reported to form spawning aggregations. *Lutjanus purpureus* is known to have a protracted spawning period extending from April to September. Even though we are not aware of specific studies on *Epinephelus flavolimbatus*, information presented for the Caribbean (Thompson and Munro 1983b; Robertson 1991) indicates that several serranid species spawn in the first and last months of the year. These observations are consistent with our results regarding handline CPUE for both species and, to a lesser degree, for that on longlines.

Acknowledgements

We wish to thank Mr. José Silva from the Departamento de Biología Pesquera, Instituto Oceanográfico, Universidad de Oriente, for his assistance in data processing.

References

- Anon. 1990. Resultados de talleres sobre la pesca en Venezuela. Ministerio de Agricultura y Cría, Dirección General Sectorial de Pesca y Acuicultura, Caracas, 126 p.
- Celaya, J. and L. González. 1988. Descripción de la pesquería de altura del pargo del Estado Nueva Esparta, Venezuela. Contrib. Cient. Centro de Investigaciones Científicas, Universidad de Oriente. 17, 72 p.
- González, L. 1990. Edad y crecimiento del pargo colorado *Lutjanus purpureus* e índice de abundancia de la pesquería de media altura pargo-mero en la Región Oriental de Venezuela. Trabajo de Ascenso, Universidad de Oriente, Boca de Río, Edo. Nva. Esparta. 73 p.
- Kawaguchi, K. 1974. Handline and longline fishing explorations for snapper and related species in the Caribbean and adjacent waters. Mar. Fish. Rev. 36(9):8-31.
- Lugo, T. 1986. Aspectos de la reproducción del pargo colorado, *Lutjanus purpureus*, (Poey, 1875) (Pisces : Lutjanidae) de la región oriental de Venezuela. Universidad de Oriente, Cumaná. 96 p. Thesis.
- Robertson, D.R. 1991. The role of adult biology in the timing of spawning of tropical reef fishes, p. 356-386. In P.F. Sale (ed.) The ecology of fishes on coral reefs. Academic Press, New York.
- Thompson, R. and J.L. Munro. 1983a. The biology, ecology and bionomics of the snappers, Lutjanidae, p. 94-109. In J.L. Munro (ed.) Caribbean coral reef fishery resources. ICLARM Stud. and Rev. 7, 276 p.
- Thompson, R. and J.L. Munro. 1983b. The biology, ecology and bionomics of the hinds and groupers, Serranidae, p. 59-81. In J.L. Munro (ed.) Caribbean coral reef fishery resources. ICLARM Stud. and Rev. 7, 276 p.

ENTERED IN NAGA

APR 14 1998

Trends in Commercial Fishery Landings of Groupers and Snappers in Bermuda from 1975 to 1992 and Associated Fishery Management Issues

B.E. LUCKHURST

Division of Fisheries

P.O. Box CR 52

Crawl CRBX, Bermuda

LUCKHURST, B.E. 1996. Trends in commercial fishery landings of groupers and snappers in Bermuda from 1975 to 1992 and associated fishery management issues [*Tendencias en los desembarques de la pesquería comercial de meros y pargos en Bermudas, de 1975 a 1992 y aspectos asociados al manejo de la pesquería*], p. 277-288. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

From 1975 to 1981, the reported landings of six commercially important species of grouper (four *Mycteroperca* spp., two *Epinephelus* spp.) declined between 68% and 95%. The largest percentage decline (representing approximately 32 t) was in fishing for the Nassau grouper, *Epinephelus striatus*, whose spawning aggregations were heavily fished during these years. The only species which exhibited signs of a significant recovery in subsequent years was the black grouper (*M. bonaci*). Landings of two smaller species of grouper, the coney (*Cephalopholis fulva*) and the creole-fish (*Paranthias furcifer*) increased markedly from 1984-1985 to April 1990 when a ban on the use of fish pots was implemented. As a consequence of this ban, line fishing effort for these and other species has increased in an effort to maintain catch levels.

Of the species of snapper taken by the commercial fishery, the yellowtail snapper (*Ocyurus chrysurus*) has dominated catches with landings varying over time from 10 t to over 35 t. Gray snapper (*Lutjanus griseus*) and lane snapper (*Lutjanus synagris*) landings have shown a general increase over time with a significant increase in fishing effort for lane snapper after the fish pot ban. Landings from line fishing effort directed at lane snapper doubled to 20 t between 1990 (the year of the fish pot ban) and 1992. A deepwater snapper fishery which developed in 1981 as a result of a fishing gear innovation lasted less than two years due to overfishing of a limited bathymetric zone around the Bermuda seamount.

Resumen

Durante el periodo de 1975 a 1981, los desembarques reportados de seis especies de mero de importancia comercial (cuatro *Mycteroperca* spp., dos *Epinephelus* spp.) decrecieron entre 68% y 95%. El mayor porcentaje de decremento (representado por aproximadamente 32 000 kg) ocurrió en la cherna criolla (*Epinephelus striatus*) cuyas agregaciones reproductivas fueron fuertemente explotadas durante esos años. La única especie que presentó signos de una recuperación significativa en años subsecuentes fue el cuna bonaci (*M. bonaci*). Los desembarques de dos especies más pequeñas de meros, la cherna cabrilla (*Cephalopholis fulva*) y el cuna lucero (*Paranthias furcifer*) aumento en forma marcada de 1984-1985 a Abril de 1990, cuando una prohibición en el uso de encierros fue implementada. Como una consecuencia de esta prohibición, el esfuerzo de pesca con línea para estas y otras especies ha incrementado en un intento por mantener los niveles de captura.

*De las especies de pargo tomadas por la pesca comercial, la rabirubia (*Ocyurus chrysurus*) ha dominado las capturas con descargas variando en el tiempo de 10 a mas de 35 toneladas. Los desembarques de pargo prieto (*L. griseus*) y pargo blajaiba (*L. synagris*) han mostrado un incremento marginal en el tiempo, con un incremento significativo en el esfuerzo de pesca para el pargo blajaiba después de la implementación de la prohibición del uso de los encierros para peces. Los desembarques del esfuerzo de pesca con línea, dirigido al pargo blajaiba, duplicó a 20 toneladas entre 1990 (el año de la implementación de la prohibición) y 1992. Una pesquería de pargos de aguas profundas que se desarrolló en 1981 como resultado de una innovación a las artes de pesca duró menos de dos años debido a la sobrepesca de una área batimétrica alrededor de la montaña marina de las Bermudas.*

Introduction

In an historical context, Bermuda's fishery has been dominated by groupers. Bardach et al. (1958) discussed the abundance and importance of groupers to the island while providing information on aspects of their biology. They estimated that groupers comprised approximately 70% of total food fish landings during the period of their study (middle 1950s), with snappers contributing 20% to the total. In 1975, a fisheries statistics program became fully operational providing catch and effort data from the industry on a compulsory basis. In this first year of the program, groupers comprised 47.6% of the total landed weight of food fish (431 t) while snappers contributed 9.8% (Luckhurst and Ward 1996). By 1989, total food fish catch had increased to 623 t but the species composition of the catch had changed significantly with the grouper landings being reduced to 18.7% of the total, while snappers were largely unchanged at 10.1%. The well-documented decline of Bermuda's grouper stocks from 1975 to 1981 was used by Bannerot et al. (1987) as an empirical data set to compare against simulated yield curves generated by various computer models examining the resiliency of protogynous and gonochoristic populations to exploitation. In general, protogynous populations such as groupers should be favored provided that males are not limiting. However, as mortality reduces the frequency of contact

between males and females, relative reproductive success of groupers is expected to decline. Russ (1991) discussed several studies in which large declines occurred in both grouper and snapper populations as a result of intense fishing pressure (see also Cuellar et al.; Diaz-Ruiz et al.; Sullivan and Sluka, this vol.).

Methods

The data used in these analyses are derived from the fishery statistical database established by the Division of Fisheries in 1975. They have subsequently been modified and refined over the past 18 years in response to changes in the fishery. Changes in reporting categories over time can compromise the interpretation of landing figures, but this is considered primarily a problem with smaller species which may often be filleted for marketing purposes. As reporting practices vary in the fishery in response to different factors, it is not possible to quantify this effect when using reported landings. However, knowledge of the operation of the fishery and the market has been used in the interpretation of the figures in an attempt to reduce this possible error. The various fishery management plans and issues referred to in this paper and an analysis of trends in landings in the commercial fishery, up to and including 1990, is given in Luckhurst and Ward (1996).

Results and Discussion

Total landings

The overall pattern in landings of groupers is a sharp decline from over 200 t in 1975 to approximately 58 t in 1981 (Fig. 1a), followed by an increasing trend until 1989. However, the species composition of the grouper catch changed markedly during the 1980s with two smaller species comprising almost 50% of total landings in 1989 (Luckhurst and Ward 1996). A fish pot ban was put into effect in April 1990 in an effort to allow the recovery of coral reef fish stocks which had been subjected to heavy fishing pressure with fish pots. As a result of the fish pot ban, the total grouper landings level declined by 58% and has remained stable through 1992. An analysis of the trends in individual grouper species (next section) indicates the relative contribution of each species to this general pattern.

In contrast, the pattern of landings in all the snapper species combined shows a more stable trend over the 18-year period, ranging from under 25 t to 70 t (Fig. 1a). As the yellowtail snapper (*Ocyurus chrysurus*) often comprised 50% or more of the total snapper landings, it is clear that variations in the landing figures of this species have a significant effect on the overall snapper pattern.

In the past three years, the total landings of groupers and snappers have been very similar with little variation between them.

Grouper landings by species

The pattern of landings for the larger grouper species (*Myctoperca* spp.) shows a similar trend in the four species with large declines from 1975 to 1981 (Fig. 1b). The landings of the black grouper (*M. bonaci*) declined 78.4% during this period while the next most abundant species, the tiger

grouper (*M. tigris*) dropped 91.7%. From 1982 to 1984, the black grouper and the yellowmouth grouper (*M. interstitialis*) showed parallel increasing trends but these trends diverged in 1985 with the black grouper continuing to increase while the yellowmouth grouper steadily declined again. The fish pot ban in April 1990 brought a dramatic drop in the landings of black grouper (Fig. 1b) while having little impact on the remaining three species whose landings had already declined to little more than incidental catch levels.

The landings of groupers of the genus *Epinephelus* (Fig. 1c) show the same steep decline from 1975 to 1981 but with only two species of commercial significance. The red hind (*E. guttatus*) had the largest landing figures of all the grouper species starting at just under 70 t in 1975. Landings of this species declined by 67.8% over the seven-year period. This was followed by a significant increase in 1983 and apparent stabilization before a large drop in 1990. In contrast, the Nassau grouper (*E. striatus*) underwent a precipitous decline from over 33 t in 1975 to less than 2 t in 1981 (Fig. 1c), a drop of 95.0% in landings. The species has not shown any evidence of a subsequent recovery. The spawning aggregation sites on the Bermuda platform and on the offshore banks were intensively fished with fish pots during this period and it appears that the spawning stock biomass was reduced below a critical but unknown level so that the population has apparently been unable to recover (see Sadovy 1996).

Red hind spawning aggregation sites have been afforded a measure of protection since 1974 when these sites and surrounding areas were seasonally closed to all fishing during the summer spawning period. The enforcement of these area closures has been continuous since their inception, but with varying effectiveness, which probably increased in recent years. This may have helped to maintain spawning stock biomass and will possibly allow a partial recovery of the

stock now that it is subject only to line fishing pressure. Some of the Nassau grouper aggregation sites were relatively close to the red hind sites (24-28 m depth) but on the seaward side in deeper water (36-40 m). These deeper sites were not included in the area closures and were therefore intensively fished. Anecdotal information from fishers indicates that the density of fish pots set for Nassau groupers in these small areas during the aggregation period (May-June) was so high that the buoy ropes of adjacent fish pots often became tangled as fishers attempted to maximize catch during this brief period of high catchability.

The misty grouper (*E. mystacinus*) attained a peak in landings in 1979 at over 7.4 t but declined after 1981 to a negligible level. The "Other" category is comprised primarily of the red grouper (*E. morio*), the rock hind (*E. adscensionis*) and the graysby (*E. cruentatus*). This group reached a peak in 1985 at almost 6 t but as these species were lumped in the original statistical reporting form, it is not possible to determine what proportional contribution each species has made to the overall figure. It is thought that the 1981 figure was increased significantly by the inclusion of wreckfish (*Polyprion americanus*) in the "Other" category as a result of an intense but short-lived vertical longline fishery which targeted primarily snappers. The wreckfish were taken in deeper water than the snappers but using the same gear. Wreckfish were included as a separate entry in the reporting form as of 1982.

The landings of two smaller grouper species, the coney (*C. fulva*) and the creole-fish (*Paranthias furcifer*) increased dramatically from 1984 to 1989 reaching levels of 25 t and almost 33 t, respectively (Fig. 1d). Most of this catch can be attributed to the increased fishing power of fish pots which came about as a result of technological innovations in the fish pot fishery. Despite the implementation of a full

limited entry fish pot fishery in 1986 with reductions in numbers of fish pots, effective fishing effort with fish pots did not appear to decline and these smaller grouper species became increasingly important for the established local fresh fillet market. The fish pot ban in 1990 witnessed steep declines in both species but the landings level of the coney returned to its previous level the next year, while the creole-fish continued to decline (see section on analysis by gear type).

Snapper landings by species

The dominant snapper species landed in Bermuda is the yellowtail snapper (*Ocyurus chrysurus*). The landings have fluctuated over the 18-year period of this analysis from 10 t to 36 t (Fig. 1e). This large range is probably the result of a combination of natural variability and changes in fishing effort over time. However, the highest sustained catch levels occurred from 1984 to 1989 during which period fish potting effort was high. The decline in 1990 and the two subsequent years is probably the combined result of the fish pot ban and the seasonal closure of portions of the Bermuda platform to all fishing activities (Luckhurst and Ward 1996). These closed areas are considered to be very productive, particularly for yellowtail snappers and other species which are fished along the edge of the platform during the summer months. Gray snapper (*Lutjanus griseus*) landings increased through the 1980s reaching a peak in 1987 at just over 23 t (Fig. 1e) before plunging to approximately 7 t in 1990 mainly in response to the fish pot ban. It has remained at a similar level for the past two years.

The lane snapper (*L. synagris*) has shown a slower but steady climb over the years, peaking in 1987 but, unlike the gray snapper, landings did not decline in 1990 (Fig. 1e). In the past two years, landings have

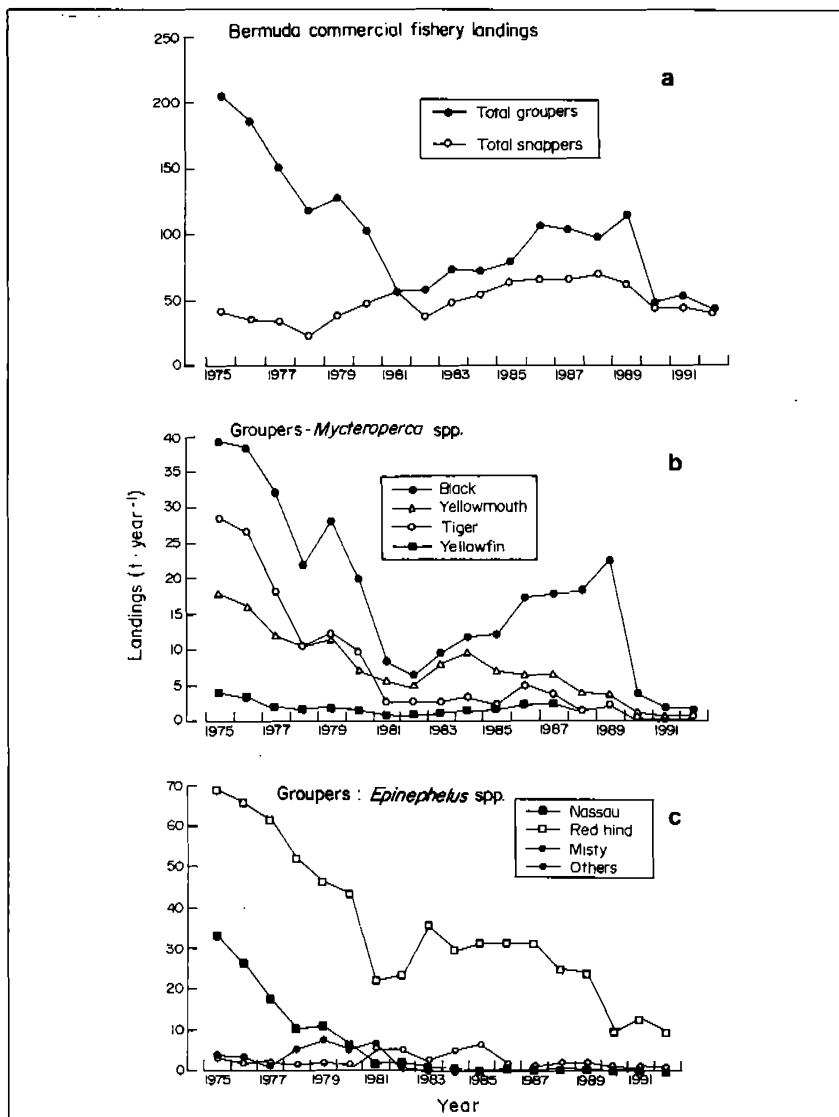
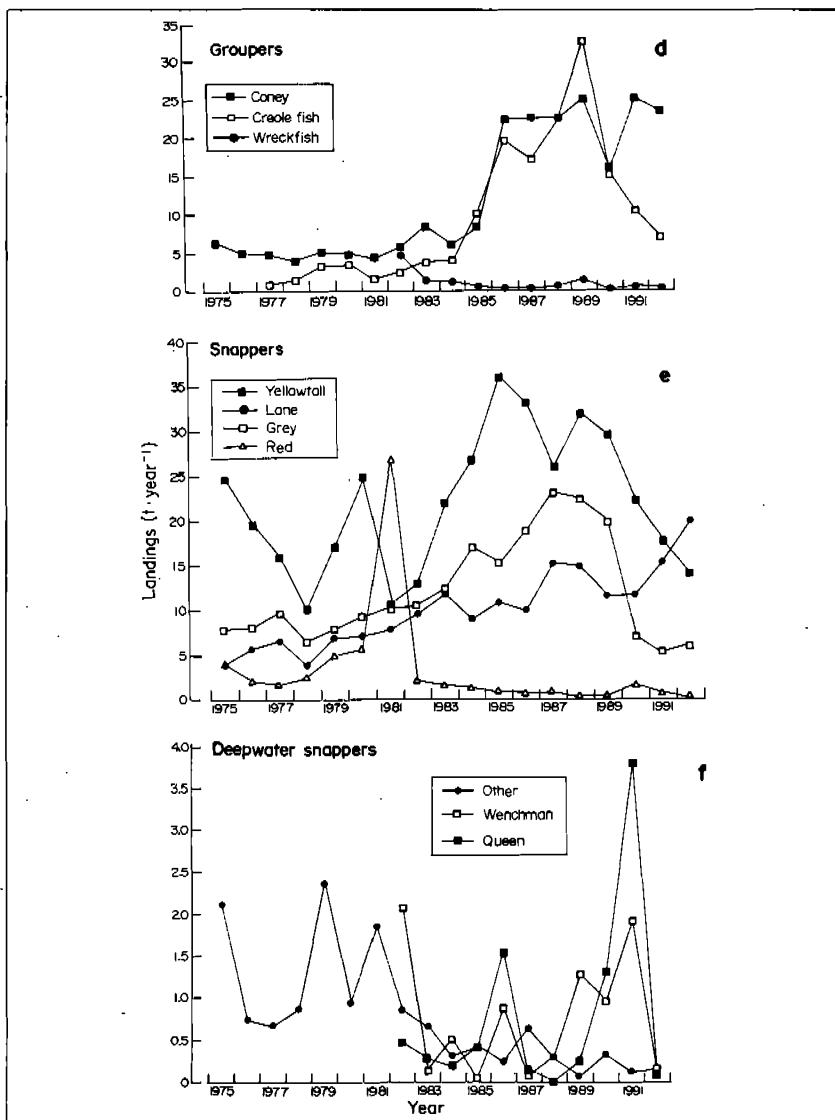


Fig. 1. Grouper and snapper landings reported from the Bermuda commercial fishery from 1975 to 1992: [Descargas comerciales de meros y pargos reportadas en la pesquería de Bermuda de 1975 a 1992:]

- Total grouper (Serranidae) and snapper (Lutjanidae) landings [Total de meros (Serranidae) y pargos (Lutjanidae).]
- Groupers of the genus *Mycteroperca*: black (*M. bonaci*); yellowmouth (*M. Interstitialis*); tiger (*M. tigris*); and yellowfin (*M. venenosa*) [Merlos del género *Mycteroperca*: cuna bonaci (*M. bonaci*); cuna amarilla (*M. Interstitialis*); cuna gata (*M. tigris*); y cuna de piedra (*M. venenosa*).]
- Groupers of the genus *Epinephelus*: Nassau (*E. striatus*); red hind (*E. guttatus*); misty (*E. mystacinus*); other species [Merlos del género *Epinephelus*: cherna criolla (*E. striatus*); mero colorado (*E. guttatus*); mero listado (*E. mystacinus*); y otras especies.]

**Fig. 1. (cont.)**

- d) Other grouper species: coney (*Cephalopholis fulva*); creole-fish (*Paranthias furcifer*); wreckfish (*Polyprion americanus*) [Otras especies de meros: cherna cabrilla (*Cephalopholis fulva*); cuna lucero (*Paranthias furcifer*); cherna (*Polyprion americanus*)]
- e) Snappers: yellowtail (*Ocyurus chrysurus*); grey (*Lutjanus griseus*); lane (*L. synagris*); red (*L. vivanus*) [a] Pargos: rabirubia (*Ocyurus chrysurus*); pargo prieto (*Lutjanus griseus*); pargo blajalba (*L. synagris*); pargo de lo alto (*L. vivanus*)]
- f) Deepwater snappers: "wenchman" (*Pristipomoides macrourus*); queen (*Etelis oculatus*); other species [Pargos de aguas profundas: panchito ojón (*Pristipomoides macrourus*); pargo cachucho (*Etelis oculatus*); y otras especies]

increased by over 8 t in response to increased line fishing effort.

The red snapper category was comprised primarily of the silk snapper (*L. vivanus*) from 1975 to 1980, although vermillion snapper (*Rhomboplites aurorubens*) was also caught. The dramatic peak in 1981 (Fig. 1e) is an artifact of the statistical reporting system. A vertical longline fishery for queen snapper (*Etelis oculatus*) and the "wenchman"^a snapper (*Pristipomoides macrourhalmus*) rapidly developed in 1981 and fishers reported the catches of these two species under the red snapper category in that year. By 1982, these two species were included on the reporting form and their landings were reported separately from that year onward (Fig. 1f). Landings of red snapper for the last 11 years have been at a low level showing no sign of a recovery.

The vertical longline fishery for deepwater snappers (queen and "wenchman") lasted less than two years due to overfishing of the narrow shelf edge around the Bermuda platform (Luckhurst and Ward 1996). The combined catch of these two species in 1981 is estimated at approximately 22 t and, by 1983, the reported landings of both species were negligible. It appears that these two species have been subjected to pulse fishing over the years with concurrent landings peaks in 1986 and 1991 (Fig. 1f). These peaks in landings are almost certainly effort-related and probably reflect fishery responses to management actions in effect at the time. In 1986, the limited entry fish pot fishery (for full-time fishers only) was implemented, displacing many part-time pot fishers who turned to various forms of line fishing in an attempt to maintain their catch levels. The larger peak in 1990-1991 is probably a direct result of the fish pot ban because former fish pot fishers were forced to shift their efforts into line and net fishing. Anecdotal evidence suggests

that a number of fishers decided to fish for deepwater snappers again because they felt that the stocks had probably an opportunity to recover after being largely unfished for several years. Catches did increase in 1991 with queen snapper reaching over 3.8 t but landings plummeted again in 1992.

Analysis of landings by gear type for groupers

In order to assess the full impact of the 1990 fish pot ban on catches of groupers and snappers, it is necessary to determine the proportion of the catch taken by fish pots for each species in the years leading up to the ban. It is also desirable to determine whether apparent increased line fishing effort for a given species following the fish pot ban has resulted in the maintenance of landing levels.

On the basis of landing statistics, four grouper species were chosen for this analysis. The reported landings by fish pots and by various forms of line fishing were determined from the fishery statistical database (Luckhurst and Ward 1996) for the three years prior to the fish pot ban and then extended through 1992, two years after the ban had been in effect.

The black grouper (*M. bonaci*) was chosen from amongst the four species of *Mycteroperca* because it was the only large grouper with a significant landing level before the fish pot ban. The analysis showed that the catch by fish pots completely dominated the landings in 1987-1989, comprising over 95% of the landed weight in each of the three years (Fig. 2a). The same analysis of the other three species of *Mycteroperca* (see Fig. 1b) revealed a similar trend. This clearly demonstrates the dependence of the fishery on fish pots to efficiently harvest

^a *P. macrourhalmus* is designated as the cardinal snapper by both the Food and Agriculture Organization and the American Fisheries Society in their list of official common names. Hence, wenchman in quotes as this is the official common name of *P. aquilonaris*.

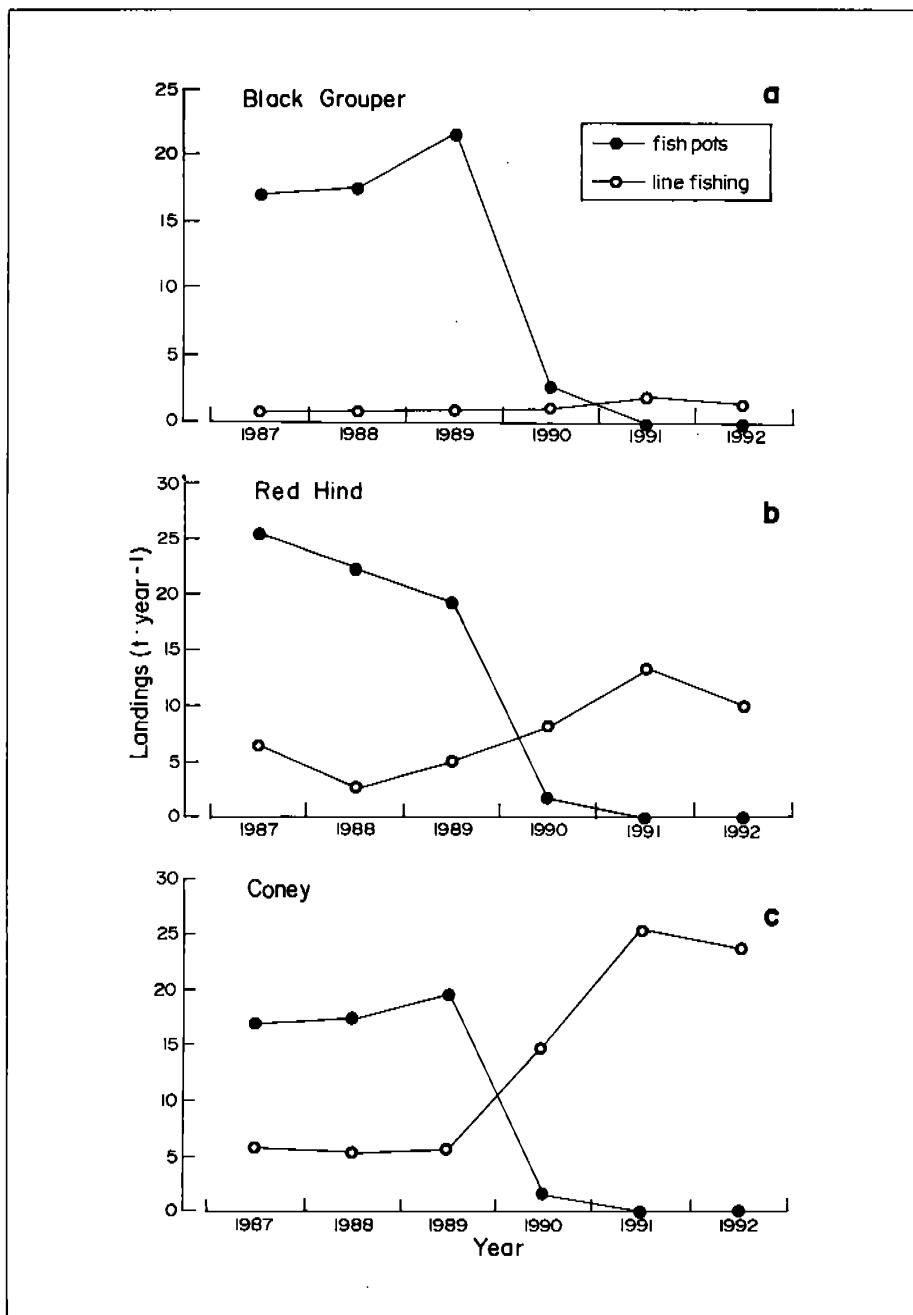
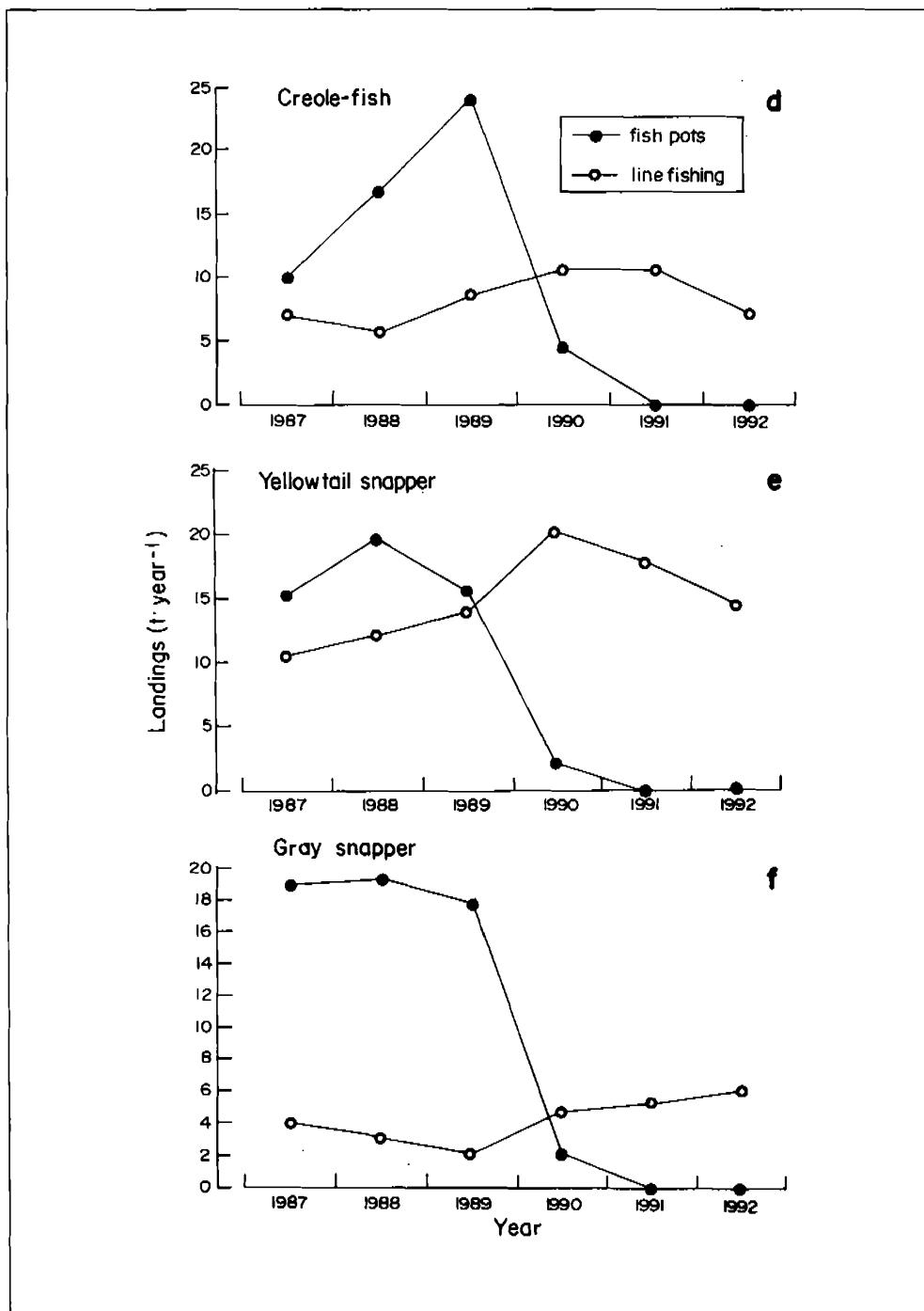


Fig. 2. Grouper and snapper landings by gear type from 1987 to 1992. The fish pot ban came into effect in April 1990. [Descargas comerciales de meros y pargos por tipo de arte de 1987 a 1992. La prohibición del uso de encierros fue implementada en Abril de 1990.]

- a) Black grouper (*M. bonaci*) [*cuna bonaci* (*M. bonaci*)]
- b) Red hind (*E. guttatus*) [*mero colorado* (*E. guttatus*)]
- c) Coney (*C. fulva*) [*cherna cabrilla* (*C. fulva*)]

**Fig. 2. (cont.)**

- d) Creole-fish (*P. furcifer*) [*cuna lucero* (*P. furcifer*)]
- e) Yellowtail snapper (*O. chrysurus*) [*rabirrubia* (*O. chrysurus*)]
- f) Gray snapper (*L. griseus*) [*pargo prieto* (*L. griseus*)]

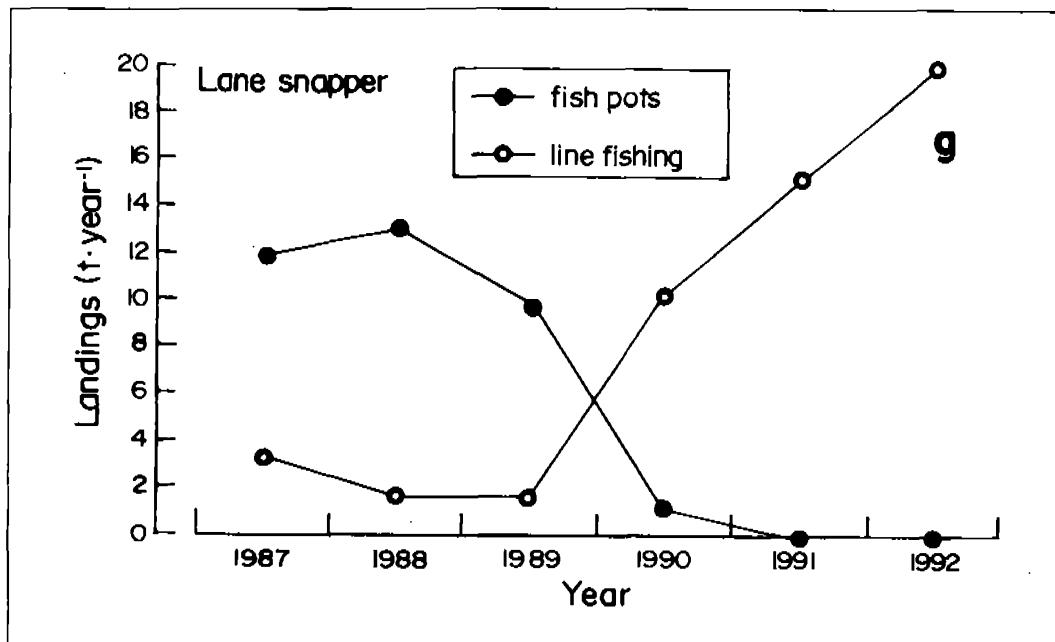


Fig. 2. (cont.)

g) Lane snapper (*L. synagris*) [*pargo blajalba* (*L. synagris*)]

large groupers. Anecdotal evidence indicates that greater fishing effort has been directed at black groupers by handline fishers since the fish pot ban, but it is considered to be a specialized fishery and the landings from line fishing have remained at the same low level since 1990 as they were before the fish pot ban.

The red hind figures indicate that the catch by fish pots ranged from 79 to 89% of the total landings before the fish pot ban, while line fishing landings increased substantially in 1991 before falling back to a lower level in 1992 (Fig. 2b). The effectiveness of increased line fishing effort for red hinds was probably limited by the closure of the expanded seasonally protected areas which went into effect as part of the 1990 Fisheries Management Plan. These areas include known red hind spawning aggregation sites, as well as a considerable area of prime fishing bottom.

The coney landing figures provide evidence of a major shift in fishing effort with the advent of the fish pot ban in April 1990 (Fig. 2c). From 1987 to 1989, fish pot landings comprised 75-78% of the total, but by 1991 landings from line fishing alone equaled the total landings achieved when fish pots were in use. This level was sustained in 1992 indicating that the high catchability of conies on handlines and their ubiquitous distribution have made the coney one of the principal species of the commercial fishery.

The other small grouper species, the creole-fish, provides a dramatic contrast to the coney. Although landings by fish pots increased from 10 t in 1987 to over 24 t in 1989, comprising 74% of creole-fish landings in that year, line fishing landings increased only marginally in 1990 and then declined significantly in 1992 (Fig. 2d). As catch-per-unit-effort of the creole-fish by

line fishing is generally not as high as the coney, many fishers have moved to target other species where the landed weight per unit of fishing time is higher.

Analysis of landings by gear type for snappers

The three most commercially important species of snapper provide interesting contrasts in landing patterns in relation to the fish pot ban. The yellowtail snapper was taken in larger quantities by fish pots than by lines in 1987-1988 but line fishing landings were still very significant and increased steadily from 1987 to 1990 (Fig. 2e). From 1989 to 1991, 0.4-0.5 t were reported landed with seine nets but this netting effort is generally sporadic and opportunistic in nature. Landings declined in the two years following the fish pot ban but still achieved the levels of fish pot landings alone confirming high catchability by the line fishery. Thus, the fishery was able to compensate for the loss of fish pots and catch levels have generally been maintained during this largely seasonal summer fishery.

The gray snapper landing pattern indicates a strong dependence on fish pots, with this gear providing 83-90% of total landings in the three years before the fish pot ban (Fig. 2f). Netting of gray snappers with seine nets traditionally occurred in inshore waters but was banned in 1983. Although the line fishing catch increased in 1990 to over 4.8 t, it remained almost level for the next two years. Gray snappers are notoriously difficult to catch in quantity by line fishing and the fishery has, to date, been unable to surpass the 6 t landing level. This is approximately one-third of the landing levels achieved with fish pots before the fish pot ban.

Although the catch of lane snappers by fish pots (78-89%) was at a similar level to gray snappers, the line fishing catch rose steeply in 1990 to 10 t (a five-fold increase

from the year before) as the fishery exploited the vulnerability of lane snappers to line fishing effort, particularly by night fishing (Fig. 2g). Anecdotal evidence indicates that line fishing effort continued to increase in 1991-92 reaching a catch level of almost 20 t, the highest recorded landings of lane snapper in the statistical database. Recreational fishing effort has also increased markedly in the past few years but no landings figures are available.

Summary and Conclusions

The dominance of groupers in the Bermuda commercial fishery in 1975 is indicated by total landings of over 200 t vs. 42 t for snappers. By 1981, grouper landings had declined to 58 t while snappers had increased to almost this same level. Despite an increasing trend in total grouper landings during 1983-1989, which was largely the result of the contribution of two smaller species, the landing level only reached about 116 t before the fish pot ban was imposed in April 1990. The majority of the grouper species stocks had not effected any recovery over this period; in fact, several species had become commercially extinct e.g., Nassau grouper. The fishing industry's strong dependence on fish pots to catch groupers was dramatically illustrated when total landings plunged to under 50 t the year that the fish pot ban took effect. Additional line fishing effort in 1991-1992 was unable to increase landings to compensate for the loss of fish pot catches.

Total snapper landings have oscillated in a smaller range than groupers with an overall increasing trend up to the fish pot ban. The yellowtail snapper has been the dominant species in the commercial fishery with landings ranging up to 36 t. However, there has been a significant decline in landings since 1989 with the 1992 figure standing at under 15 t. Since the fish

pot ban, the landings of lane snapper have almost doubled surpassing the figure for yellowtail snapper for the first time. Anecdotal evidence suggests that there has been a significant increase in directed line fishing effort for this species by both commercial and recreational fishers due to its high catchability by line fishing and ready access to the fishing grounds on the Bermuda platform by smaller fishing vessels.

It appears that most of the larger grouper species suffered high levels of fishing mortality when subjected to heavy fishing pressure with fish pots. The species which form discrete spawning aggregations, such as Nassau grouper and tiger grouper, seem to be particularly vulnerable to exploitation. When these spawning aggregations are heavily fished, spawning stock biomass is significantly reduced. When population size falls below some minimum level, disrupting reproductive behavior patterns, it is probable that the stock will suffer a spawning collapse. In protogynous hermaphroditic species such as groupers, where there is typically a female-biased sex ratio, the number of males available to spawn may become the limiting factor. The minimum or threshold size of a spawning aggregation for reproductive success is largely unknown. Several of Bermuda's grouper stocks appear to have suffered such a collapse and have not recovered.

The gonochoristic snappers have been more resilient under the high fishing effort imposed on Bermuda's stocks. Although vulnerable to fish potting pressure, the different reproductive ecology and behavior of snappers seems to have allowed these species to maintain stock levels under the Bermuda fishing regime without suffering the dramatic declines witnessed in many of the grouper species.

Acknowledgements

I thank Norbert Simmons for reviewing the manuscript and providing an historical perspective on aspects of the fisheries statistics program. Fishers Linwood Outerbridge and John P. Ingham shared their knowledge from years of fishing experience with fish pots and helped me interpret some of the landing patterns. Neville Trott willingly produced slides for my presentation on short notice.

References

- Bannerot, S., W.W. Fox, Jr. and J.E. Powers. 1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and Caribbean, p. 561-603. *In* J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Bardach, J.E., C.L. Smith and D.W. Menzel. 1958. Bermuda Fisheries Research Program. Final Report. Bermuda Trade Development Board, Hamilton, Bermuda. 59 p.
- Luckhurst, B.E. and J.A. Ward. 1996. Analysis of trends in Bermuda's fishery statistical database from 1975-1990 with reference to fishery management measures implemented during this period. Proc. Gulf Caribb. Fish. Inst. 44:306-324.
- Russ, G.R. 1991. Coral reef fisheries: effects and yields, p. 601-635. *In* P.F. Sale (ed.) The ecology of fishes on coral reefs. Academic Press, San Diego, California.
- Sadovy, Y. 1996. The case of the disappearing grouper, *Epinephelus striatus*, the Nassau grouper, in the Caribbean and western Atlantic. Proc. Gulf Caribb. Fish. Inst. 45:5-22.

ENTERED IN NAGA

APR 14 1998

Catch, Effort and Sustainable Yield for Australia's Northern Trawl Fishery

D.C. RAMM

Y. XIAO

Fisheries Division

Department of Primary Industry and Fisheries

GPO Box 990, Darwin NT 0801

Australia

RAMM, D.C. and Y. XIAO. 1996. Catch, effort and sustainable yield for Australia's northern trawl fishery [*Captura, esfuerzo y rendimiento sostenible para la pesquería de arrastre del norte de Australia*], p. 289-306. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) *Biology, fisheries and culture of tropical groupers and snappers*. ICLARM Conf. Proc. 48, 449 p.

Abstract

Australia's northern trawl fishery is a multispecies, multifleet shelf fishery operating on the Northwest Shelf (114-123°E), and in the Timor (123-129°E) and Arafura (131-142°E) Seas. Groundfish resources have been fished continuously since 1971, and total annual retained catches reached 37 100 t on the Northwest Shelf in 1973; 9 100 t in the Timor Sea in 1974; and 9 000 t in the Arafura Sea in 1983. Red Lutjanidae, mainly *Lutjanus malabaricus*, dominated catches in the Arafura ($\leq 4\ 191\text{ t}\cdot\text{year}^{-1}$) and Timor Seas ($\leq 1\ 091\text{ t}\cdot\text{year}^{-1}$), and were a major catch component on the Northwest Shelf ($\leq 2\ 182\text{ t}\cdot\text{year}^{-1}$). Other major commercial categories included *Nemipterus* spp. ($\leq 8\ 377\text{ t}\cdot\text{year}^{-1}$), *Saurida* spp. ($\leq 4\cdot276\text{ t}\cdot\text{year}^{-1}$) and *Lethrinus* spp. ($\leq 4\ 076\text{ t}\cdot\text{year}^{-1}$) on the Northwest Shelf, and *Ariomma indica* and *Psenopsis humerosa* ($\leq 3\ 057\text{ t}\cdot\text{year}^{-1}$) and *Nemipterus* spp. ($\leq 2\ 811\text{ t}\cdot\text{year}^{-1}$) in the Arafura Sea. Catch-per-unit effort data were standardized and maximum sustainable yields estimated, where possible, using the surplus production model.

Resumen

La pesquería de arrastre del Norte de Australia es una pesquería multiespecífica multiflota que opera sobre la plataforma continental noroeste (114-123°E) y en el mar de Timor (123-129°E) y Arafura (131-142°E). Los recursos de los campos pesqueros han sido explotados continuamente desde 1971 y las capturas totales por año alcanzaron 37 100 t en la plataforma nororiental en 1973; 9 100 t en el mar de Timor en 1974; y 9 000 t en el mar Arafura en 1983. Los pargos Lutjanus malabaricus dominaron las capturas en el mar Arafura ($\leq 4\ 191\text{ t}\cdot\text{año}^{-1}$) y en el mar de Timor ($\leq 1\ 091\text{ t}\cdot\text{año}^{-1}$), y fueron el componente mayor de la captura en la plataforma nororiental ($\leq 2\ 182\text{ t}\cdot\text{año}^{-1}$). Otras categorías comerciales mayores incluyeron Nemipterus spp., ($\leq 8\ 377\text{ t}\cdot\text{año}^{-1}$); Saurida spp. ($\leq 4\cdot276\text{ t}\cdot\text{año}^{-1}$) y Lethrinus spp. ($\leq 4\ 076\text{ t}\cdot\text{año}^{-1}$) sobre la plataforma nororiental; y Ariomma indica, Psenopsis humerosa ($\leq 3\ 057\text{ t}\cdot\text{año}^{-1}$) y Nemipterus spp ($\leq 2\ 811\text{ t}\cdot\text{año}^{-1}$) en el mar Arafura. Los datos de captura por unidad de esfuerzo fueron estandarizados y los rendimientos máximos sostenibles estimados, cuando fué posible, usando modelo de producción excedente.

Introduction

Groundfish resources of the Northwest Shelf and Timor and Arafura Seas, on Australia's northern continental shelf, were fished extensively by Japanese stern trawlers during 1959-1963 (Sainsbury 1987), Taiwanese pair trawlers during 1971-1990, and Thai stern trawlers during 1985-1990. The Japanese fleet targeted Lethrinidae on the Northwest Shelf (Sainsbury 1987), while Taiwanese trawlers retained predominantly Carangidae, Lutjanidae, Nemipteridae and Synodontidae (e.g., Liu 1976; Liu et al. 1978; Chen et al. 1979; Edwards 1983; Sainsbury 1987, 1988, 1991). The fishery developed rapidly and total annual catch reached 49 200 t in 1974 (Sainsbury 1991; Sainsbury, unpubl.), representing about 30% of the then total catch from Australian waters, and 60% of the catch taken by Taiwanese distant-water pair trawlers (Liu 1976). Early estimates of maximum sustainable yield (MSY) for groundfish were based on Gulland's approximation of $MSY=0.5MB_0$, where M is natural mortality rate, and B_0 is unexploited biomass estimated using swept area method with net width as effective trawl path width. These estimates varied considerably depending on values of M , and area of trawl grounds. Liu (1976) and Liu et al. (1978) estimated MSYs of 336 000 t·year⁻¹, 250 000 t·year⁻¹ and 447 000 t·year⁻¹ for all commercial groundfish species on the Northwest Shelf, Timor Sea and Arafura Sea (Australian and Indonesian sectors), respectively, assuming $M=1.0$ year⁻¹ and that the total shelf area was exploited. Sainsbury (1982) estimated a MSY of 87 000 t·year⁻¹ for all commercial groundfish species on the Northwest Shelf using $M=0.5$ year⁻¹ and actual area trawled in 1973. Edwards (1983) assumed $M=0.3$ year⁻¹ and 'areas of concentration of effort' in estimating MSYs of 36 000 t·year⁻¹, 20 000 t·year⁻¹ and 30 000 t·year⁻¹ for all commercial groundfish species on the Northwest Shelf, Timor Sea and Arafura Sea (Australian sector only),

respectively. Sainsbury (1982, 1984) also estimated sustainable yields for major commercial categories by fitting data from the Northwest Shelf to surplus production models.

Sainsbury (1991) developed an adaptive management strategy for groundfish on the Northwest Shelf based on observed changes in community structure during 1960-1983, where relative abundances of Lethrinidae, Lutjanidae and Serranidae, and incidentally caught sponges, decreased significantly over time, while those of Nemipteridae and Synodontidae increased significantly, while those of Carangidae, Haemulidae and Sparidae did not change. Further, Sainsbury (1991) established that Lethrinidae and Lutjanidae had a higher probability of occurring in habitat with large epibenthos than in open sand habitat, while Nemipteridae and Synodontidae preferred open sand habitat. Sainsbury (1987) concluded that trawling on the Northwest Shelf may have modified benthic habitats and caused long-term changes in community structure.

Major changes in fishing practice occurred following the ratification of Australia's Fishing Zone (AFZ) in 1979. Groundfish trawling, now managed by the Federal Department of Primary Industries and Energy, was confined to management zones on the Northwest Shelf, and in the Timor and Arafura Seas. User conflicts with the domestic shrimp fishery were minimized by excluding fish trawlers from shallow, shrimp-rich waters, including the Gulf of Carpentaria. Fishing by foreign trawlers continued, under license, and effort shifted from the Northwest Shelf to the Arafura Sea to target *Lutjanus malabaricus*. Concerns were raised about the inadequacy of fishery data from the Timor and Arafura Seas (e.g., Jernakoff and Sainsbury 1990). Here, we report catch and effort data for the entire trawl fishery in northern Australia during 1972-1990, and discuss implications of our findings for management of, and future research into, that fishery.

Method

Our study covered groundfish trawl data from the Northwest Shelf (115-123°E) and the Australian sectors of the Timor (123-131°E) and Arafura (131-141°E) Seas from 1971 when fishing began in the Arafura Sea, to 1990 when foreign license arrangements were discontinued (Fig. 1). Annual retained catch and effort data to 1979 were based on Edwards (1983) and Sainsbury (1991; Sainsbury, unpubl.) (Appendix 1). The Federal Department of Primary Industries and Energy supplied tow-by-tow logbook data for 1980-1990 and observer data for box weights and species composition for commercial categories from 1 192 tows (3700h) on the Northwest Shelf and in the Arafura Sea during 1985-1987. Logbook catch data (number of boxes·tow⁻¹ by category) were converted to weight using box weights declared in logbooks or measured by observers. Distant-water fleets operating in the AFZ were also monitored by surveillance and weekly radio reports. There was a good correspondence between these sources of information and fishing activities reported by observers and logbooks

(Ramm, unpubl.), and all logbooks were assumed to be recovered. Further, logbook data quality were good, with only 0.2% of effort data missing, and 93.5% of catch data reported by commercial categories. Thus no corrections were applied to the data.

Catch-per-unit-effort (CPUE) for each commercial category was standardized by fleet, zone and year using annual catch-and-effort data (1972-1990) fitted to the multiple linear regression model

$$\log(U_{ijt}) = \log(U_{111}) + \log(\alpha_i) + \log(\beta_j) + \log(\gamma_t) + \varepsilon_{ijt},$$

where U_{ijt} is CPUE for fleet i in zone j during year t, U_{111} is CPUE for fleet 1 in zone 1 during year 1, α_i is relative fishing power of fleet i, β_j is relative abundance in zone j, γ_t is relative abundance in year t, and ε_{ijt} is an error term with a mean of zero and a constant variance (e.g., Hilborn and Walters, 1992). Standardized CPUE and effort for each zone were fitted, by multiple linear regression, into Walters and Hilborn's (1976) difference equation

$$(U_{t+1}/U_t) - 1 = r - (r/kq)U_t - qE_t,$$

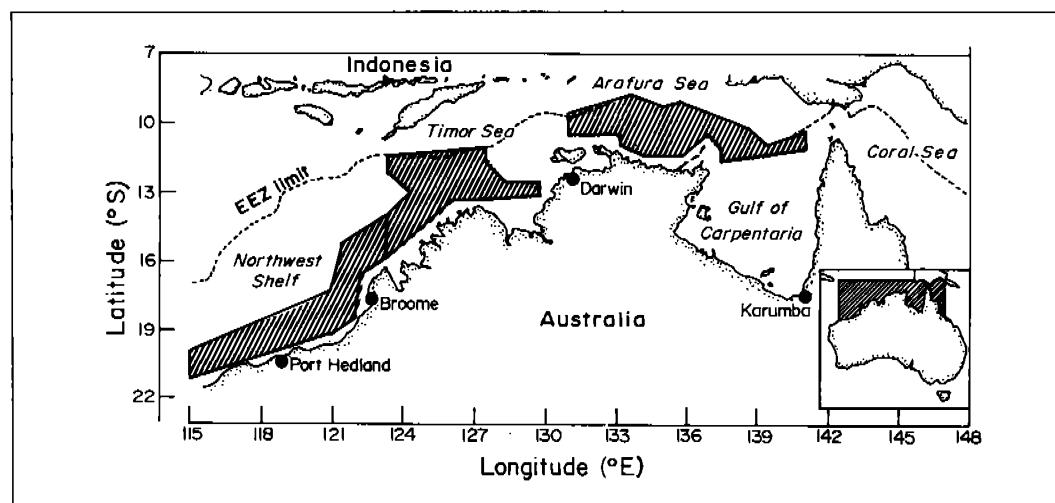


Fig. 1. Fishery management zones (shaded) in Australia's northern trawl fishery: Northwest Shelf (115-123°E), Timor Sea (123-131°E) and Arafura Sea (131-141°E). [Zonas de manejo (área sombreada) de la pesquería de arrastre del norte de Australia: Plataforma Nororiental (115-123°E), Mar de Timor (123-131°E) y Mar Arafura (131-141°E).]

where U_t and U_{t+1} are standardized CPUE during years t and $t+1$, respectively, E_t is standardized effort during year t , r is intrinsic population growth rate, q is catchability, and k is carrying capacity. Alternative fits using Polovina's (1989) extension of this model, assuming an identical intrinsic population growth rate r among zones and a time-series method (Hilborn and Walters 1992) resulted in little improvement in goodness-of-fit.

Results

Taiwanese distant-water pair trawlers (length: 36-42 m, gross tonnage: 280-350 t) dominated the fishery with effort >30 000 h·year⁻¹ during 1973-1986 (Table

1; Edwards 1983; Sainsbury 1991) mostly on the Northwest Shelf between 116-119°E and 19-21°S, and Arafura Sea between 136-138°E and 9-11°S (Fig. 2a). Thai stern trawlers (26-42 m, 115-350 t) fished in the Arafura Sea during 1985-1990 with effort >30 000 h·year⁻¹ during 1988-1990, mostly between 133-137°E and 10-11°S (Table 1, Fig. 2b). Another Chinese pair trawler fleet, from Zhejiang Province, fished on the Northwest Shelf and in the Timor Sea during 1989 with a total effort of 6 251 hours, and a fledgling Australian stern trawl fleet has operated sporadically in the Arafura Sea for a total of 2 793 hours during 1987-1990 (Table 1).

Taiwanese trawlers generally fished on the Northwest Shelf (depth fished: 50-80 m)

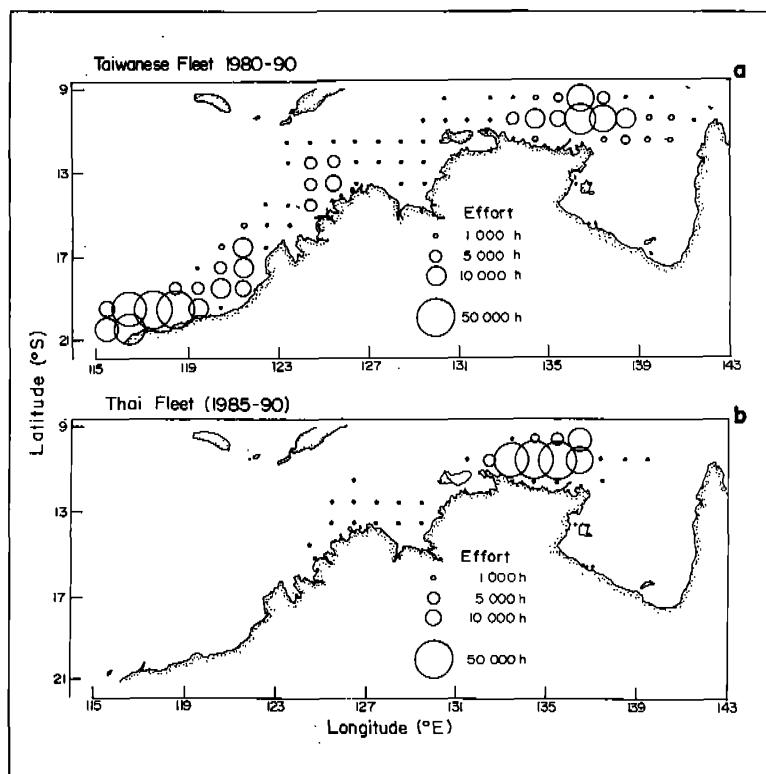


Fig. 2. Total fishing effort, by degree grid, for (a) Taiwanese and (b) Thai fleets in Australia's northern trawl fishery during 1980-1990. [Esfuerzo de pesca total, por cuadrante de un grado, para las flotas de (a) Taiwan y (b) Thallandia, de la pesquería de arrastre del norte de Australia durante 1980-1990.]

Table 1. Total number of licensed trawlers and fishing effort (h) in Australia's northern trawl fishery during 1980-1990.
[Número total de arrastreros con licencia y esfuerzo de pesca (h) de la pesquería de arrastre del norte de Australia durante 1980-1990.]

Fleet	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990
Number of licensed trawlers											
Australian	0	0	0	0	0	0	0	2	2	8	3
Thai	0	0	0	0	0	3	7	7	13	14	11
Taiwanese	104	72	72	72	80	64	44	22	18	12	4
Zhejiang	0	0	0	0	0	0	0	0	0	8	0
Effort on Northwest Shelf											
Australian	0	0	0	0	0	0	0	0	0	0	0
Thai	0	0	0	0	0	0	0	0	0	0	0
Taiwanese	36 448	31 379	38 996	29 891	38 546	38 022	12 203	4 960	7 153	10 139	665
Zhejiang	0	0	0	0	0	0	0	0	0	1 974	0
Effort in Timor Sea											
Australian	0	0	0	0	0	0	0	0	0	0	0
Thai	0	0	0	0	0	0	27	0	103	389	0
Taiwanese	2 242	1 944	1 687	2 672	6 959	6 188	2 991	1 449	569	981	367
Zhejiang	0	0	0	0	0	0	0	0	0	4 277	0
Effort in Arafura Sea											
Australian	0	0	0	0	0	0	0	58	1 399	0	1 336
Thai	0	0	0	0	0	2 597	17 924	25 672	31 413	61 317	41 739
Taiwanese	17 959	9 881	13 948	28 219	29 935	7 173	16 862	3 941	2 610	22	1 470
Zhejiang	0	0	0	0	0	0	0	0	0	0	0

during April-August and in the Timor (60-90 m) and Arafura (40-75 m) Seas during October-March (Fig. 3). Trip and tow duration averaged 59.1 days ($SE=1.3$ day, $n=447$) and 2.2 h ($SE<0.01$ hours, $n=186$ 278), respectively. Interestingly, fishing was conducted throughout the day on the Northwest Shelf and Timor Sea ($7 \text{ tows} \cdot \text{day}^{-1}$), and from dawn to dusk in the Arafura Sea (0530-1930 hours, $5 \text{ tows} \cdot \text{day}^{-1}$). In contrast, Thai trawlers fished throughout the day ($6 \text{ tows} \cdot \text{day}^{-1}$) and year in the Arafura Sea (50-75 m), with a mean trip and tow duration of 27.6 days ($SE=0.8$ day, $n=319$) and 4.0 hours ($SE<0.01$ hours, $n=45,709$), respectively.

Twenty-four commercial categories, representing at least 69 species of fish, squid and cuttlefish, were identified from observer data (Appendix 2). Most categories were dominated by single species such as *Lethrinus lentjan* (Lethrinidae), *Lutjanus malabaricus* (red Lutjanidae), *Lutjanus vittus* (small Lutjanidae), *Nemipterus furcosus*

(Nemipteridae), *Pristipomoides multidens* (goldband Lutjanidae), *Psenopsis humerosa* (butterfish), *Saurida undosquamis* (Synodontidae) and *Trichiurus lepturus* (Trichiuridae). Total retained catch for all fleets during 1972-1990 was approximately 229 000 t on the Northwest Shelf, 47 000 t in the Timor Sea and 126 000 t in the Arafura Sea (Table 2a-c, Appendix 1). Nemipteridae was the dominant category on the Northwest Shelf ($8\ 377 \text{ t} \cdot \text{year}^{-1}$), while red Lutjanidae dominated catches in the Timor ($1\ 091 \text{ t} \cdot \text{year}^{-1}$) and Arafura Seas ($4\ 191 \text{ t} \cdot \text{year}^{-1}$). Other important categories included Lethrinidae ($4\ 076 \text{ t} \cdot \text{year}^{-1}$) and Synodontidae ($4\ 276 \text{ t} \cdot \text{year}^{-1}$) on the Northwest Shelf, Carangidae ($1\ 528 \text{ t} \cdot \text{year}^{-1}$) in the Timor Sea, and butterfish ($3\ 057 \text{ t} \cdot \text{year}^{-1}$) and Nemipteridae ($2\ 811 \text{ t} \cdot \text{year}^{-1}$) in the Arafura Sea.

Observer data indicated that the proportion of the total catch retained by trawlers varied little between fleets and zones, with Taiwanese vessels retaining 67%, by weight,

of the catch ($SE=12\%$, $n=61$) on the Northwest Shelf and 53% ($SE=14\%$, $n=101$) in the Arafura Sea, and Thai trawlers retaining 63% ($SE=16\%$, $n=109$) in the Arafura Sea. However, marked differences existed in discard practices, at the category level, between fleets particularly in the Arafura Sea where butterfish, Trichiuridae and Rachycentridae were retained by Taiwanese trawlers but discarded by Thai vessels, while Ariidae were retained by Thai vessels but discarded by Taiwanese vessels (Table 2a-c, Fig.4).

Standardization of CPUE revealed marked variation in fishing power between fleets, zones and years (Table 3). The fishing power of Thai

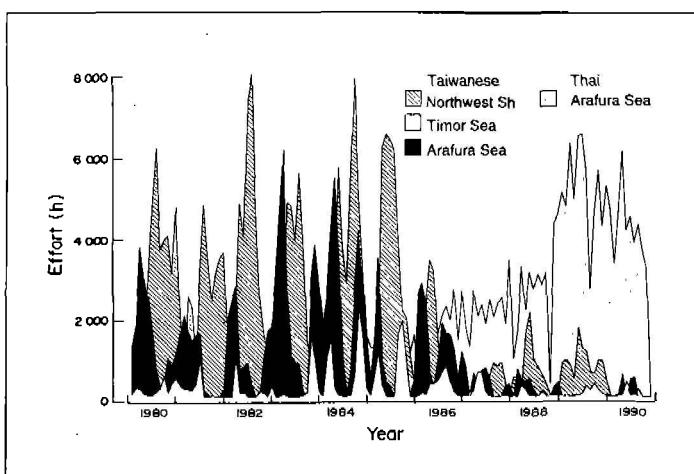


Fig. 3. Monthly effort for Taiwanese and Thai fleets in Australia's northern trawl fishery during 1980-1990. Taiwanese fleet on the Northwest Shelf (cross hatch), and in the Timor (white) and Arafura Seas (black); Thai fleet in the Arafura Sea (stipple). [Esfuerzo mensual para las flotas de Taiwan y Thal de la pesquería de arrastre del norte de Australia durante 1980-1990. La flota de Taiwan de la plataforma nororiental (achurada), y en los mares de Timor (blanco) y Arafura (negro); y la flota de Thal en el mar Arafura (stipple).]

Table 2. Retained catch (t) by fleet in Australia's northern trawl fishery during 1980-1990 on (a) Northwest Shelf, (b) Timor Sea and (c) Arafura Sea. Data by category inadequate for Thai and Australian fleets in the Arafura Sea during 1985-1986 and 1987-1988, respectively. [Captura retenida (t) por flota de la pesquería de arrastre del norte de Australia durante 1980-90 en: (a) Plataforma Nororiental; (b) Mar de Timor; (c) Mar Arafura. Datos por categoría Inadecuados para las flotas Thal y Australiana en el mar Arafura durante 1985-1986 y 1987-1988, respectivamente.]

(a) Catch (t) on Northwest Shelf [(a) Captura (t) en la plataforma nororiental]

Category	Taiwanese										Zhejiang	
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1989
Ariidae	35	18	32	0	1	0	0	0	0	0	0	0
Butterfish	2	2	2	2	0	4	2	0	1	1	0	1
Carangidae	820	746	842	469	485	578	128	45	66	45	1	13
Formionidae	58	165	45	28	38	40	5	2	1	28	0	11
Haemulidae	223	100	149	133	131	126	19	9	10	139	0	122
Lethrinidae	1 729	1 164	1 855	1 114	944	1 004	226	138	186	410	19	954
<i>Loiffo</i> spp.	42	67	133	50	62	78	14	4	7	9	1	0
Lutjanidae small	546	580	917	680	832	761	136	69	197	234	25	15
Lutjanidae goldband	172	117	253	94	367	260	60	13	101	170	20	12
Lutjanidae red	636	409	717	364	411	561	95	39	130	284	22	141
Mullidae	484	654	784	652	678	696	129	87	53	93	12	5
Nemipteridae	3 665	4 008	3 884	3 634	3 853	3 115	829	291	677	563	48	18
Priacanthidae	306	316	303	153	173	216	47	37	51	56	6	4
Rachycentridae	139	171	51	61	2	20	39	0	12	9	0	0
Sciaenidae	6	9	2	1	4	3	0	0	0	1	0	0
Scombridae	13	1	42	1	3	9	1	1	1	3	0	7
Sepiidae	285	422	821	609	536	413	79	29	70	104	3	0
Serranidae	261	109	272	238	214	208	29	50	81	102	16	17
Sharks and rays	298	264	400	246	284	224	52	19	35	52	2	13
Sparidae	247	136	180	125	115	126	39	13	75	61	0	2
Sphyraenidae	103	70	124	44	50	49	14	1	5	2	0	0
Synodontidae	887	739	558	387	557	651	271	104	324	118	3	7
Trichiuridae	13	18	5	0	0	2	0	1	0	0	0	0
Mixed taxa	1 610	813	1 048	661	712	864	165	45	132	136	25	236
Total retained catch	12 579	11 098	13 418	9 745	10 451	10 007	2 378	998	2 212	2 618	201	1 575

(continued)

Table 2. (continued)(b) **Catch (t) in Timor Sea [(/b) *Captura (t) en el mar de Timor*]**

Category	Taiwanese										Zhejiang	1989	1989
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990		
Ariidae	3	1	0	0	0	0	0	0	0	0	0	0	0
Butterfish	0	4	0	4	10	7	1	6	1	0	0	12	0
Carangidae	74	94	25	76	120	61	5	8	12	3	1	3	1
Formionidae	8	37	0	0	3	22	24	1	0	1	0	6	0
Haemulidae	34	94	31	136	201	54	25	7	12	24	0	196	9
Lethrinidae	88	41	57	138	250	172	56	36	38	64	15	228	2
<i>Loligo</i> spp.	2	3	0	0	0	2	1	5	0	1	1	0	0
Lutjanidae small	36	38	36	117	168	139	24	33	19	7	6	219	2
Lutjanidae goldband	27	37	139	146	446	336	78	124	29	46	13	237	1
Lutjanidae red	100	100	153	202	578	382	69	98	27	140	28	631	18
Mullidae	1	2	5	11	38	39	6	14	7	1	1	2	0
Nemipteridae	103	78	22	120	172	182	79	24	39	12	20	2	1
Priacanthidae	26	18	17	25	66	62	21	6	5	4	3	6	0
Rachycentridae	13	2	1	3	1	9	0	0	2	0	0	0	0
Sciaenidae	0	0	0	26	57	1	0	0	0	0	0	0	0
Scombridae	6	0	0	0	8	1	0	1	2	1	0	4	0
Sepiidae	22	8	6	29	76	68	21	12	5	6	2	5	1
Serranidae	11	6	6	25	30	29	2	8	3	9	2	24	2
Sharks and rays	63	25	9	25	91	38	11	11	5	17	7	38	0
Sparidae	2	15	5	22	20	22	4	3	0	1	0	0	0
Sphyraenidae	15	5	3	3	14	3	0	1	0	0	0	0	0
Synodontidae	23	47	9	2	108	118	38	2	4	3	0	17	0
Trichiuridae	6	1	3	1	1	1	0	0	0	0	0	0	0
Mixed taxa	307	109	50	90	224	248	56	52	13	15	13	229	0
Total retained catch	971	765	577	1 201	2 684	1 995	524	450	225	354	114	1 834	40

Table 2. (continued)**(c) Catch (t) in Arafura Sea^a [(c) Captura (t) en el Mar Arafura]**

Category	Taiwanese												Thai					Australian	
	1980	1981	1982	1983	1984	1985	1986	1987	1988	1989	1990	1985	1986	1987	1988	1989	1990	1990	
Ariidae	23	2	13	8	15	6	0	0	0	0	0	0	0	187	248	247	189	0	
Butterfish	197	142	955	3057	323	286	894	61	82	0	37	0	0	0	0	0	0	0	
Carangidae	607	329	568	651	833	179	207	89	6	0	3	0	0	152	335	663	429	0	
Formionidae	199	85	76	98	52	32	96	35	15	0	29	0	0	46	135	255	91	0	
Haemulidae	205	90	189	258	447	80	134	37	8	0	0	0	0	139	208	385	295	2	
Lethrinidae	105	65	86	166	332	57	175	71	34	0	30	0	0	188	248	469	272	11	
<i>Loi/lo</i> spp.	329	418	735	108	98	23	13	2	1	0	0	0	0	8	5	13	11	0	
Lutjanidae small	27	61	148	94	283	82	114	44	17	0	16	0	0	121	141	224	180	2	
Lutjanidae goldband	35	8	13	128	78	16	35	14	5	0	14	0	0	39	67	122	122	1	
Lutjanidae red	978	758	923	2095	2965	721	1274	384	257	3	164	0	0	1 394	2 184	4 188	2 550	222	
Mullidae	42	60	2	5	2	3	7	2	1	0	1	0	0	14	12	12	10	0	
Nemipteridae	1 015	585	609	694	390	191	436	144	95	0	20	0	0	199	273	268	225	0	
Priacanthidae	71	13	12	3	5	2	6	3	0	0	0	0	0	21	43	98	56	0	
Rachycentridae	0	0	0	2	3	2	4	1	0	0	0	0	0	0	0	0	0	0	
Sciaenidae	39	23	122	69	39	30	22	0	10	0	0	0	0	7	15	12	2	0	
Scombridae	132	64	103	86	152	8	17	2	7	0	1	0	0	56	41	66	58	1	
Sepiidae	49	34	82	106	109	30	39	14	8	0	3	0	0	65	51	73	72	0	
Serranidae	17	5	11	21	47	6	14	4	1	0	4	0	0	33	47	96	58	1	
Sharks and rays	338	284	411	612	973	274	399	98	60	0	29	0	0	21	38	116	150	6	
Sparidae	19	29	3	2	26	2	14	5	4	0	3	0	0	2	13	34	40	1	
Sphyraenidae	57	19	25	15	37	7	15	8	12	0	0	0	0	11	7	16	17	0	
Synodontidae	62	95	50	17	8	26	31	9	4	0	4	0	0	67	39	103	134	0	
Trichiuridae	1 005	390	31	89	16	3	0	0	25	0	0	0	0	0	0	0	0	0	
Mixed taxa	841	222	295	620	614	234	346	100	56	0	42	0	0	78	120	327	347	8	
Total retained catch	6 392	3 782	5 464	9 004	7 848	2 299	4 293	1 126	710	4	398	337	2 691	3 499	4 290	7 787	5 308	249	

^a Data by category inadequate for Thal fleet during 1985-1986, and Australian fleet during 1987-1988.

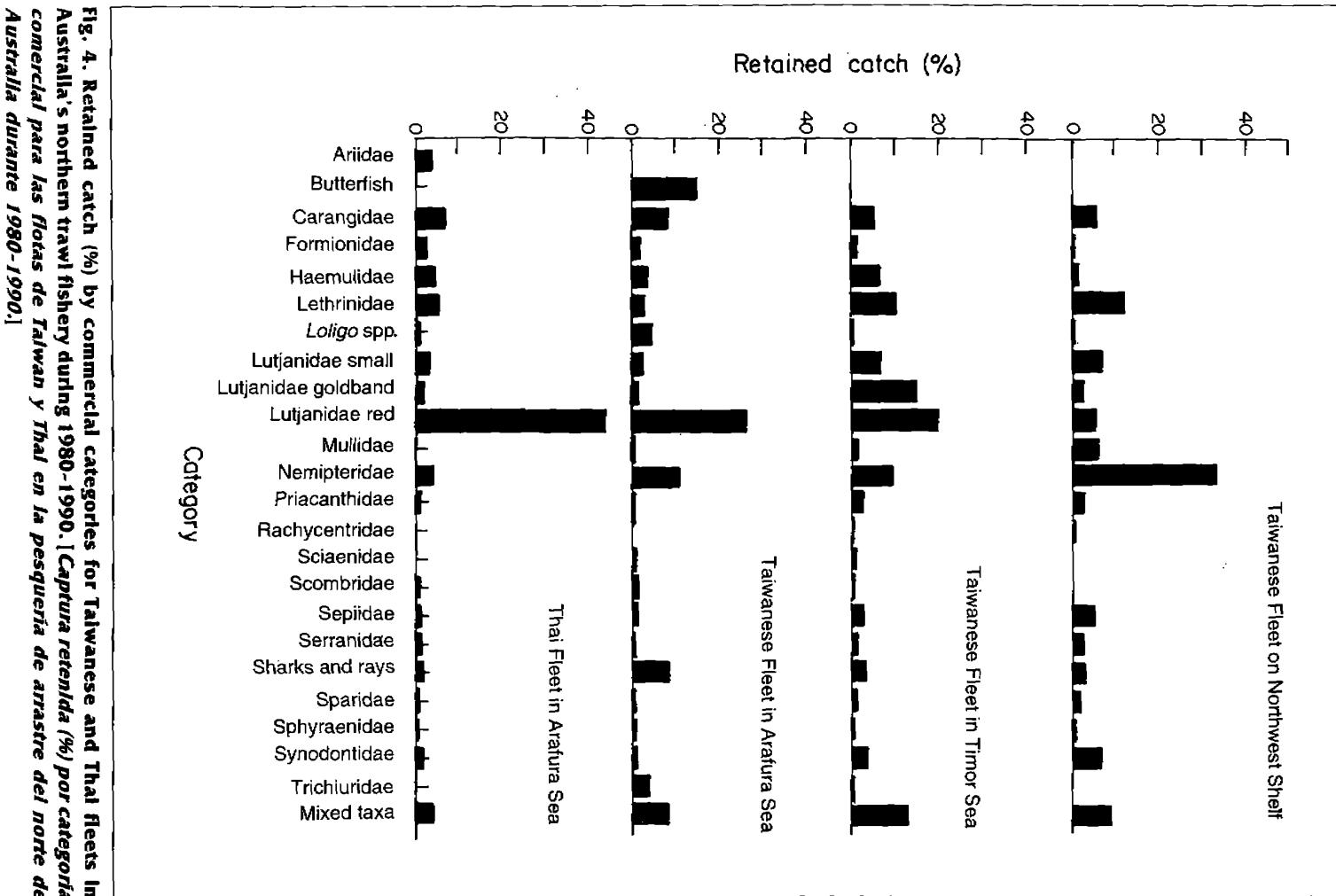


Fig. 4. Retained catch (%) by commercial categories for Taiwanese and Thai fleets in Australia's northern trawl fishery during 1980-1990. [Captura retenida (%) por categoría comercial para las flotas de Taiwán y Tailandia en la pesquería de arrastre del norte de Australia durante 1980-1990.]

Table 3. Standardization of CPUE ($\text{kg} \cdot \text{h}^{-1}$) for Taiwanese and Thal fleets in Australia's northern trawl fishery during 1972-1990.
 Annual catch and effort data were fitted to $\log(U_{ijt}) = \log(U_{111}) + \log(\alpha_1) + \log(\beta_1) + \log(\gamma_t) + \varepsilon_{ijt}$, where U_{ijt} is CPUE for fleet i in zone j during year t , U_{111} is CPUE for the Taiwanese fleet on the Northwest Shelf during 1972, α_1 is relative fishing power of the Thal fleet, β_1 is relative abundance in the Timor (2) and Arafura (3) Seas, and γ_t is relative annual abundance during 1973-1990, and ε_{ijt} is an error term. Annual catch and effort during 1972-1979 were based on Edwards (1983) and Sainsbury (1991; unpubl.). [CPUE estandarizada ($\text{kg} \cdot \text{h}^{-1}$) para las flotas de Taiwan y Thal en la pesquería de arrastre al Norte de Australia durante 1972-1990. Datos anuales de captura y esfuerzo fueron calculados de $\log(U_{ijt}) = \log(U_{111}) + \log(\alpha_1) + \log(\beta_1) + \log(\gamma_t) + \varepsilon_{ijt}$, donde U_{ijt} es la CPUE para la flota i en la zona j durante el año t . U_{111} es la CPUE para la flota Taiwanesa sobre la plataforma nororiental durante 1972, α_1 es el poder de pesca relativo de la flota Thal y β_1 es la abundancia relativa en el mar de Timor (2) y Arafura (3), y γ_t es la abundancia anual relativa durante 1973-1990, y ε_{ijt} es un término de error. Captura y esfuerzo anuales durante 1972-1979 fueron basados en Edwards (1983) Sainsbury (1992; datos no publicados).]

Category	Regression						Standardization Parameters																		
	F	P	Adj r ²	U_{111}	α_1	β_1	γ_{13}	γ_{14}	γ_{15}	γ_{16}	γ_{17}	γ_{18}	γ_{19}	γ_{10}	γ_{81}	γ_{82}	γ_{83}	γ_{84}	γ_{85}	γ_{86}	γ_{87}	γ_{88}	γ_{89}	γ_{90}	
Ariidae	8.038	0.056	0.847	1.02	5.63	1.14	0.79	1.00	1.00	1.00	1.00	1.00	1.00	1.22	0.40	0.94	0.38	0.62	1.00	1.00	1.62	1.76	0.89	1.00	
Butterfish	17.920	0.000	0.894	0.09	1.00	12.97	268.88	1.00	1.00	1.00	1.00	1.00	1.00	0.68	1.02	1.70	1.78	0.70	1.15	1.03	1.44	1.25	1.07	1.00	
Carangidae	3.788	0.001	0.535	36.02	1.47	1.54	1.67	0.36	1.27	0.54	1.14	0.92	1.07	0.51	0.59	0.68	0.48	0.44	0.37	0.32	0.12	0.16	0.15	0.09	0.05
Formionidae	2.813	0.024	0.440	1.33	0.57	2.35	6.55	1.00	1.00	1.00	1.00	1.00	1.00	1.21	2.89	0.75	0.52	0.27	0.79	0.80	0.40	0.35	0.83	1.00	
Haemulidae	4.938	0.001	0.615	3.30	0.75	5.31	2.89	1.00	1.00	1.00	1.00	1.00	1.00	1.24	1.37	1.20	1.55	1.39	0.84	0.58	0.58	0.63	1.73	1.00	
Lethrinidae	7.300	0.000	0.703	39.09	0.72	1.19	0.24	1.13	1.12	0.91	1.02	0.85	1.12	0.67	0.86	0.67	0.84	0.87	0.83	0.70	0.60	0.94	1.11	1.17	1.08
Loligo spp.	3.101	0.015	0.477	1.82	0.10	0.77	2.71	1.00	1.00	1.00	1.00	1.00	1.00	1.16	2.19	4.46	0.85	0.77	0.54	0.27	0.51	0.27	0.53	1.00	
Lutjanidae small	4.890	0.000	0.593	24.58	0.76	1.24	0.27	1.12	1.07	0.80	0.26	0.83	0.85	0.48	0.42	0.77	1.02	0.87	1.00	1.01	0.50	0.90	1.02	0.54	1.03
Lutjanidae goldband	13.463	0.000	0.822	16.39	0.57	5.95	0.35	1.00	1.00	1.00	1.00	1.00	1.00	0.23	0.18	0.38	0.44	0.56	0.45	0.31	0.45	0.56	0.67	1.00	
Lutjanidae red	6.496	0.000	0.658	22.78	0.70	3.75	4.12	0.66	0.80	0.67	0.27	0.51	0.60	0.38	0.61	0.65	0.85	0.72	0.78	0.80	0.42	0.70	0.84	1.33	1.09
Mullidae	6.261	0.000	0.661	15.81	0.64	0.19	0.03	1.00	1.00	1.00	1.00	1.00	1.00	0.82	1.78	0.64	0.93	0.75	1.27	0.72	1.58	1.21	0.50	1.00	
Nemipteridae	7.430	0.000	0.696	147.46	0.21	0.47	0.50	1.40	1.25	0.86	0.67	0.88	0.68	0.38	0.70	0.74	0.42	0.56	0.35	0.44	0.39	0.39	0.64	0.26	0.39
Priacanthidae	7.074	0.000	0.723	10.83	2.31	1.21	0.08	0.23	1.22	0.48	0.39	0.91	0.96	0.33	1.44	0.98	0.82	0.33	0.40	0.51	0.44	0.52	0.66	0.49	0.68
Rachycentridae	4.243	0.019	0.641	0.90	1.00	0.82	0.19	1.00	1.00	1.00	1.00	1.00	1.00	5.76	2.85	1.08	1.24	0.20	1.24	2.01	1.71	2.99	1.00	1.00	
Sciaenidae	2.555	0.110	0.496	0.10	0.12	18.68	17.96	1.00	1.00	1.00	1.00	1.00	1.00	1.63	2.04	2.29	2.75	1.53	0.66	0.75	1.44	2.30	1.00	1.00	
Scombridae	5.775	0.001	0.697	0.10	0.94	5.40	10.01	1.00	1.00	1.00	1.00	1.00	1.00	5.19	6.38	8.86	2.94	2.14	0.92	0.98	1.29	2.17	1.83	1.00	
Sepiidae	8.549	0.000	0.737	6.51	0.63	0.72	0.32	1.00	1.00	1.00	1.00	1.00	1.00	1.48	1.43	1.92	2.37	2.05	2.00	1.18	1.51	1.51	1.24	1.00	
Serranidae	4.824	0.000	0.612	3.33	1.07	0.81	0.15	1.14	0.95	1.48	4.70	1.85	1.41	1.41	1.92	1.07	1.65	2.28	2.05	1.67	0.67	2.35	1.98	3.15	3.80
Sharks and rays	9.805	0.000	0.766	6.55	0.07	1.72	4.37	1.00	1.00	1.00	1.00	1.00	1.00	1.27	1.14	0.91	0.93	1.14	0.87	0.56	0.61	0.74	1.06	1.00	
Sparidae	3.696	0.005	0.523	15.21	0.39	0.63	0.15	1.00	1.00	1.00	1.00	1.00	1.00	0.27	0.66	0.20	0.22	0.29	0.22	0.22	0.22	0.59	0.30	1.00	
Sphyraenidae	2.627	0.035	0.422	0.83	0.36	1.25	1.32	1.00	1.00	1.00	1.00	1.00	1.00	3.97	2.24	2.21	0.95	1.48	0.88	1.04	0.73	1.20	0.42	1.00	
Synodontidae	7.498	0.000	0.702	66.20	1.07	0.51	0.18	1.26	1.77	1.15	1.49	1.03	0.75	0.62	0.32	0.59	0.22	0.06	0.14	0.35	0.26	0.15	0.20	0.13	0.15
Trichiuridae	5.959	0.010	0.724	0.33	1.00	3.92	28.88	1.00	1.00	1.00	1.00	1.00	1.00	2.44	1.42	0.46	0.32	0.06	0.12	1.00	0.60	1.00	1.00	1.00	
Mixed taxa	15.117	0.000	0.840	27.85	0.24	1.65	1.16	1.00	1.00	1.00	1.00	1.00	1.00	1.90	0.93	0.74	0.73	0.67	0.90	0.50	0.53	0.57	0.48	1.00	
Total retained catch	8.896	0.000	0.728	434.61	0.56	1.38	0.98	1.10	1.20	0.99	0.97	0.99	0.91	0.62	0.78	0.78	0.75	0.75	0.75	0.63	0.61	0.47	0.55	0.64	0.53

trawlers, relative to Taiwanese trawlers, ranged from 0.10 for *Loligo* spp. to 5.63 for Ariidae, with an overall value of 0.56. Geographic variations in relative abundances were also marked, with categories such as Ariidae, Carangidae and Sphyraenidae occurring throughout the fishery, Mullidae and Nemipteridae being predominant on the Northwest Shelf, Haemulidae and goldband Lutjanidae occurring mostly in the Timor Sea, and butterfish and Trichiuridae being predominant in the Arafura Sea. Coefficients of relative annual abundance varied widely for many categories during 1980–1982. Estimation of MSY from annual catch and effort data fitted to Walters and Hilborn's (1976) difference equation was attempted for all categories and zones, but was obtained only for about 24 of the possible 75 combinations of category and zone (Table 4). MSY was estimated for 9 commercial categories (e.g., Lethrinidae 5 288 t·year⁻¹, red Lutjanidae 1 528 t·year⁻¹, Nemipteridae 4 520 t·year⁻¹) on the Northwest Shelf, 12 categories (e.g., Lethrinidae 1 168 t·year⁻¹, red Lutjanidae 750 t·year⁻¹, Nemipteridae 377 t·year⁻¹) in the Timor Sea, and butterfish (3 018 t·year⁻¹) in the Arafura Sea.

Discussion

Although only 69 species of fish were identified from observer data, many more species are taken in Australia's northern trawl fishery. Sainsbury et al. (1984) reported 531 species commonly taken in trawls between 30 and 150 m on the Northwest Shelf and Timor and Arafura Seas. Russell and Houston (1989) concluded that 231 species of fish were caught by groundfish trawlers in the Arafura Sea, of which about 100 species were retained, with 23 species accounting for 70% of total catch by weight. While most species are widespread within the Indo-Pacific, distinct changes in fish fauna occur near 123°E (Sainsbury 1991) and 132°E (Ramm et al. 1990). Thus Nemipteridae was

the dominant catch component on the Northwest Shelf and a major commercial category at other grounds, while Lethrinidae and Synodontidae were important on the Northwest Shelf, red Lutjanidae dominated catches in the Timor and Arafura Seas, Carangidae was important in the Timor Sea, and butterfish occurred predominantly in the Arafura Sea.

MSY estimates for Lethrinidae, red Lutjanidae and Nemipteridae on the Northwest Shelf are within the range of values determined by Sainsbury (1987, 1991) for various model scenarios. Whilst there are previous estimates of sustainable yield for groundfish in the Timor and Arafura Seas (e.g., Edwards 1983; Dalzell and Pauly 1989), none have previously been attempted for individual species or species groups. Our analyses indicated that the majority of available fishery data was inadequate for use in stock assessment, particularly in the Arafura Sea. Many factors contributed to this problem, including long-term changes in discard practice, targeting and management regimes. Edwards (1983) reported low logbook recovery rates prior to the declaration of the AFZ, and complete recovery thereafter. He also reported that effort increased in the Arafura Sea during 1978–1979 due to targeting of *Loligo* spp. Other operational changes included an increase in minimum codend mesh size, from about 45 mm (stretched mesh) prior to 1979, through 60 mm during 1979–1989, to 90 mm thereafter (Jernakoff and Sainsbury 1990). Sainsbury and Ramm (1988 in Jernakoff and Sainsbury 1990) identified limitations in the observer data and concluded that available data were insufficient to interpret logbook data and estimate sustainable yields. They recommended that quality of data on fishing operations, retained catch and total catch, species composition of retained and discarded catch and length-frequency distributions of key species be improved for viable stock assessment. Finally, assessments for the Arafura Sea also require fishery

Table 4. Annual catch and effort in Australia's northern trawl fishery during 1972-1990 fitted to Walters and Hilborn's (1976) difference equation $(U_{t+1}/U_t) - 1 = r - (r/kq)U_t - qE_t$, where U_t and U_{t+1} are CPUE ($\text{kg} \cdot \text{h}^{-1}$) during years t and $t+1$ respectively, E_t is effort (h) during year t , r is intrinsic population growth rate, q is catchability (h^{-1}), k is carrying capacity (t) and MSY is annual maximum sustainable yield ($\text{t} \cdot \text{year}^{-1}$). Standardized data were fitted by multiple linear regression, and annual catch and effort during 1972-1979 were based on Edwards (1983) and Sainsbury (1991; unpubl.). [Captura y esfuerzo anual de la pesquería de arrastre del Norte de Australia durante 1972-90 calculados de las ecuaciones en diferencias de Walters y Hilborn (1976) $(U_{t+1}/U_t) - 1 = r - (r/kq)U_t - qE_t$, donde U_t y U_{t+1} son CPUE ($\text{kg} \cdot \text{h}^{-1}$) durante el año t y $t+1$, respectivamente. E_t es el esfuerzo (h) durante el año t , r es la tasa intrínseca de crecimiento poblacional, q es capturabilidad (h^{-1}), k es la capacidad de carga (t) y MSY es el rendimiento máximo sostenible anual ($\text{t} \cdot \text{año}^{-1}$). Los datos estandarizados fueron calculados por regresión lineal múltiple, y la captura y el esfuerzo anual durante 1972-79 estuvieron basados en Edwards (1983) y Sainsbury (1991; datos no publicados).]

Category	Northwest Shelf							Timor Sea							Arafura Sea							
	F	P	Adj·R ²	r	q*	k	MSY	F	P	Adj·R ²	r	q*	k	MSY	F	P	Adj·R ²	r	q*	k	MSY	
Arilidae	0.000	0.000	0.000	2.35	0.0000000	0	0	0.000	0.000	0.000	-0.67	0.0000000	0	0	0.413	0.682	-0.202	0.46	0.0000044	1422	162	
Butterfish	0.586	0.631	-0.261	1.16	0.0000065	24		7	13.775	0.068	0.865	1.65	0.0000162	98	41	6.656	0.039	0.618	1.21	0.0000038	9977	3018
Carangidae	5.026	0.021	0.321	-0.61	-0.00000281	1893	-287	0.489	0.623	-0.064	0.31	-0.0000129	-2061	159	0.260	0.774	-0.195	0.18	0.0000048	4590	210	
Formionidae	1.516	0.293	0.114	0.30	-0.0000126	-60	-4	47.690	0.102	0.969	3.32	0.0002930	33	27	0.972	0.424	-0.006	0.18	-0.0000112	-493	-22	
Haemulidae	0.991	0.425	-0.002	0.90	0.0000101	617	139	1.467	0.303	0.105	0.79	0.0001240	444	88	1.636	0.261	0.124	0.09	-0.0000168	-118	-3	
Leiithrididae	4.056	0.039	0.264	0.76	0.0000014	27 824	5 288	3.988	0.041	0.260	0.74	0.0000074	6 287	1 168	5.455	0.021	0.389	0.94	0.0000017	4883	1153	
Loligo spp	1.707	0.249	0.136	0.96	0.0000157	436	105	0.511	0.703	-0.484	2.85	0.00008820	5	3	6.671	0.024	0.558	-1.01	-0.0000369	1026	-259	
Lutj. small	10.400	0.002	0.525	1.71	-0.0000017	-12 360	-5 294	20.665	0.000	0.698	1.99	0.0000400	769	383	9.784	0.003	0.557	1.58	-0.0000063	-767	-303	
Lutj. goldband	1.230	0.349	0.049	1.04	0.0000119	1170	303	1.864	0.224	0.161	0.69	0.0000795	1 692	293	1.299	0.331	0.062	0.68	-0.0000050	-415	-70	
Lutjanidae red	5.288	0.017	0.323	1.01	0.0000034	6 068	1 528	6.972	0.007	0.399	1.03	0.0000268	2 915	750	6.248	0.010	0.368	9.52	-0.0000759	-742	-1767	
Mullidae	7.440	0.019	0.589	1.95	0.0000051	3 954	1 932	6.989	0.022	0.571	1.76	0.0000146	254	112	6.980	0.022	0.571	1.02	-0.0000073	-53	-14	
Nemipteridae	3.819	0.044	0.238	1.91	0.0000191	9 477	4 520	2.598	0.105	0.151	0.45	0.0000187	3 342	377	2.700	0.098	0.159	-0.30	-0.0000153	8 583	-642	
Priacanthidae	4.594	0.026	0.285	1.74	-0.0000044	-1 965	-854	4.704	0.025	0.292	2.08	0.0000182	627	326	1.516	0.284	0.103	0.63	-0.0000089	-75	-12	
Rachycentridae	2.077	0.241	0.264	3.17	0.0000398	114	90	3.547	0.220	0.560	-1.12	-0.0008260	3	-1	9.547	0.223	0.851	-0.45	-0.0000667	5	-1	
Sciaenidae	0.271	0.787	-0.574	-1.00	-0.0000136	-25	6	0.000	0.000	0.000	-0.73	0.0000000	0	0	0.178	0.840	-0.223	0.31	0.0000048	603	47	
Scombridae	0.518	0.620	-0.137	0.25	0.0000026	177	11	0.000	0.000	0.000	2.00	0.0000867	14	7	6.667	0.543	-0.080	0.38	0.0000081	760	71	
Sepiidae	3.472	0.090	0.354	0.52	-0.0000091	-791	-104	0.697	0.529	-0.072	0.29	0.0000230	425	31	0.034	0.966	-0.273	-0.01	0.0000019	-2 568	6	
Serranidae	2.428	0.122	0.144	1.35	0.0000062	1 522	514	2.086	0.159	0.113	1.03	0.0000051	1 367	352	10.408	0.008	0.677	1.36	-0.0000382	-16	-5	
Sharks and rays	2.074	0.196	0.193	0.53	0.0000028	2 595	346	3.241	0.101	0.332	0.46	0.0000559	273	31	1.197	0.357	0.042	-0.75	-0.0000122	-4 649	873	
Sparidae	1.386	0.320	0.088	1.14	0.000019	3 431	978	1.285	0.371	0.087	1.18	0.0000624	73	22	6.064	0.030	0.530	0.44	-0.0000165	-25	-3	
Sphyraenidae	0.979	0.429	-0.005	0.21	-0.0000018	-423	-22	0.777	0.563	-0.126	0.59	0.0000501	47	7	4.399	0.058	0.430	-0.25	-0.0000174	134	-8	
Synodontidae	1.217	0.322	0.023	1.94	0.0000186	5 428	2 635	0.898	0.428	-0.012	0.42	-0.0000125	-2 295	-240	5.953	0.012	0.355	-0.02	-0.0000321	9	0	
Trichiuridae	0.000	0.000	0.000	-1.04	0.0000000	0	0	57.918	0.017	0.966	-1.24	-0.0001770	-40	12	0.281	0.780	-0.561	-0.26	-0.0000159	360	-23	
Mixed taxa	2.065	0.197	0.191	0.57	0.0000032	8 241	1 183	2.056	0.198	0.190	0.57	0.0000210	2 011	286	10.662	0.007	0.682	-0.65	-0.0000206	-19 276	3 142	
Total retained catch	6.448	0.009	0.377	113.24	-0.0004040	-806	-22 814	6.543	0.008	0.381	200.91	-0.0032610	-143	-7182	6.267	0.010	0.369	606.72	0.0079550	62	9421	

*Negative values are meaningless and indicate problems in fitting data to the model (see text).

data for the Indonesian sector, which are presently lacking.

Although the results from this study are generally inconclusive, the analyses have directed recent research on groundfish in the Timor and Arafura Seas (e.g., Blaber et al. 1992). Identification of large uncertainties in interpreting logbook data had led to fishery-independent trawl surveys in the Timor and Arafura Seas between 127 and 137°E (D.C. Ramm, unpubl.) and Gulf of Carpentaria (S.J.M. Blaber, unpubl.), and the development of a project aimed at collating fishery catch and operational data for groundfish fisheries in both Australian and Indonesian sectors of the Arafura Sea (D.C. Ramm and D.J. Staples, unpubl.). Alternative assessments of groundfish stocks are now underway using biomass data from trawl surveys.

Acknowledgements

We gratefully acknowledge AFZ observers, especially Messrs. Bill Anderson, Jeff Wessel, Mick Baron and Phil Schubert, and AFZ fishery manager Dr. Rusty Branford, of the Federal Department of Primary Industries and Energy, for logbook and observer data during 1980-1990. We also thank masters and crew members of trawlers and observer platforms, including Capt. David Tomlinson of *RV Flamingo Bay* (observer platform 1985-1988), for their collaboration in acquiring data. This study was partly funded by grant 86/049 from the Federal Fishing Industry Research and Development Council.

References

- Blaber, S., D. Staples, K. McLoughlin, G. Newton, R. Campbell, D. Brewer, J. Stevens, D. Ramm, R. Buckworth, R. Slack-Smith, N. Hall, G. Johnson, S. Adisukresno, N. Naamin, M. Badrudin and I. Muchsin. 1992. Stock Assessment Working Group Report, Australia-Indonesia Workshop on Arafura Sea Fisheries, 9-13 November 1992, Darwin.
- Chen, S.C., C.H. Chen, T.H. Chi, K.C. Fan, D.C. Liu and R.Y. Tsay. 1979. Demersal fish resources investigation on trawl grounds off the northwest coast of Australia. Bull. Taiwan Fish. Res. Inst. 93 p.
- Dalzell, P. and D. Pauly. 1989. Assessment of the fish resources of southeast Asia, with emphasis on the Banda and Arafura Seas. Neth. J. Sea Res. 24:641-50.
- Edwards, R.R.C. 1983. The Taiwanese pair trawler fishery in tropical Australian waters. Fish. Res. 2:47-60.
- Hilborn, R. and C.J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics and uncertainty. Chapman and Hall, New York.
- Jernakoff, P. and K.J. Sainsbury. 1990. CSIRO's northern demersal finfish stock assessments: 1980-89. Bureau of Rural Resources, Canberra. Information Paper IP/6/90, 169 p.
- Liu, H.-C. 1976. The demersal fish stocks of the waters of north and northwest Australia. Acta Oceanogr. Taiwan 6:128-134.
- Liu, H.-C., H.-L. Lai and S.-Y. Yeh. 1978. General review of demersal fish resources in the Sunda Shelf and the Australian waters. Acta Oceanogr. Taiwan 8:109-140.
- Polovina, J.J. 1989. A system of simultaneous dynamic production and forecast models for multispecies or multiarea applications. Can. J. Fish. Aquat. Sci. 46:961-963.
- Ramm, D.C., P.J. Pender, R.S. Willing and R.C. Buckworth. 1990. Large-scale spatial patterns of abundance within the assemblage of fish caught by prawn trawlers in northern Australian waters. Aust. J. Mar. Freshwat. Res. 41:79-95.
- Russell, B.C. and W. Houston. 1989. Offshore fishes of the Arafura Sea. The Beagle, Records of the Northern Territory Museum of Arts and Sciences 6:69-84.
- Sainsbury, K.J. 1982. The biological management of Australia's multispecies tropical demersal fisheries: a review of problems and some approaches. Aust. CSIRO Mar. Lab. Rep. 147, 16 p.
- Sainsbury, K.J. 1984. Optimal mesh size for tropical multispecies trawl fisheries. J. Cons. CIEM 41:129-39.
- Sainsbury, K.J. 1987. Assessment and management of the demersal fishery on the continental shelf of northwestern Australia, p. 465-503. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers:

- biology and fisheries management. Westview Press, Boulder.
- Sainsbury, K.J. 1988. The ecological basis of multispecies fisheries, and the management of a demersal fishery in tropical Australia, p. 349-82. In J.A. Gulland (ed.) Fish population dynamics: the implications for management (second edition). John Wiley & Sons, Chichester.
- Sainsbury, K.J. 1991. Application of an experimental approach to management of a tropical
- multispecies fishery with highly uncertain dynamics. ICES Mar. Sci. Symp. 193:301-20.
- Sainsbury, K.J., P.S. Kailola and G.G. Leyland. 1984. Continental shelf fishes of Northern and North Western Australia. Clouston & Hall and Peter Pownall Fisheries Information Service, Canberra.
- Walters, C.J. and R. Hilborn. 1976. Adaptive control of fishing systems. J. Fish. Res. Board Can. 33:145-159.

Appendix 1

Effort (h) for the Taiwanese fleet in Australia's northern trawl fishery during 1972-1979 on (a) Northwest Shelf, (b) Timor Sea and (c) Arafura Sea based on Edwards (1983) and Sainsbury (1991; unpubl.). [Esfuerzo (h) para la flota de Taiwan en la pesquería del norte de Australia durante 1972-1979 sobre (a) plataforma noroeste, (b) Mar de Timor, (c) Mar Arafura, basados en Edwards (1983) y Sainsbury (1991); datos no publicados].

Ground	1972	1973	1974	1975	1976	1977	1978	1979
Northwest Shelf	500	64 545	79 860	57 767	46 592	56 413	40 998	33 500
Timor Sea	2 017	1 512	8 673	6 664	5 911	7 063	8 324	8 357
Arafura Sea	17 425	19 334	19 083	14 412	18 208	25 951	29 250	23 544

Retained catch (t) for the Taiwanese fleet in Australia's northern trawl fishery during 1972-1979 on (a) Northwest Shelf, (b) Timor Sea and (c) Arafura Sea based on Edwards (1983) and Sainsbury (1991; unpubl.). Zeros may be missing values. [Captura (ton) obtenida por la flota de Taiwan en la pesquería de arrastre del Norte de Australia durante 1972-1979 sobre (a) plataforma nororiental; (b) Mar de Timor; (c) Mar Arafura, basado en Edwards (1983) y Sainsbury (1991; datos no publicados). Los valores cero pueden ser valores perdidos.]

(a) Catch (t) on Northwest Shelf [(a) Captura (ton) de la plataforma norte]

Category	1972	1973	1974	1975	1976	1977	1978	1979
Ariidae	0	0	0	0	0	0	0	0
Butterfish	0	0	0	0	0	0	0	0
Carangidae	34	866	1 462	685	1 168	1 060	889	595
Formionidae	0	0	0	0	0	0	0	0
Haemulidae	0	0	0	0	0	0	0	0
Lethrinidae	30	4 076	2 653	2 866	1 841	2 000	1 701	754
<i>Loligo</i> spp.	0	0	0	0	0	0	0	0
Lutjanidae small	13	1 762	1 281	1 148	469	777	755	411
Lutjanidae goldband	0	0	0	0	0	0	0	0
Lutjanidae red	21	2 182	1 487	1 107	336	557	596	297
Mullidae	0	0	0	0	0	0	0	0
Nemipteridae	39	8 377	7 935	5 034	4 531	4 518	3 432	2 169
Priacanthidae	12	70	618	369	327	318	392	209
Rachycentridae	0	0	0	0	0	0	0	0
Sciaenidae	0	0	0	0	0	0	0	0
Scombridae	0	0	0	0	0	0	0	0
Sepiidae	0	0	0	0	0	0	0	0
Serranidae	3	374	226	275	168	193	121	156
Sharks and rays	0	0	0	0	0	0	0	0
Sparidae	0	0	0	0	0	0	0	0
Sphyraenidae	0	0	0	0	0	0	0	0
Synodontidae	16	2 711	4 276	3 356	3 062	3 199	1 952	1 937
Trichiuridae	0	0	0	0	0	0	0	0
Total retained catch	273	37 143	31 256	21 289	18 929	19 080	14 488	10 764

(continued)

Appendix 1 (continued)**(b) Catch (t) In Timor Sea [(b) Captura (ton) del Mar de Timor]**

Category	1972	1973	1974	1975	1976	1977	1978	1979
Ariidae	0	0	0	0	0	0	0	0
Butterfish	0	0	0	0	0	0	0	0
Carangidae	59	29	1 528	322	611	640	873	239
Formionidae	0	0	0	0	0	0	0	0
Haemulidae	0	0	0	0	0	0	0	0
Lethrinidae	61	55	598	416	425	640	627	197
<i>Loligo</i> spp.	0	0	0	0	0	0	0	0
Lutjanidae small	58	52	467	456	18	492	431	187
Lutjanidae goldband	0	0	0	0	0	0	0	0
Lutjanidae red	109	40	1 091	329	62	503	958	522
Mullidae	0	0	0	0	0	0	0	0
Nemipteridae	162	168	955	389	159	942	602	167
Priacanthidae	12	10	236	34	18	148	114	21
Rachycentridae	0	0	0	0	0	0	0	0
Sciaenidae	0	0	0	0	0	0	0	0
Scombridae	0	0	0	0	0	0	0	0
Sepiidae	0	0	0	0	0	0	0	0
Serranidae	3	3	25	27	327	64	50	32
Sharks and rays	0	0	0	0	0	0	0	0
Sparidae	0	0	0	0	0	0	0	0
Sphyraenidae	0	0	0	0	0	0	0	0
Synodontidae	76	42	392	295	327	444	371	177
Trichiuridae	0	0	0	0	0	0	0	0
Total retained catch	871	785	9 121	5 550	4 496	6 333	7 381	2 597

(c) Catch (t) In Arafura Sea [(c) Captura (ton) del Mar Arafura]

Category	1972	1973	1974	1975	1976	1977	1978	1979
Ariidae	0	0	0	0	0	0	0	0
Ariidae	0	0	0	0	0	0	0	0
Butterfish	0	0	0	0	0	0	0	0
Carangidae	0	0	0	0	0	0	0	0
Formionidae	0	0	0	0	0	0	0	0
Haemulidae	0	0	0	0	0	0	0	0
Lethrinidae	0	0	0	59	116	83	221	230
<i>Loligo</i> spp.	0	0	0	0	0	0	0	0
Lutjanidae small	0	0	0	28	53	77	95	46
Lutjanidae goldband	0	0	0	0	0	0	0	0
Lutjanidae red	1 402	1 158	771	841	907	912	685	427
Mullidae	0	0	0	0	0	0	0	0
Nemipteridae	2 110	2 811	2 597	1 371	1 560	1 266	1 130	784
Priacanthidae	0	0	0	0	0	0	0	0
Rachycentridae	0	0	0	0	0	0	0	0
Sciaenidae	0	0	0	0	0	0	0	0
Scombridae	0	0	0	0	0	0	0	0
Sepiidae	0	0	0	0	0	0	0	0
Serranidae	0	0	0	0	0	0	0	0
Sharks and rays	0	0	0	0	0	0	0	0
Sparidae	0	0	0	0	0	0	0	0
Sphyraenidae	0	0	0	0	0	0	0	0
Synodontidae	396	907	1 190	234	454	220	162	123
Trichiuridae	0	0	0	0	0	0	0	0
Total retained catch	8 165	9 536	8 817	5 090	6 026	9 150	7 689	6 073

Appendix 2

Species composition of commercial categories in Australia's northern trawl fishery based on observer data for Taiwanese and Thai fleets during 1985-1987. [Composición por especies de categorías comerciales de la pesquería de arrastre del Norte de Australia basado en datos observados de las flotas de Taiwán y Tailandia durante 1985-1987.]

Category/Family	Species	Relative abundance (% weight of category)
Ariidae	<i>Arius thalassinus</i>	100
Butterfish		
Ariommataidae	<i>Ariomma indica</i>	21
Centrolophidae	<i>Psenopsis humerosa</i>	79
Carangidae	<i>Alepes</i> sp.	4
	<i>Carangooides uii</i>	11
	<i>Carangooides chrysophrys</i>	11
	<i>Carangooides gymnostethus</i>	18
	<i>Carangooides humerosus</i>	4
	<i>Carangooides malabaricus</i>	4
	<i>Caranx bucculentus</i>	11
	<i>Gnathanodon speciosus</i>	4
	<i>Megalaspis cordyla</i>	22
	<i>Selar boops</i>	7
	<i>Selaroides leptolepis</i>	2
Formionidae	<i>Apolectus niger</i>	100
Haemulidae	<i>Diagramma pictum</i>	100
Lethrinidae	<i>Lethrinus choeronychus</i>	29
	<i>Lethrinus fraenatus</i>	2
	<i>Lethrinus lentjan</i>	64
	<i>Lethrinus nebulosus</i>	1
	<i>Lethrinus nematacanthus</i>	4
<i>Loligo</i> spp.	<i>Loligo</i> spp.	100
Lutjanidae small	<i>Lutjanus russelli</i>	6
	<i>Lutjanus vittus</i>	94
Lutjanidae goldband	<i>Pristipomoides multidens</i>	91
	<i>Pristipomoides typus</i>	9
Lutjanidae red	<i>Lutjanus argentimaculatus</i>	1
	<i>Lutjanus erythropterus</i>	24
	<i>Lutjanus johni</i>	3
	<i>Lutjanus malabaricus</i>	70
	<i>Lutjanus sebae</i>	2
Mullidae	<i>Parupeneus pleurospilus</i>	100
Nemipteridae	<i>Nemipterus celebicus</i>	1

(continued)

Appendix 2 (continued)

Category/Family	Species	Relative abundance (% weight of category)
	<i>Nemipterus furcosus</i>	69
	<i>Nemipterus hexodon</i>	28
	<i>Nemipterus virgatus</i>	1
	<i>Scolopsis monogramma</i>	1
Priacanthidae	<i>Priacanthus hamrur</i>	21
	<i>Priacanthus tayenus</i>	79
Rachycentridae	<i>Rachycentron canadus</i>	100
Sciaenidae	<i>Protonotaria diacanthus</i>	80
	<i>Argyrosomus</i> sp.	20
Scombridae	<i>Rastrelliger kanagurta</i>	100
Sepiidae	<i>Sepia</i> spp.	100
Serranidae	<i>Epinephelus areolatus</i>	38
	<i>Epinephelus coioides</i>	24
	<i>Plectropomus maculatus</i>	38
Sharks and rays		
Carcharhinidae	<i>Carcharhinus dussumieri</i>	29
	<i>Rhizoprionodon acutus</i>	6
	<i>Rhizoprionodon taylori</i>	6
Hemigaleidae	<i>Hemipristis elongatus</i>	6
Dasyatidae	<i>Himantura uarnak</i>	12
Rhynchobatidae	<i>Rhynchobatus djiddensis</i>	41
Sparidae	<i>Argyrops spinifer</i>	100
Sphyraenidae	<i>Sphyraena putnamiae</i>	100
Synodontidae	<i>Saurida micropectoralis</i>	18
	<i>Saurida</i> sp.1	5
	<i>Saurida undosquamis</i>	77
Trichiuridae	<i>Trichiurus lepturus</i>	100
Mixed taxa		
Labridae	<i>Choerodon cephalotes</i>	28
	<i>Choerodon schoenleinii</i>	6
	<i>Choerodon</i> sp.	6
Haemulidae	<i>Hapalogenys kishinouyei</i>	6
Glaucosomatidae	<i>Glaucosoma burgeri</i>	6
Lethrinidae	<i>Gymnocranius elongatus</i>	6
Ephippidae	<i>Platax batavianus</i>	6
Scaridae	<i>Scarus ghobban</i>	12
Carangidae	<i>Seriola nigrofasciata</i>	6
Siganidae	<i>Siganus fuscescens</i>	12
Teraponidae	<i>Terapon jarbua</i>	6

ENTERED IN NAGA

APR 14 1998

Reproduction in Gag (*Mycteroperca microlepis*) (Pisces: Serranidae) in the Eastern Gulf of Mexico and the Consequences of Fishing Spawning Aggregations

C.C. KOENIG

F.C. COLEMAN

Florida State University

Department of Biological Sciences

Tallahassee, Florida 32306-2043, USA

L.A. COLLINS

National Oceanic and Atmospheric Administration

National Marine Fisheries Service

Southeast Fisheries Science Center

Panama City Laboratory

3500 Delwood Beach Road

Panama City, Florida 32408, USA

Y. SADOVY

Department of Zoology

University of Hong Kong

Pokfulam Rd., Hong Kong

P.L. COLIN

Chuuk Atoll Research Laboratory

PO Box 70, Weno, Chuuk State

Federated States of Micronesia 96942

KOENIG, C.C., F.C. COLEMAN, L.A. COLLINS, Y. SADOVY and P.L. COLIN. 1996. Reproduction in gag (*Mycteroperca microlepis*) (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations [Reproducción del cuna agujaí (*Mycteroperca microlepis*) (Pisces: Serranidae) en el este del Golfo de México y las consecuencias de la pesca de las agregaciones de desovadores], p. 307-323. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Spatial and temporal spawning patterns of gag (*Mycteroperca microlepis*) in the eastern Gulf of Mexico were investigated by: (1) offshore cruises to suspected spawning sites; (2) interviews with grouper fishers; (3) the analysis of gag gonads; and (4) the analysis of daily incremental growth in juvenile gag otoliths. The gag spawning season extends from early February to late April, but the majority of spawning occurs in March. Spawning aggregations in the eastern Gulf are concentrated along the 80-m isobath in the area south of Apalachicola to west of Tampa, Florida. Sex-size-frequency data from gag collection in 1991, 1992 and 1993 indicated several changes in population structure

compared with sex-size data collected by other investigators before the 1980s. The comparisons indicated that the present population shows a reduction in: (1) the average size of females; (2) the average size of males; and (3) the proportion of males (from about 17% to <2%). An increase in fishing pressure on gag spawning aggregations during the 1980s and observations by other investigators strongly suggest that a fishing selection for males during the spawning season is in large part responsible for the observed changes in the gag population. Probable mechanisms are discussed to explain the fishing-induced suppression of compensatory sex-change in these protogynous hermaphrodites.

Resumen

Patrones de desove espacial y temporal del cuna agujaí (Mycteroperca microlepis) en el este del Golfo de México fueron investigadas por: (1) cruceros mar afuera y sitios donde se sospechaba que ocurrían desoves; (2) entrevistas con pescadores de mero; (3) análisis de gonadas del cuna agujaí; (4) análisis de crecimiento usando incrementos diarios en otojitos de juveniles. La temporada de desove se extiende de inicios de Febrero a fines de Abril, pero la mayoría de los desoves ocurren en Marzo. Agregaciones de desovadores en el este del Golfo se concentran a lo largo de la isobata de 80 m en el área sur de Apalachicola, al oeste de Tampa, Florida. Los datos de frecuencia de tallas por sexo del cuna agujaí fueron colectados en 1991, 1992 y 1993, indicando varios cambios en la estructura de la población cuando fueron comparados con datos de talla por sexo colectados por otros investigadores antes de los 1980s. Las comparaciones indicaron que la población actual muestra una reducción en: (1) el tamaño promedio de las hembras; (2) el tamaño promedio de machos; y (3) la proporción de machos (de cerca de 17% a <2%). Un incremento en la presión de pesca sobre las agregaciones de desovadores del cuna agujaí en los 1980s y observaciones efectuadas por otros investigadores sugieren fuertemente que la selección de pesca sobre los machos durante la estación de desove es en gran parte responsable de los cambios observados en la población. Se discuten probables mecanismos para explicar la supresión inducida por la pesca del cambio de sexo compensatorio en estos hermafroditas protogineos.

Introduction

The shallow water groupers (Family Serranidae), including gag (*Mycteroperca microlepis*), black grouper (*M. bonaci*), scamp (*M. phenax*), and red grouper (*Epinephelus morio*), support major commercial and recreational fisheries in the southeastern United States (Huntsman and Waters 1987; Bullock and Smith 1991) (see also Collins et al., this vol.). In the Gulf of Mexico, red groupers rank first among reef fish species in mean annual harvest (4.5 million kg). Gag are ranked seventh, at 1.15 million kg, but should probably be ranked second, with annual landings of about 2 million kg because fishers often misidentify gag as black grouper, resulting in landing reports that grossly underestimate catches of gag (Eklund 1993; Koenig, pers. comm.).

All species of groupers examined have proven to be protogynous hermaphrodites (Shapiro 1987), in which males result from sex change of mature females. The reproductive mode that a species exhibits may

have significant population-level consequences when that species is subject to exploitation. For instance, Bannerot (1984) and Bannerot et al. (1987), using fishery simulation models, concluded that protogynous hermaphrodites may be more susceptible to overexploitation than gonochorists (separate sexes) if fishing pressure served to reduce the normal proportion of males in the population. A significantly depressed male:female ratio could potentially restrict reproductive capacity and ultimately result in population declines.

The primary objective of this study was to define precisely the timing and location of gag spawning in the Gulf of Mexico and to gain insight into the nature of the gag mating system. Because we noted a significant decline in the number of males occurring in our samples relative to samples taken by other investigators over a decade ago, we compare historical and recent sex-ratio and size-frequency data for Gulf and Atlantic populations of gag against a background of information on temporal and

spatial reproductive patterns. We explain observed sex and size changes in gag populations in the context of known patterns and mechanisms of sex change in other species and of recent documented increases in fishing effort and landings, particularly on spawning aggregations.

Materials and Methods

Spatial and temporal spawning patterns of gag were investigated by the analysis of gonads collected by Florida State University (FSU) researchers over a two-year period (1991 through 1992). Data obtained for each gonad included size of fish (mm total length, TL) and collection date, location and depth (m). Cooperation from commercial fishers of northwest Florida was essential to this study. Data collected independently by the National Marine Fisheries Service (NMFS), Panama City Laboratory, in 1991, 1992 and 1993 were used for comparisons of sex ratio and size-frequency distributions.

Samples were collected year-round in 1991 ($N = 991$) before we were aware of the location of spawning aggregations. We obtained gonads from fish houses and from recreational and commercial fishers operating in relatively shallow waters (< 40 m) primarily in the area between and south of Apalachicola and St. Marks, Florida.

Samples were collected in 1992 ($N = 536$) from January through August in both shallow water sites (< 40 m, 30% of samples) and offshore spawning sites (50 - 120 m, 70% of samples). The shallow-water samples collected in 1992 were from the same general area as those collected in 1991.

Samples from spawning aggregations were collected by hook-and-line, mostly in the area to the north and west of the Middle Grounds (southeast of Apalachicola) between the 40 and 120 m isobaths, but

some samples were taken from the same depth range to the southwest of the Middle Grounds. These gonads came from catches taken by five commercial fishers who, because they derive a significant portion of their annual income from fishing the gag spawning aggregations, would give general locations of capture, including depth, but would not release exact locations. We chartered four trips with commercial fishers to spawning sites during the peak spawning period (discussed below).

Both historical and recent data sets are comparable in terms of fishing method and the geographical areas of coverage. The historical Gulf data (Hood and Schlieder 1992) were collected primarily from hook-and-line commercial fishers operating in the area of the Middle Grounds (R. Schlieder, pers. comm.), but also from recreational fishers. The historical Atlantic data (Collins et al. 1987) was collected by the same methods in various depths of water off South Carolina.

Gonad analysis

Gonads collected both years were used to determine spawning season, depth and location and to determine size-frequency distributions. Only gonads from 1992 were used to determine sex, size at sexual maturity, spawning patterns and sex ratios. Gonads were removed from freshly killed fish and either immediately placed on ice and brought back to the laboratory where they were frozen or they were preserved in Davidson's solution. All frozen gonads were thawed and weighed to the nearest 0.1 g.

Gonadosomatic indices (GSI), used to identify spatial and temporal variation in reproductive states, were calculated using the following equation:

$$GSI = 100(\text{ovary weight}/\text{total body weight})$$

Conversions of lengths to weights were made using the following equation from Bullock and Smith (1991):

$$W = 2.680 \times 10^{-8} SL^{2.958}$$

where W = weight in kg and SL = standard length in mm.

Sex was determined microscopically for both the FSU- and NMFS-collected specimens because gross examination was unreliable. Freshly frozen ripe gonads were adequate for identifying sex and for staging oocyte development, whereas histological sections were required for identifying pre- or postspawning individuals and staging.

Frozen gonads were examined by preparing squashes, in which a bit of thawed tissue was squashed between two microscope slides and then covered with a cover slip. Each squash was examined under a compound microscope for sex, stages of oocyte development (see Moe 1969), range of oocyte size per stage, and presence or absence of late-stage atresia, if possible. Whenever sex was questionable, quick hematoxylin and eosin stains of new squashes were made, following Link (1980). This method also facilitated identification of transitionals (= individuals in the process of changing sex from female to male). The presence of live sperm in thawed testes confirmed reproductive activity.

Preserved gonads were sectioned at 10 μm , mounted on slides, and stained with hematoxylin and eosin. Oocytes were examined for stage and degree of development following Moe (1969). Fish were considered immature if the gonads were small, extremely compact, and contained oogonia, stage 1 and small stage 2 oocytes. Gonads were considered ripe if they contained stage 3 or more advanced oocytes.

Inactive fish (mature, nonreproductive), which could be identified reliably only by histological examination, contained stages 1 and 2 oocytes which were loosely held

in a stroma or showed evidence of the early stages of oocyte degeneration; the gonadal wall (tunica) was typically thick, indicating, but not confirming, prior spawning activity. Individuals so classified may or may not have spawned before in their lifetime. Postspawning individuals could be identified histologically by the presence of early stage degeneration of vitellogenic oocytes or postovulatory follicles.

Landings data

Gag landings data for the Gulf coast of Florida were obtained from the Marine Fisheries Information System of the Florida Marine Research Institute, Department of Environmental Protection, St. Petersburg, Florida. A problem with the gag landings data is that gag catches are commonly recorded as black grouper. It is well known, however, that black groupers (*M. bonaci*) are rare on the west coast of Florida north of the Florida Keys (Bullock and Smith 1991). Therefore, to estimate the actual gag landings, we combined gag with black grouper landings data, but excluded Monroe County (Florida Keys) landings from our estimates.

Results

Spawning season, depth, location and pattern

GSIs of gonads collected in 1991 were low throughout the year, but suggested that gags were reproductively active from December through mid-May (Fig. 1a). GSIs of gonads collected in 1992 (most from spawning aggregations) clearly indicated that gags were reproductively active from February through April, with peak spawning from mid-February through March, followed by a gradual decline from late March through April (Fig. 1b). These spawning times were corroborated by the analysis of juvenile otolith daily increments from

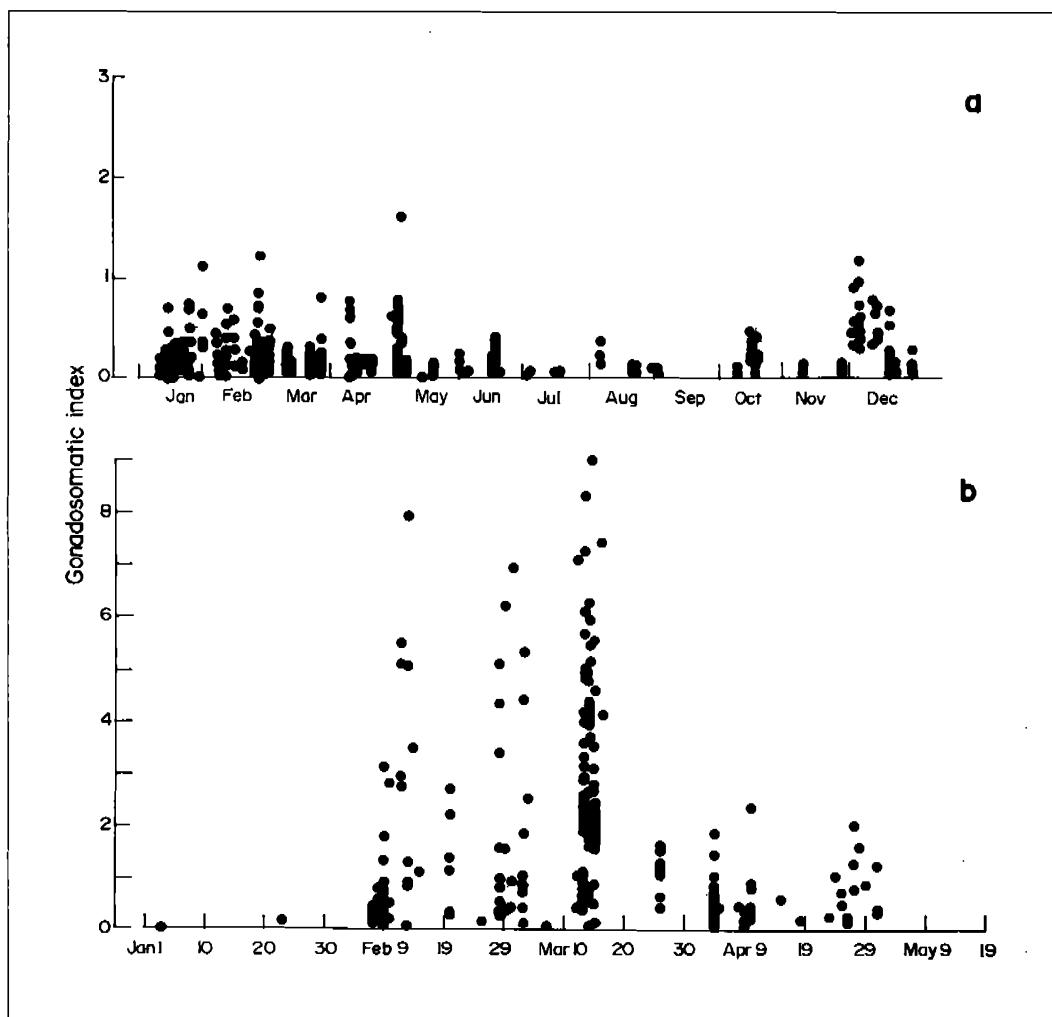


Fig. 1. Seasonal pattern of gonadosomatic Indices of gag (*Mycteroperca microlepis*) (a) 1991 data collected year-round in depths less than 50 m; (b) 1992 data collected during spawning season mostly from aggregation sites. [Patrón estacional de los índices gonadosomáticos del cuna agujaí (*Mycteroperca microlepis*) (a) datos colectados a lo largo del año 1991 en profundidades menores a 50 m; (b) Datos colectados durante la estación de desove en 1992, mayormente de sitios de agregación.]

fish collected over a broad geographic and temporal range (Koenig, unpubl.).

Spawning occurs on offshore reefs from southeast of Apalachicola to west of Tampa (and possibly further to the south) (Fig. 2). Spawning aggregations were concentrated at depths of about 80 m (range: 50 m to 120 m). GSIs of fish caught in shallow water (1992) were higher in February than in March, but GSIs of both groups (February

and March) were much smaller than those recorded for gags captured at depths greater than 50 m (Fig. 3). During peak spawning, most mature females (i.e., >550 mm SL) caught at depths >50 m (Fig. 1b) had large, active gonads whereas those caught at the same time in shallower waters (<50 m) had relatively small gonads (Fig. 1a). Fish collected from spawning aggregations in March tended to be larger than fish collected

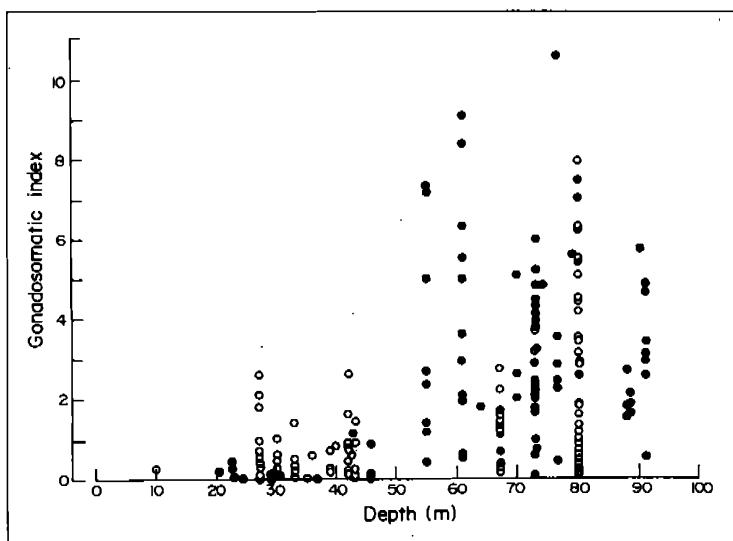
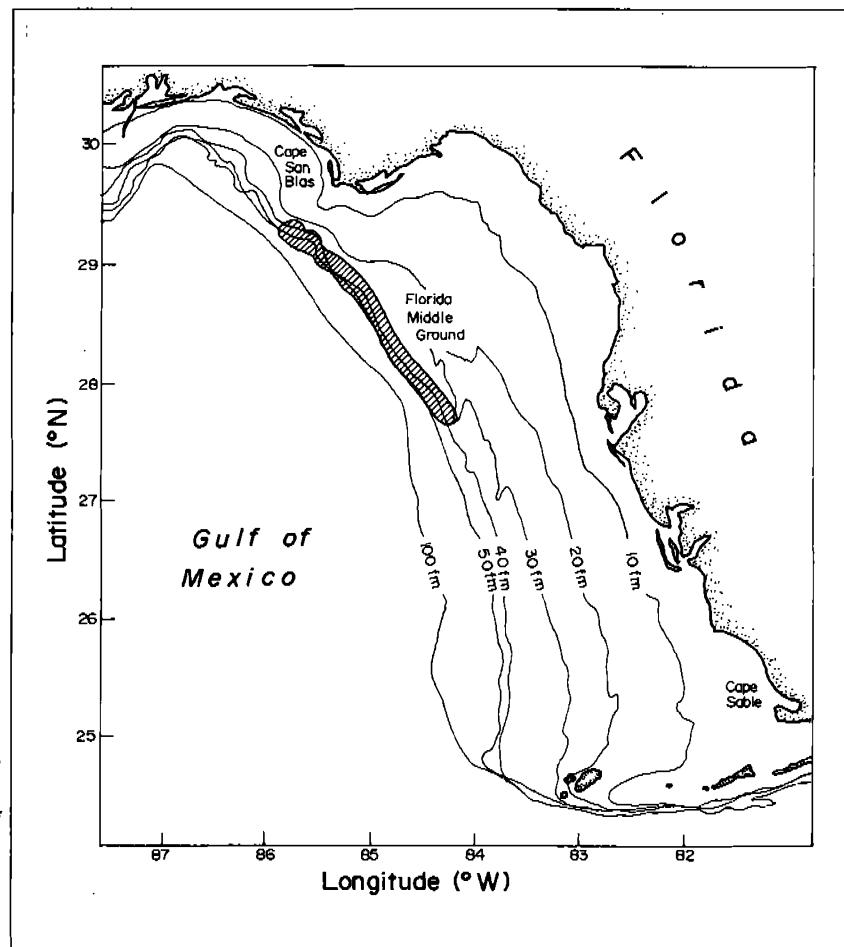


Fig. 3. Distribution of gonadosomatic indices relative to depth of capture for gag (*Mycterooperca microlepis*) during peak spawning (February = open circles; March = closed circles) in 1992. [Distribución de los índices gonadosomáticos en relación a la profundidad de captura del cuna agujaí (*Mycterooperca microlepis*) durante el pico de desove (Febrero = círculos claros; Marzo = círculos oscuros) en 1992.]

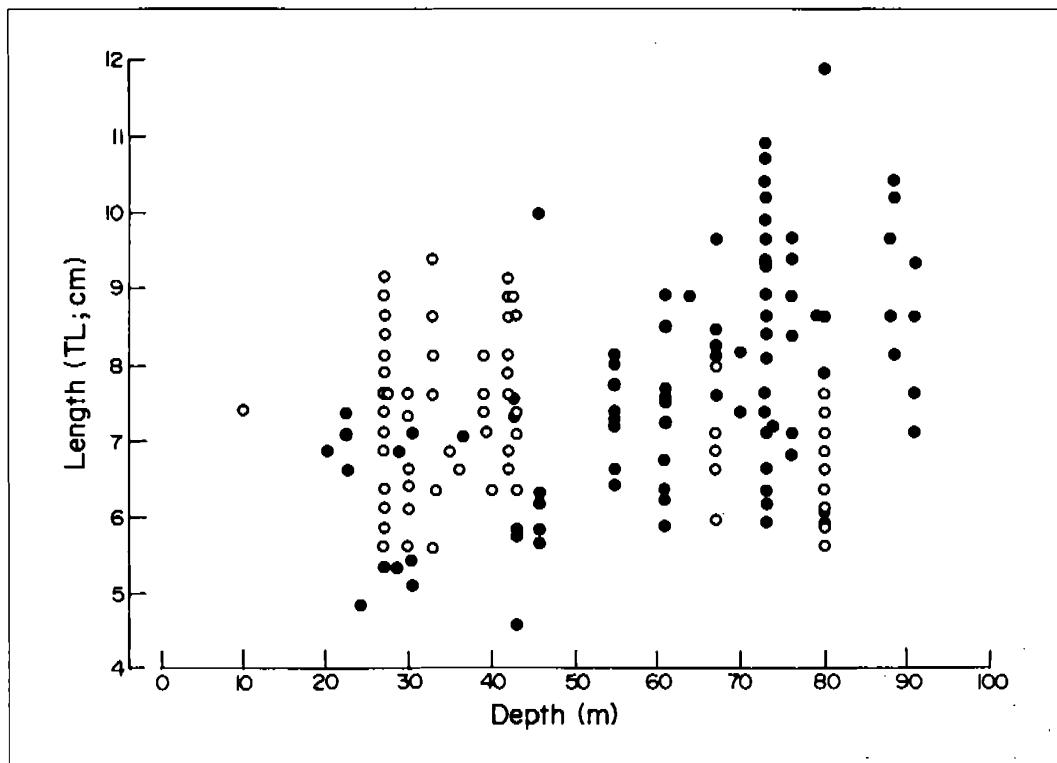


Fig. 4. Distribution of total length (cm) relative to depth of capture for gag (*Mycteropterus microlepis*) during peak spawning (February = open circles; March = closed circles). [Distribución de la longitud total (cm) en relación a la profundidad de la captura del cuna aguafí (*Mycteropterus microlepis*) durante el pico de desove (Febrero= círculos claros; Marzo=círculos oscuros).]

in shallow (<50 m) water (Fig. 4), but this pattern appeared reversed in February.

Gonads examined histologically ($N = 112$) included 110 females, no males, and 2 transitionals. Nineteen of the fish were immature, 67 were inactive (47 mature, 20 uncertain), and 24 were mature and ripe. The inactive category includes fish that are clearly sexually mature but are not in spawning condition ($N = 43$) and fish for which level of maturity could not be determined. The smallest mature fish examined was 400 mm SL, 50% of the fish between 500 and 550 mm SL had matured, and 100% of the fish larger than 550 mm SL were mature.

The inactive gonads, most of which were collected from mature fish ($N = 47$) in shallow water (<50 m) during peak spawning periods, provide limited but highly suggestive

information about the spawning condition of females in shallow water. Spawning condition could be determined clearly in 15 of these fish: 10 (67%) showed no indication of either imminent or past spawning activity, 3 (20%) collected in February had developing oocytes suggesting a prespawning condition, and the remaining 2 (13%) collected in March were in postspawning condition. These data, combined with the data presented in Figs. 3 and 4, suggest that gags found in February in relatively shallow water consist of two types of mature females, those that will not spawn and those that will migrate to the spawning sites. In March, mature females in shallow waters consist of both nonspawners and those that have spawned and left the spawning sites.

Sex ratio and size frequency

The two data sets, historical and recent, show marked differences in both sex ratio and size frequency (Table 1). In both historical data sets the percentage of males among mature fish was 17%. The 95% confidence interval (binomial) for the historical Gulf data (13% to 21%) was narrower than the historical Atlantic data (11% to 23%) because of the smaller sample size of the latter. In the recent data sets, the percent males among mature fish was much lower, ranging from 2.7% to 1.3% (Table 1). The 95% confidence interval about the mean (2.2%) of the recent data sets was about 0.9% to 3.5%.

A comparison of the FSU-1991 size-frequency distribution and the FSU-1992 size-by-sex-frequency distributions with those of Hood and Schlieder (1992) (Fig. 5a and 5b, respectively) shows that a distinct loss of large fish has occurred over the 1980s (along with a reduction in the proportion and average size of males).

Fig. 6 shows size-by-sex-frequency distributions of data collected by NMFS (Panama City Laboratory) in 1991, 1992 and 1993. It shows a distinct reduction in average size compared with the historical data.

Transitional were rare in all samples, historical and recent (Table 1). The size (mm TL) range of transistionals in the historical samples were: Gulf, 850 - 1 150 and Atlantic, 857 - 904. In the recent samples the size ranges of transistionals were: FSU-1992, 660 - 864; NMFS-1991, 725; NMFS-1992, 1 025 - 1 149; NMFS-1993, 525 - 1 175.

Gags have sexually dimorphic color patterns at least during the spawning season (Gilmore and Jones 1992). All of the large males we examined exhibited this pattern, which fishers have variously called "copperbelly", "charcoalbelly", or "rustybelly". Such pigment patterns persist even after capture. The smallest males in our sample apparently did not exhibit this pattern because they were not recognized as males until the gonads were examined microscopically. Only one male in the FSU-1992 collection (607 mm TL), was collected shallower than 50 m (29 m). In addition, the two smaller of the three FSU-1992 transistionals were collected shallower than 50 m.

We examined monthly variation in the average catch data for the Florida Gulf coast landings (1986-1992) and found that the highest catches occurred during the period immediately prior to, during and after peak

Table 1. Historical and recent sex ratio and size frequency of gag (*Mycteroperca microlepis*) (Pisces: Serranidae) in the eastern Gulf of Mexico. [Proporción de sexos histórica y reciente, y frecuencia de tallas del cuna aguají (*Mycteroperca microlepis*) (Pisces: Serranidae) en el este del Golfo de México.]

Study	Collection dates	Collection areas	Males		Transistionals		Mature females		
			No.	%	No.	%	No.	%	Median sz
Hood and Schlieder (1992)	1977-1980	N.E. Gulf	134	17	6	0.8	659	82	850-900
Collins et al. (1987)	1977-1982	off South Carolina	51	17	4	1.3	253	82	800-850
Panama City Laboratory	1991	N.E. Gulf	12	2.7	1	0.2	427	97	800-849
	1992		8	2.5	2	0.6	309	97	750-799
	1993		8	1.3	2	0.3	613	98	700-749
FSU Laboratory	1992	N.E. Gulf	9	1.9	3	0.6	457	98	750-799

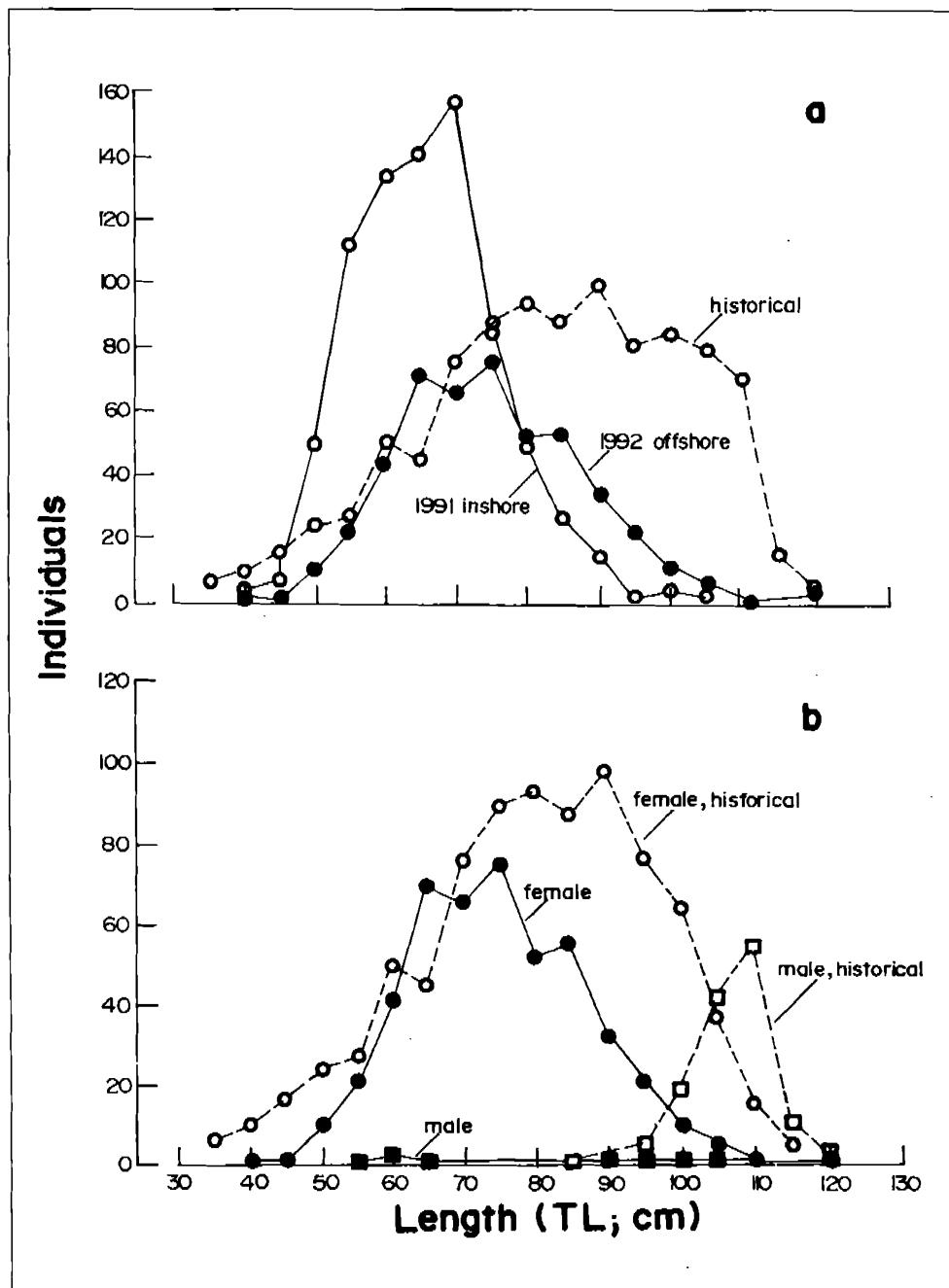


Fig. 5. (a) Size-frequency distributions for gag (*Mycteroperca microlepis*) collected by FSU in 1991 (<50 m) and 1992 (>50 m) and by Hood and Schlieder (1992) in 1977-1980; (b) Size-frequency distributions by sex for gag (*Mycteroperca microlepis*) collected by FSU in 1992 (>50 m) and by Hood and Schlieder (1992) in 1977-1980. [*(a) Distribución de frecuencia de tallas del cuna agujaí (*Mycteroperca microlepis*) colectada por FSU en 1991 (<50 m) y 1992 (>50 m) y por Hood y Schlieder (1992) en 1977-1980; (b) Distribución de frecuencia por sexo para el cuna agujaí (*Mycteroperca microlepis*) colectadas por FSU en 1992 (>50 m) y por Hood y Schlieder (1992) en 1977-1980.]*

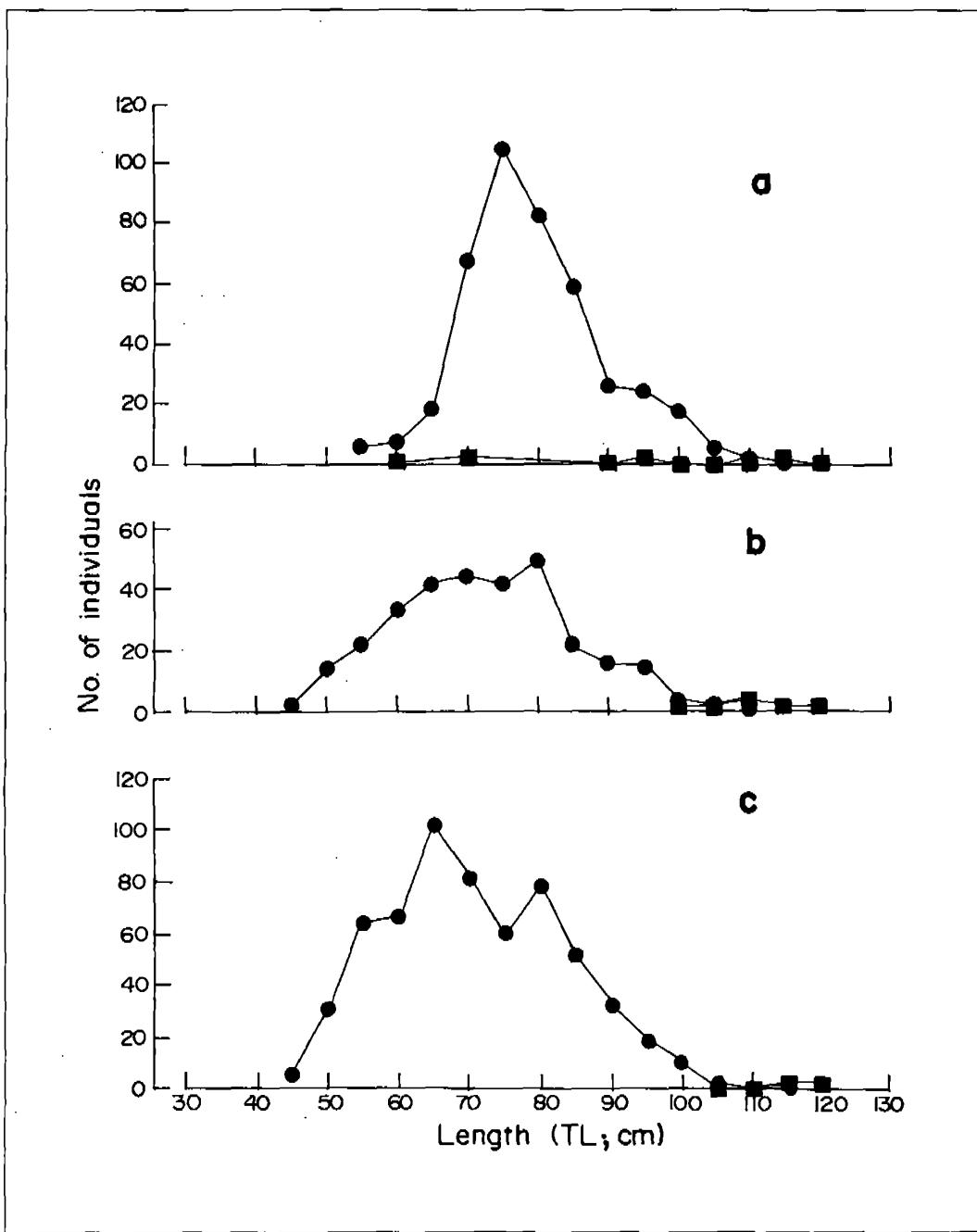


Fig. 6. Size-frequency distributions by sex for gag (*Mycteroperca microlepis*), NMFS, Panama City Laboratory data: (a) 1991, (b) 1992, (c) 1993. [Distribución de frecuencia por tallas por sexo para el cuna aguají (*Mycteroperca microlepis*), NMFS, datos de laboratorio de Panamá City: (a) 1991, (b) 1992, (c) 1993.]

spawning (Fig. 7a). The mean number of trips was lowest during February and March, probably due to the high incidence of storms and danger associated with fishing these areas during that time of year (Fig. 7b). But clearly, the catch-per-unit effort (Fig. 7c) is highest exactly during peak spawning, indicating a high vulnerability of gags during this time.

Discussion

The peak spawning season in the Gulf population of gag is February through March and spawning aggregations occur in water depths from 50 to 120 m. Keener et al. (1988) showed similar spawning times for the Atlantic population of gags through the back-calculation of daily increments of juvenile otoliths, and Gilmore and Jones (1992) observed putative spawning aggregations within the same depth range as those in the Gulf off the east coast of Florida. Mitochondrial DNA analyses (Koenig and Ptacek, unpubl.) of Atlantic and Gulf populations of gags demonstrated a lack of genetic differentiation within and between populations. Thus, it appears that Atlantic and Gulf gag comprise a single genetic population with similar patterns of spawning and probably similar responses to exploitation. Burton (NMFS, Beaufort, unpubl.) showed that fishery landings of gag peaked during the time of gag spawning off the east coast of Florida. Although there are no recent studies of sex ratios of Atlantic gag, we found neither males nor transitionals in a sample (collected during the spawning season, 1993) supplied by commercial fishers ($N = 170$, Koenig, Coleman and Carr, unpubl.).

Several species of groupers have been shown to undergo annual migrations to well-defined spawning sites (Colin et al. 1987; Shapiro 1987; Waschkevitz and Wirtz 1990; Sadovy, in press). Van Sant et al. (1990) described a gag spawning migration

southwards to the east coast of Florida, based on tagging studies. Although no spawning migrations have been described for gag in the Gulf, they are implied from the consistent annual timing and location of the aggregations.

Gilmore and Jones (1992; pers. comm.) observed individual scamp returning to the same aggregation site in consecutive years. These investigators did not present direct observations of individual gag returning annually to the same sites, although they did observe consistent annual site-specific aggregations.

The occurrence of prespawning groups in gag has been observed and videotaped (D. DeMaria and W. Parks, commercial fishers, pers. comm.). Prespawning sites were observed by Parks to occur in shallow (20–40 m) water at annually consistent sites off the south Atlantic coast of Florida typically during late December or early January. The function of the prespawning groups is unknown.

Anecdotal accounts by commercial fishers indicate that gag spawning aggregations once exceeded the present range northward to more accessible locations southeast of Pensacola and throughout the Middle Grounds. Spawning sites are now restricted to the range depicted in Fig. 2. If gag aggregation sites are traditional and the northern aggregation sites have been depleted by fishing, then it is likely that continued aggregation fishing will eliminate other aggregation sites. Such a process may lead to fishery extinction, and this process is often cited as the cause for the collapses of other grouper fisheries (Olsen and Laplace 1979; Sadovy 1994).

Spawning has not been directly observed in gag; however, evidence presented by Gilmore and Jones (1992) suggests that gag form hierarchical spawning groups with single-male, multiple-female spawning events. Our data support his observation. Ripe testes from gag are relatively small and contain small amounts of milt which indicates single

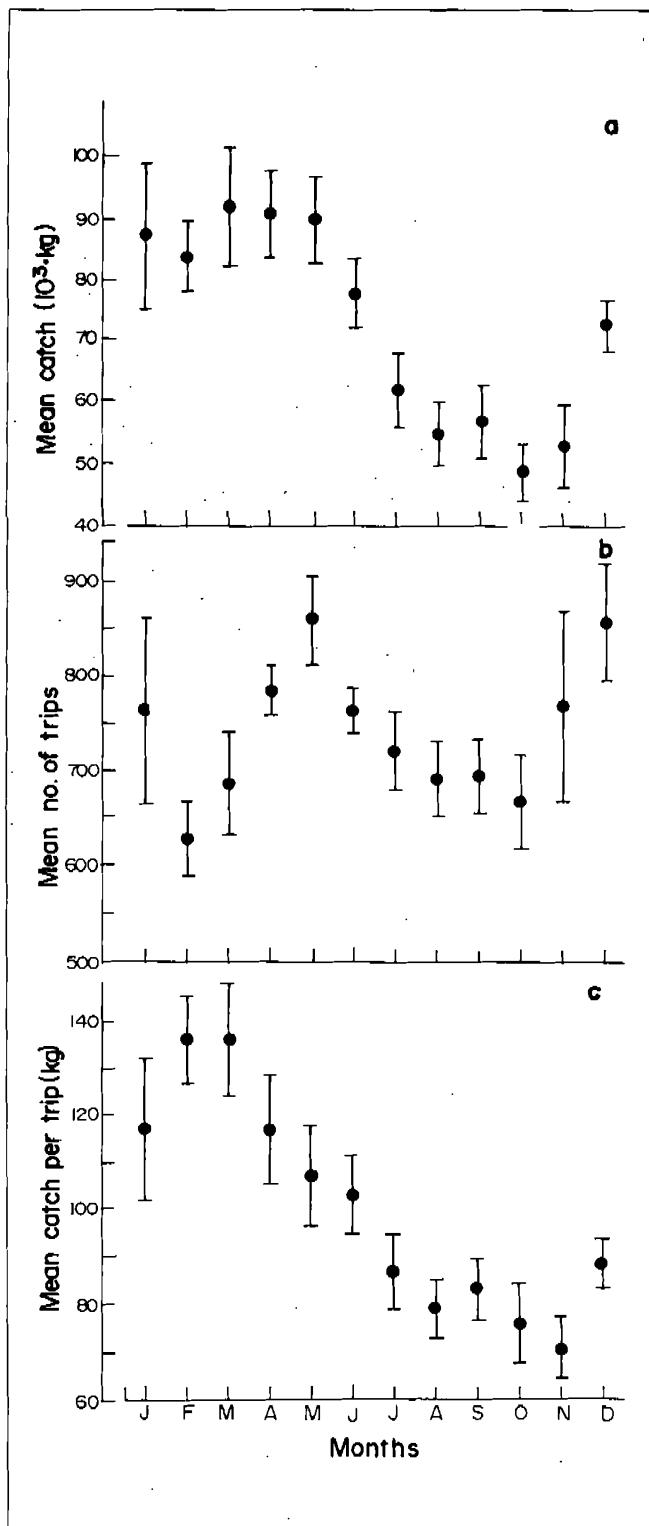


Fig. 7. Florida Gulf coast landings of gag (*Mycteroperca microlepis*) from 1986 to 1992. (a) Mean monthly landings; (b) Mean monthly commercial grouper fishing trips; (c) Mean monthly catch per trip. [Descargas en las costas del Golfo de Florida del cuna aguafí (*Mycteroperca microlepis*) de 1986-1992. (a) Descarga media mensual; (b) Media mensual de viajes de pesca comercial del mero; (c) Media mensual de la captura por viaje.]

male spawning (i.e., no sperm competition). Red hind (*Epinephelus guttatus*), also has single male spawning and males have small testes (Sadovy et al. 1994). In contrast, Nassau grouper (*Epinephelus striatus*) males, when ripe, have large, milt-filled testes and are multiple-male spawners (Colin 1992).

The proximal causes of sex change in groupers have important implications for fisheries management (Munro 1987). Management will be quite different for species in which sex change is age- or size-mediated (endogenous control, as suggested for gag by McErlean and Smith 1964) than for those exhibiting sociodemographic control (exogenous control, e.g., Shapiro 1987). To date, the only mechanism described for sex-changing reef fish species is sociodemographic control (Shapiro et al., in press).

The conditions of sex change (i.e., which fish changes sex and when) are determined in *Anthias squamipinnis*, a protogynous serranid (subfamily Anthiinae), by hierarchical associations within the social group (Shapiro 1981a). For example, removal of a territorial male from the group causes the dominant (= largest) female to change sex. It is possible that a similar process of sex change occurs in gag. Our size-by-sex-frequency data (Fig. 5b) support this contention, as no small males (<800 mm) occurred in historical samples, but were present in ours. That is, if the mechanism of sex change in gag is mediated by social or demographic factors, then smaller males and transitionals would be expected in the population as exploitation eliminated the larger size classes. However, our data do not support a hypothesis of sex change in gag which is determined by size alone.

The declines in average size and male:female sex ratios in the eastern Gulf of Mexico population of gag over the 1980s was coincident with increased fishing pressure (Ecklund 1993). Landings data for the Florida Gulf coast indicate that fishing pressure was most intense during the time

of gag spawning aggregation formation (Gilmore and Jones 1992 and anecdotal information from fishers) and that the highest catch-per-effort occurs at the time of peak spawning (Fig. 7c). In addition, northwest Florida grouper fishers report that they have experienced a steady decline in gag landings over the last 12 years. Unfortunately, stock declines cannot be verified because before 1986 all Gulf groupers were lumped in the landings data. It appears likely that, in addition to general stock declines due to heavy fishing pressure, population-level size- and sex-ratio changes are the direct result of fishing activities on the spawning aggregations. This contention is supported by the observations of Gilmore and Jones (1992 and pers. comm.), who reported that hook-and-line fishing on gag (and scamp) spawning aggregations tended to select males before females. If fishing selection for males occurs, then hook-and-line estimates of sex ratio (Table 1) actually overestimate the actual (absolute) proportion of males.

Although males may be selected by hook-and-line fishing, this observation alone does not explain how aggregation fishing could override compensatory sex-change mechanisms and reduce the proportion of male gags. If compensatory sex change mechanisms were operational in the male-deficient population, an increase in the proportion of transitionals would be expected. However, the proportion of transitionals is about the same in both historical and contemporary samples (Table 1). This observation could be explained if transitionals were also selected by fishing. Shapiro (1981b) and others have shown that among protogynous species individuals induced to undergo sex change rapidly adopt stereotypic male behaviors before they become functional males. The time necessary to complete transition in gag is unknown; however, data from artificial induction of sex change (Roberts and Schlieder 1983) suggest that it may take months.

Nevertheless, if fishing selection of males is based on male behavior, as Gilmore and Jones (1993) suggest, then transitinals, once they adopt male behaviors, will also be selected by fishing.

Selection of male and transitional gags in spawning aggregations should cause a depression of the male:female ratio, but when aggregations disperse and fishing pressure is lessened at nonspawning times of the year it would seem that the opportunities for sex change would increase. Therefore, if sex change could be induced at all times of the year, a higher frequency of males and/or transitinals would be expected in the population during nonspawning times. This increase in males (and/or transitinals) should be reflected in the catch at the beginning of the spawning season. However, no such increases in males nor transitinals were observed. If, on the other hand, males and females were segregated during nonspawning times of the year, the only opportunity for female "assessment" of the altered sex ratio would occur when the two sexes reunited at the time of spawning. Shapiro et al. (in press) described a similar system of sex segregation in the red hind and discussed possible mechanisms which could account for the lack of sex change among all-female groups during nonspawning times. Anecdotal evidence suggests that large male gags remain offshore; commercial fishers say that it is rare to catch large males that are distinctively colored ("copperbellies") in water shallower than 40 m. Our data support this contention, but the possibility of males lacking characteristic color patterns exists in our data set. Clearly, the temporal and spatial distribution of males needs further investigation. Assuming that males remain offshore throughout the year and females disperse after spawning to inshore sites (and sex change is socially mediated), then sex change would likely be initiated only at the time of spawning. It is possible that prespawning aggregations play a role

in sex change, but these ephemeral aggregations are completely unstudied.

Selection of males and transitinals from spawning aggregations could explain the relatively rapid depletion of large adults from the Gulf population of gag. The largest fish in the population are in the spawning aggregations and the largest individuals of each spawning aggregation are males, transitinals and dominant females. Removal by fishing of the males and transitinals presumably induces sex change in the dominant females, then these too are selected. Although size reduction in exploited fish populations is a general phenomenon (Bohnsack 1989) based on increased probability of capture with age (size), it would probably not act as rapidly as the direct removal of the largest individuals.

Several points are important to consider in relation to the comparison of historical and recent data sets. Although random sampling cannot be assumed for the overall data sets, bias would be minimized if the data were stratified by season and depth because large gag and males tend to occupy deeper water, especially during the spawning season. Thus, our 1991 size-class data are biased towards the smaller sizes of adult gags because samples were taken from shallow water. By contrast, our 1992 size-class data are biased towards larger sizes (and probably a high male:female sex ratio) because most of the samples came from deepwater during the spawning season. It is likely that historical samples were not taken from spawning aggregations because the GSIs were relatively small during the spawning season (Hood and Schlieder's mean peak GSI value was less than 2.0). Thus, our 1991 and 1992 data sets bracket the 'true' population size frequency (Fig. 5a) and the 1992 data set is biased in favor of a higher male:female sex ratio. In addition, the data set collected by the NMFS Panama City Laboratory had an additional bias toward more males because

"copperbellies" were selected from the catch (at the fish house) before the catch was sampled. Thus, males are probably even rarer in the population than our data indicate.

The question remains: What does a reduced proportion of males in the gag population mean in terms of reproductive capacity and ultimately recruitment? Intuitively, fewer males than is evolutionarily adaptive for a particular mating system would seem to restrict spawning opportunities for females in that system. As far as we know, there is a complete lack of information on this subject, except for the simulation models of Bannerot (1984) which compared the response, in terms of reproductive capacity, of the gonochorist and protogynist reproductive modes at various levels of exploitation. Bannerot found protogynists generally superior to gonochorists in reproductive capacity; however, under reduced male:female sex ratios the reproductive capacity of the protogynists dropped precipitously. Clearly, the relationship of sex ratio to reproductive capacity (and/or recruitment) needs to be examined in detail.

The response of gag to fishing pressure serves as an example of the importance to fishery management of knowledge of the details of reproductive strategies of exploited species. Even within the protogynous hermaphroditic mode of reproduction there may be widely different responses to fishing pressure, especially if that pressure is applied to the spawning fish. For example, we compared red grouper size-by-sex ratios of fish collected in the early 1960s ($N = 594$, Moe 1969) with our red grouper collections of 1991 and 1992 ($N = 450$, unpublished data). Both data sets were collected in a similar manner and in overlapping areas. We found no significant difference in size distribution or in sex ratios (22% males [plus transitionals] in Moe's sample and 24% males [plus transitionals]

in ours) even though red groupers are subject to exploitation rates at least as great as those of gags and at all times of the year (Goodyear and Schirripa 1993).

Effective management depends on detailed information concerning the complex life histories of exploited species at many levels of biological organization. Such detailed information is difficult, time consuming, and expensive to gain. An immediate management measure for gag, given the evidence presented in this paper on the effects of fishing spawning aggregations, should involve closure of either the spawning areas or season. Before, during and after the closure, gag should be monitored for sex ratio, gonad condition (e.g., rates of atresia) and recruitment success (Koenig and Colin, in press). If our hypotheses are correct about the timing and nature of gag sex change induction and fishing selection then the proportion of males should rise the second year after fishing of spawning aggregations stops.

Acknowledgements

We thank the following people for their participation in this work. M.P. Chasar was indispensable in all phases of the field work. Ann Kiefert, Shawna Stewart, Lou Spataro and Shannon Owens provided technical support. Sandy Handy (FSU) and Dan Marciewicz volunteered many hours. Peter Hood (FMRI, St. Petersburg) supplied unpublished data on gag. Lew Bullock (FMRI, St. Petersburg) provided field support on offshore trips to identify spawning aggregations. Jim Bohnsack (NMFS, Miami) provided advice and support during various phases of this project. The following commercial fishers were invaluable in providing gonads and leading us to the spawning grounds of gag: Clay Bailey (Apalachicola), Brian Garrity (Crawfordville), Bob Dickey and Phil Mathis (Panacea), Steve Smeby

(Panama City) and Don DeMaria (Key West). This research project was funded by MARFIN (NA90AA-H-MF748) and the Florida Department of Natural Resources (now Department of Environmental Regulation).

References

- Bannerot, S.P. 1984. The dynamics of exploited groupers (Serranidae): an investigation of the protogynous hermaphroditic reproductive strategy. University of Miami, Coral Gables, Florida. 392 p. Ph.D. dissertation.
- Bannerot, S.P., W.W. Fox and J.E. Powers. 1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and Caribbean, p. 295-327. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Bohnsack, J.A. 1989. The potential of marine fishery reserves for reef fish management in the US Southern Atlantic. NOAA Tech. Mem. NMFS-SEFC-261, 40 p.
- Bullock, L.H. and G.B. Smith. 1991. Seabasses (Pisces: Serranidae). Memoirs of the Hour-glass Cruises VIII (II), 243 p.
- Colin, P.L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. Env. Biol. Fish. 34:357-377.
- Colin, P.L., D.Y. Shapiro and D. Weiler. 1987. Aspects of the reproduction of two groupers, *Epinephelus guttatus* and *E. striatus*, in the West Indies. Bull. Mar. Sci. 40:220-230.
- Collins, M.R., C.W. Waltz, W.A. Roumillat and D.L. Stubbs. 1987. Contribution to the life history and reproductive biology of gag, *Mycteroperca microlepis* (Serranidae) in the South Atlantic Bight. US Fish. Bull. 85:648-653.
- Ecklund, A.M. 1993. A literature review of the gag grouper, *Mycteroperca microlepis*. National Marine Fisheries Service, SE Fisheries Science Center, Miami. Contribution MIA 92/93-72.
- Gilmore, R. G. and R. J. Jones. 1992. Color variation and associated behavior in the epinepheline groupers, *Mycteroperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. Bull. Mar. Sci. 51(1):83-103.
- Goode, C.P. and M.J. Schirripa. 1993. The red grouper fishery of the Gulf of Mexico. National Marine Fisheries Service, SE Fisheries Science Center, Miami Contribution MIA-90/91-86.
- Hood, P.B. and R.A. Schlieder. 1992. Age, growth and reproduction of gag *Mycteroperca microlepis* (Pisces: Serranidae), in the eastern Gulf of Mexico. Bull. Mar. Sci. 51(3):337-352.
- Huntsman, G.R. and J.R. Waters. 1987. Development of management plans for reef fishes-Gulf of Mexico and US South Atlantic, p. 533-560. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Keener, P., G.D. Johnson, B.W. Stender, E.B. Brothers and H.R. Beatty. 1988. Ingress of postlarval gag, *Mycteroperca microlepis* (Pisces: Serranidae) through a South Carolina barrier island inlet. Bull. Mar. Sci. 42(3):376-396.
- Koenig, C.C. and P.L. Colin. Absolute abundance, and survival of juvenile gag grouper, *Mycteroperca microlepis*, in seagrass beds of the northeastern Gulf of Mexico. Proc. Gulf Caribb. Fish. Inst. 45. (In press).
- Link, G.W., Jr. 1980. Age, growth, reproduction, feeding, and ecological observations on the three species of *Centropristes* (Pisces: Serranidae) in North Carolina waters. The University of North Carolina, Chapel Hill. 277 p. Ph. D. dissertation.
- McErlean, A.J. and C.L. Smith. 1964. The age of sexual succession in the protogynous hermaphrodite *Mycteroperca microlepis*. Trans. Am. Fish. Soc. 93(3):301-302.
- Moe, M.A., Jr. 1969. Biology of the red grouper (*Epinephelus morio* Valenciennes) from the eastern Gulf of Mexico. Prof. Pap. Ser., Fla. Mar. Lab, 10, 95 p.
- Munro, J.L. 1987. Workshop synthesis and directions for future research, p. 639-659. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Olsen, D.A. and J.A. Laplace. 1979. A study of a Virgin Islands grouper fishery based on

- a breeding aggregation. Proc. Gulf Carib. Fish. Inst. 31:130-144.
- Roberts, D.E., Jr. and R.A. Schlieder. 1983. Induced sex inversion, maturation, spawning, and embryogeny of the protogynous grouper, *Mycteroperca microlepis*. J. World Maricult. Soc. 14:639-649.
- Sadovy, Y. 1994. Grouper stocks of the Western central Atlantic: the need for management and management needs. Proc. Gulf Caribb. Fish. Inst. 43:43-64.
- Sadovy, Y. The case of the disappearing grouper: *Epinephelus striatus*, the Nassau grouper, in the Caribbean and Western Atlantic. Proc. Gulf Caribb. Fish. Inst. 45. (In press).
- Sadovy, Y., P.L. Colin and M.L. Domeier. 1994. Aggregation and spawning in the tiger grouper, *Mycteroperca tigris* (Pisces: Serranidae). Copeia: 511-516.
- Shapiro, D.Y. 1981a. Size, maturation and the social control of sex reversal in the coral reef fish *Anthias squamipinnis*. J. Zool. Lond. 193:105-128.
- Shapiro, D.Y. 1981b. Behavioural changes of protogynous sex reversal in a coral reef fish in the laboratory. Anim. Behav. 29:1185-1198.
- Shapiro, D.Y. 1987. Reproduction in groupers, p. 295-327. In J.J. Polovina and S. Ralston (eds.). Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Shapiro, D.Y., G. Garcia-Moliner and Y. Sadovy. Social system of an inshore sub-population of the red hind grouper, *Epinephelus guttatus* (Pisces: Serranidae). Env. Biol. Fish. (In press).
- Van Sant, S.B., M.R. Collins and G. Sedberry. 1990. Preliminary evidence from a tagging study for a gag (*Mycteroperca microlepis*) spawning migration with notes on the use of oxytetracycline for chemical tagging. Proc. Gulf Caribb. Fish. Inst. 43:417-428.
- Waschkewitz, R. and P. Wirtz. 1990. Annual migration and return to the same site by an individual grouper, *Epinephelus alexandrinus* (Pisces: Serranidae). J. Fish Biol. 36(5):781-782.

ENTERED IN RASA

APR 14 1998

Assessment of a Snapper Complex (*Lutjanus* spp.) of the Eastern Tropical Pacific

M. CRUZ-ROMERO^a

E.A. CHÁVEZ^b

E. ESPINO^a

A. GARCÍA^a

^a*Instituto Nacional de la Pesca, Centro Regional de
Investigación Pesquera, A.P. 591, Manzanillo, Colima México*

^b*Centro Interdisciplinario de Ciencias Marinas
Instituto Politecnico Nacional
A.P. 592, 23000 La Paz, Baja California Sur, Mexico*

CRUZ-ROMERO, M., E.A. CHÁVEZ, E. ESPINO and A. GARCÍA. 1996. Assessment of a snapper complex (*Lutjanus* spp.) of the eastern tropical Pacific [Evaluación del recurso de un complejo de pargos (*Lutjanus* spp.) del Pacífico occidental tropical]. p. 324-330. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Paulty (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Three stocks (*Lutjanus peru*, *L. guttatus* and *L. argentiventralis*) from a ten-snapper species complex were assessed after a year of weekly samplings of commercial landings. The length-weight relationship parameters, von Bertalanffy growth parameters, ages, stages of gonad maturity, fecundities, seasonal spawning patterns, natural mortalities and stock sizes were estimated. Population sizes, fishing mortality and exploitation rates were estimated for each stock. An age-structured simulation model for each stock was created such that fishing mortality strategies could be proposed to ensure a sustainable yield in the long term. In one case, changes in observed yields through time could not be explained to be a result of changes in recruitment or fishing mortality. However, the three stocks analyzed were found to be underexploited and yields can be expanded to about 70 t above current levels. Thus, further annual increases in fishing intensity at a rate equivalent to that of human population growth are recommended until the maximum sustainable yield level is reached to ensure the creation of new jobs at the same rate as they are required by new generations of fishers.

Resumen

Tres poblaciones de un complejo de diez especies de pargos (*Lutjanus* *peru*, *L. guttatus* y *L. argentiventralis*) fueron analizadas a partir de muestras semanales de descargas comerciales tomadas a lo largo del año. Parámetros de la relación peso-longitud, parámetros de crecimiento de von Bertalanffy, edad, estadios de madurez, fecundidad, patrones estacionales de desove, mortalidad natural y tamaños de las poblaciones fueron estimados para cada población. Un modelo de simulación basado en la estructura por edades de

la población fué creado, tal que las estrategias de pesca pudieran ser propuestas con el objeto de asegurar un rendimiento sostenible a largo plazo. En un caso, cambios observados a través del tiempo no pudieron ser explicados únicamente como resultado de cambios en el reclutamiento y mortalidad por pesca. Sin embargo, las tres poblaciones analizadas se consideran subexplotadas de tal forma que los rendimientos pudieran ser aumentados en cerca de 70 t sobre el nivel actual. De esta forma, incrementos futuros en la intensidad de pesca anual equivalente a la tasa de crecimiento de la población humana es recomendada hasta que el nivel de rendimiento máximo sostenible sea alcanzado, con el objeto de asegurar la creación de nuevos empleos en la misma proporción conforme sea requerido por las nuevas generaciones de pescadores.

Introduction

Tropical artisanal fisheries are typically multispecific and often yield relatively low catches on a per-species basis. The snapper fishery on the coast of Colima, west-central Mexico, is just a portion of a complex that includes 109 species, and whose total yearly catches exceed 2 000 t in some years (see Cuellar et al.; Diaz-Ruiz et al., this vol.). Amongst these, red snapper (*Lutjanus peru*) is the most important for its commercial value, as well as its yields (Cruz-Romero et al. 1988). The snapper complex comprises nine species of *Lutjanus* and one belonging to the genus *Hoplopagrus*. The three species discussed here are the red snapper or "huachinango" (*Lutjanus peru*), the "alazán" snapper (*Lutjanus argentiventris*) and the "lunarejo" or "flamenco" snapper (*Lutjanus guttatus*). They have a Panamic distribution, from the west coast of Baja California, in the vicinity of Bahía Magdalena, to Peru. The role of fisheries management is the conservation of exploited resources based upon monitoring of stocks and through a continuous reorientation of management policies (Holling 1978; Gulland 1982). Thus, the goal of the present paper is to contribute to the management of snapper resources based upon the principles of population dynamics integrated in a simulation model for each species.

The fishery

The shoreline of the State of Colima is characterized by a mixture of rocky coast and sandy beaches and a narrow continental

shelf. Mean sea surface temperatures range from 27.4 to 28.7°C. The continental shelf is narrow and fishing activities here began only recently. There are about 360 fishers mostly using hook-and-line, although gill nets, longlines and fish traps are also used. Most of the fishing boats used are 7.3 m (24 feet long) with outboard motors. Fishing trips take only a few hours every day and fishing grounds are spread over most of the rocky coastline of the State. Catch of the full species complex ranged from 3 686 t in 1980 to 1 177 t in 1986, with the number of fishing trips ranging from 1 246 in 1984 to 10 772 in 1980. Snappers represent 40-60% of total catch, and the red snapper represents more than 90% of all snappers (Cruz-Romero et al. 1988). The latter authors mention that there was a decline in catches from 1980 to 1985, with a partial recovery in 1986; fishing effort also showed a similar trend. Estimates of maximum sustainable yield (MSY) for the red snapper and other species of snappers have been presented previously (Cruz-Romero et al. 1988) as obtained by the application of the models of Schaefer and Fox (Doi 1973; Ricker 1975; Pauly 1988). These estimates gave MSY values ranging from 333 to 382 for the red snapper, with optimum effort ranging from 1 761 to 2 214 one-day trips. In the case of other snappers, considered as a single stock, maximum yield was estimated as 26 to 48, with optimum effort ranging from 170 to 173 trips. They concluded that the current catches are near-MSY levels, and that the declining catches were not the result of low stock biomass but rather that administrative problems constrain the development of the fishery.

Materials and Methods

Data on commercial landings were used in addition to one year of weekly samplings of the length-frequencies of the total catch at Manzanillo harbor and twice monthly at Boca de Apila. Length-weight data and stages of gonad maturity were also recorded for subsamples. Sex composition was determined at the sampling time, as well as confirmed in the laboratory with specimens whose gonads were also collected. Ovaries were analyzed using the maturity scale of Sokolov and Wong (1973). Fecundity was evaluated by the gravimetric method, based on the countings of 0.3 g subsamples of mature ova taken from the fore, medium and posterior ends of the right ovaries. Resulting values were raised to the total weight of the ovary and logarithmic regressions establishing the relationship between fecundity and body weight were derived for each species.

The growth parameters of the von Bertalanffy growth were estimated from the length-frequency data using ELEFAN I (Pauly 1987). After growth rates had been estimated, an age-length key was used to estimate the age structure of each stock. Then, natural mortality was determined by the equation of Pauly (1983). Length-weight relationships were established by means of logarithmic regressions.

Once the growth parameters (L_{∞} , K) and natural mortality (M) were estimated, the catch data for eight years were used to run an age-structured simulation model implemented on a spreadsheet, which reconstructed the population throughout the time period covered by the catch records. The model is based upon the estimated age structure of the stock in the year when the records showed the greatest catch. For this year, an estimate was made of the population size of each age class per age class (P_t). The exploitation rate (E, in this case the proportion of the unexploited stock

that is exploited each year), the fishing mortality (F) and its correspondence with the most likely catch value (C) were established, using the equations:

$$C = P_t \cdot E,$$

$$P_t = \sum T_i n_i w_i \text{ and}$$

$$E = (F/M+F)[1-\exp(-(F/M+F))].$$

Then, an iterative process involving different F values was implemented until the maximum likelihood was found between recorded and estimated catches; this also led to fishing mortality estimates for each year, as well as to the most likely number of one-year old recruits. The latter values were used to fit the Ricker (1954) recruitment model, used to simulate the effects of exploitation after the last catch records, and to identify the most appropriate exploitation strategy.

To establish the relationship among cohorts through time, it was necessary to define a relationship of dependence between the number of parents in one year (P) and the number of one-year old recruits (R) the following year. In order to accomplish this task, the number of one-year old recruits was determined empirically through the iterative process used also to obtain the best estimate of catch and fishing mortalities throughout the time period when catch data were available, as explained previously. Then the number of one-year old fish was fitted to the recruitment model by Ricker (1954)

$$R = \alpha \cdot A \cdot \exp(-(\beta \cdot A))$$

where α expresses density-independent mortality and β expresses density-dependent mortality. Cushing (1977) has discussed the meaning of the parameters of this model. Once parameter values were found, the alpha parameter of each stock was transformed by multiplication by a normally distributed random variable. The amplitude of variation used was +30% around the mean

parameter value, equivalent to the average number of recruits at that adult number the year before.

Parameter values for each stock were used to simulate the most likely development of exploitation of each stock twelve years after the last year of catch records.

Results and Discussion

Male:female ratios showed non-significant differences from unity in two of the three stocks analyzed, being of 1:1.05 for *L. guttatus*, and 1:0.9 for *L. argentiventris*. However, in *L. peru* it was 1:0.68. Minor seasonal differences were observed; for instance, in *L. guttatus* females are slightly more abundant than males during the spawning period from July through October.

L. guttatus spawns throughout the year, while in the case of *L. argentiventris*, spawning was observed to occur in April-May and from September through November. No mature females of *L. peru* were recorded from samples and spawning apparently occurs in deeper waters where females are not accessible to fishing gears. Ruiz et al. (1985) found that males of this species were more abundant during the spawning season, but our findings showed these differences to be more frequent throughout the year. The species is apparently iteroparous and a spawning period probably occurs in April and another one in September.

Although it is known that there is an exponential relationship between the size of females and their fecundity, and the snappers here studied may spawn several times throughout the year, an accurate estimate of the reproductive contribution of different age classes is still unknown.

Mean sizes observed in commercial catches range between 200 and 280 mm, corresponding to ages of 2.5-3 years. Minimum sizes of maturity were 170-180 mm in *L. guttatus*, 190-200 mm in *L.*

argentiventris and 220 mm in *L. peru*. Growth patterns are similar in the three stocks. In addition, it was found that 62% of the catch of *L. peru* are immature, which should be carefully examined in order to avoid the risk of premature overexploitation of juvenile fish. In contrast, in *L. argentiventris* and *L. guttatus* only 6 and 7% of the catch are immature.

In the case of *L. argentiventris* fecundity ranged from $0.759 \cdot 10^5$ to $3.56 \cdot 10^5$ in females whose standard lengths were 240 and 565 mm, respectively. In *L. guttatus* it was an order of magnitude larger and it ranged from $0.0664 \cdot 10^6$ to $2.17 \cdot 10^6$ in specimens whose standard lengths were from 200 to 490 mm. No data are available for *L. peru*. Tables 1 and 2 present our growth parameters and related estimates.

The estimates of fishing mortality (*F*) obtained independently for each stock throughout each of the years when catch records were available, i.e., from 1980 to 1988, and through a 12-year projection, are shown in Table 3, Fig. 1. They ranged from 0.01 to 0.32 year⁻¹ for *L. argentiventris*; from *F* = 0.11 to 0.4 year⁻¹ for *L. guttatus* and from *F* = 0.3 to 0.36 year⁻¹ for *L. peru*. These values lead us to interpret that the last mentioned species probably is the main

Table 1. Parameter values of the Ricker model for stock and recruitment [$R = \alpha \cdot A \cdot \exp^{-\beta \cdot A}$], establishing the relationship between adult numbers (A) and one-year old recruits (R) of three *Lutjanus* spp. from the west coast of Mexico. [Valores de los parámetros del modelo de Ricker para el stock y el reclutamiento ($R = \alpha \cdot A \cdot \exp^{-\beta \cdot A}$), estableciendo las relaciones entre el número de adultos (A) y reclutas de un año de edad (R) de tres especies de *Lutjanus* spp. de la costa occidental de México.]

Species	α	β
<i>L. argentiventris</i>	1.184	0.00009
<i>L. guttatus</i>	6.08	0.00001
<i>L. peru</i>	0.8	0.00008

Table 2. Asymptotic sizes (L_∞ , W_∞), K, length-weight relationship (a;b) and natural mortality (M) in three important species of *Lutjanus* from the west coast of Mexico. [Tallas asintóticas (L_∞ , W_∞), K, relación peso-longitud (a;b) y mortalidad natural (M) en tres especies de *Lutjanus* spp. de importancia en la costa occidental de México.]

Species	L_∞ (SL; cm)	W_∞ (g)	K (year ⁻¹)	a	b	M (year ⁻¹)
<i>L. argentiventralis</i>	68.5	6 676	0.155	0.070	2.75	0.33
<i>L. guttatus</i>	64.2	4 577	0.192	0.064	2.73	0.39
<i>L. peru</i>	64.0	5 536	0.156	0.061	2.75	0.33

target of the fishery, not only because of the fishing mortality values, but also because of its high catches and market value.

Values of the exploitation rates ($E = F/Z$) ranged from $E = 0.0084$ to 0.23 in the case of *L. argentiventralis*, from $E = 0.09$ to 0.28 in *L. guttatus* and from $E = 0.22$ to 0.26 for *L. peru*, showing that the latter stock has been exploited more intensely than the others. However, the three stocks are still

underexploited. It was found that in the case of *L. argentiventralis* the MSY is 6.2 and 10.9 t if $F = 0.7$, as compared to 2.06 and 3.5 if a value of $F = 0.1$ is applied in both cases, representing only 32 and 33% of the MSY value. For *E. guttatus*, the stock would be exploited to about 80% under the MSY values which would be 2.1 and 2.3 t for the same years. Finally, the MSY values for *L. peru* would be 417 and 444

Table 3. Observed/simulated catches of *L. argentiventralis*, *L. peru* and *L. guttatus*. Catch data for the years after 1988 are a 12-year simulated projection. [Capturas observadas/simuladas de *L. argentiventralis*, *L. peru* y *L. guttatus*. Datos de captura para los años posteriores a 1988 son una proyección de 12 años mediante simulación.]

Year	<i>L. argentiventralis</i>		<i>L. peru</i>		<i>L. guttatus</i>	
	Catch (t)	F	Catch (t)	F	Catch (t)	F
1980	24.66	0.32	379.81	0.33	3.21	0.4
1981	12.68	0.16	309.79	0.33	1.87	0.25
1982	3.99	0.05	215.82	0.3	0.77	0.11
1983	0.75	0.01	161.79	0.32	0.66	0.12
1984	0.65	0.01	153.51	0.34	0.64	0.15
1985	0.54	0.01	163.23	0.35	1.38	0.34
1986	2.05	0.05	204.69	0.36	2.05	0.38
1987	1.54	0.05	227.38	0.34	1.82	0.34
1988	1.32	0.05	280.20	0.35	1.72	0.35
+1	2.27	0.1	315.36	0.35	2.01	0.35
+2	2.15	0.1	354.95	0.35	2.09	0.35
+3	2.03	0.1	397.82	0.36	2.13	0.36
+4	2.08	0.1	389.91	0.36	2.38	0.36
+5	2.11	0.1	356.04	0.36	2.52	0.36
+6	2.16	0.1	337.02	0.36	2.44	0.36
+7	2.19	0.1	318.13	0.37	2.46	0.37
+8	2.44	0.1	327.12	0.37	2.47	0.37
+9	2.64	0.1	338.40	0.37	2.37	0.37
+10	2.83	0.1	334.15	0.38	2.36	0.38
+11	2.95	0.1	319.85	0.38	2.58	0.38
+12	3.15	0.1	328.24	0.38	2.65	0.38

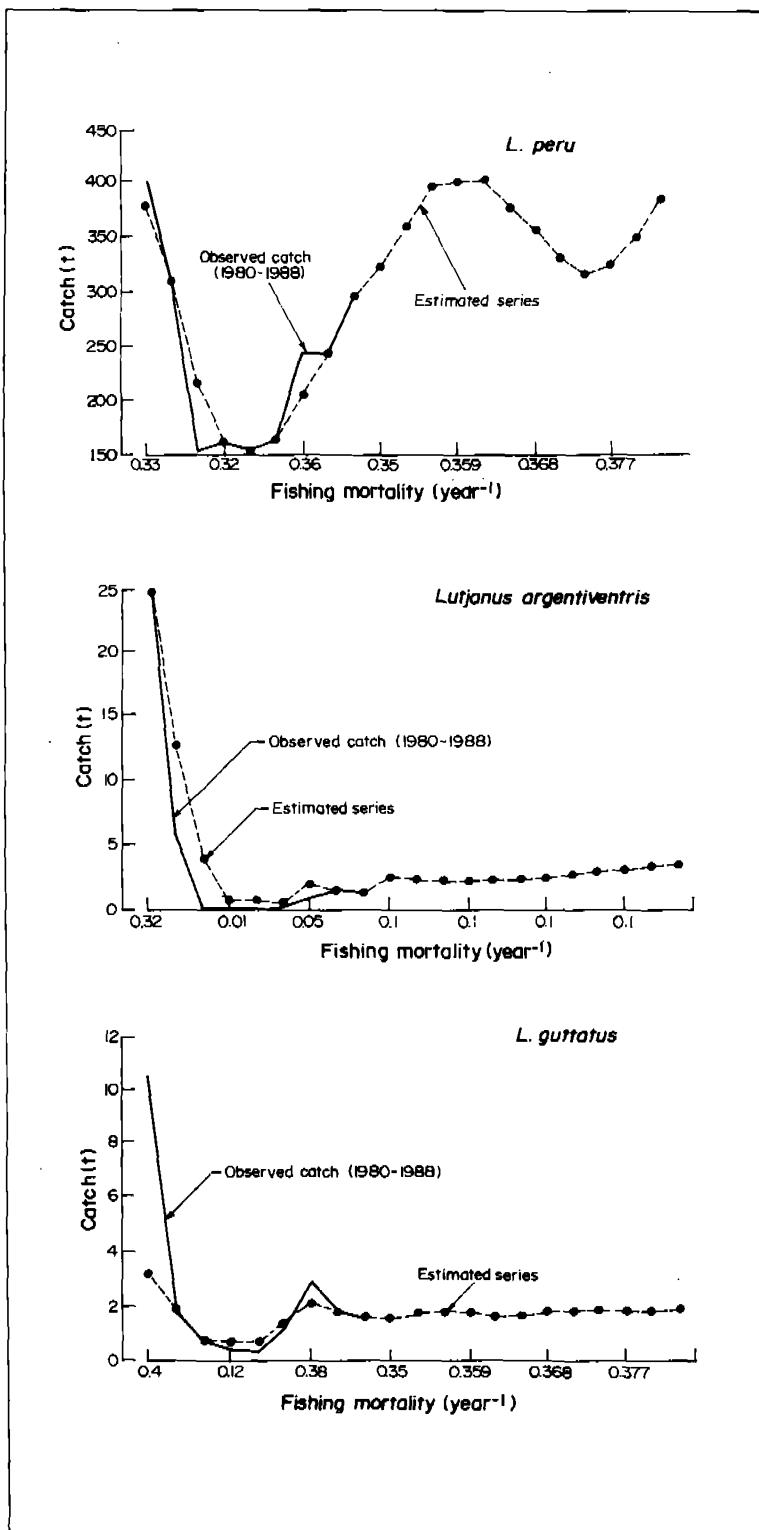


Fig. 1. Observed and simulated catch of *L. argentiventris*, *L. guttatus* and *L. peru* in West Mexico from 1980 to 1988 and in a 12-year projection. [Capturas observadas y simuladas de *L. argentiventris*, *L. guttatus* y *L. peru* en el occidente de México, de 1980 a 1988, y a lo largo de una proyección de 12 años.]

t, which would mean that the current fishery exploits only about 84% of the potential MSY.

A very common goal or strategy of management is the assessment of the F value that will produce maximum sustainable yield (MSY). In the case of *L. peru*, whose catch volumes represent about 99% of total catch, this can be expanded to about 70 t above the current level.

On the basis of the current results it is recommended that an increase of fishing effort not larger than the current population growth rate (about 2% per annum) should be maintained until the value of $F=0.7$ is reached. This policy would allow the possibility of creating jobs for new fishers at about the same rate every year. In addition, the management option chosen for this fishery should be defined every year after an assessment of the current stock size.

Sound studies on the fisheries biology of snappers must be made in other parts of their range in order to confirm the evidence presented here.

References

- Cruz-Romero, M., E. Espino and A. García. 1988. Estimación preliminar del índice de rendimiento máximo sostenible para la captura de escama ribereña. Universidad Autónoma de San Luis Potosí 10(2):109-123.
- Cushing, D.H. 1977. The problems of stock and recruitment, p. 116-133. In J.A. Gulland (ed.) Fish population dynamics. John Wiley & Sons, London.
- Doi, T. 1973. Análisis matemático de poblaciones pesqueras. Compendio para uso práctico. Instituto Nacional de la Pesca, Mexico.
- Gulland, J.A. 1982. Fish stock assessment-a manual of basic methods. FAO/Wiley Series on Food and Agriculture, Vol. I. John Wiley & Sons, New York.
- Holling, C.S., Editor. 1978. Adaptive environmental assessment and management. John Wiley & Sons, New York.
- J Pauly, D. 1983. Some simple methods for the assessment of tropical fish stocks. FAO Fish. Tech. Pap. No. 234, 52 p.
- J Pauly, D. 1987. A review of the ELEFAN system for analysis of length-frequency data in fish and aquatic invertebrates, p. 7-34. In D. Pauly and G.R. Morgan (eds.) Length-based methods in fisheries research. ICLARM Conf. Proc. 13, 468 p.
- J Pauly, D. 1988. Towards appropriate concepts and methodologies for the study of recruitment in tropical demersal communities, p. 3-14. In A. Yañez-Arancibia and D. Pauly (eds.) Proceedings of the IREP/OSLR Workshop on the Recruitment of Coastal Demersal Communities, Campeche, Mexico, 21-25 April 1986. IOC (UNESCO) Workshop Rep. No. 44.
- Ricker, W.E. 1954. Stock and recruitment. J. Fish. Res. Board Can. 11(5):559-623.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191:1-382.
- Ruiz, A., E. Giron, J. Madrid and A. Gonzalez. 1985. Determinación de edad, crecimiento y algunas constantes biológicas del huachinango del Pacífico, *Lutjanus peru* (Nichols and Murphy, 1922), p. 188-197. In Memorias del VIII Congreso Nacional de Zoología. Saltillo, Coahuila, Mexico.
- Solokov, V. and M. Wong. 1973. Programa general para la investigación de los peces pelágicos del Golfo de California. Prog. de Invest. y Fomento Pesqueros. PNUD/FAO. México, CEPOM, 51 p.

ENTREGO EN NAGA

Exploratory Fishing with Traps in Oceanic Islands off Eastern Venezuela during 1992

L.A. MARCANO

R. GUZMÁN

G.J. GÓMEZ

FONAIAP, Ctro. Inv. Agrop. Pesq. Sucre

P. O. Box 236, Cumaná 6101

Venezuela

MARCANO, L.A., R. GUZMÁN and G.J. GÓMEZ. 1996. Exploratory fishing with traps in oceanic islands off eastern Venezuela during 1992 [Pesca exploratoria con trampas en una isla oceánica del este de Venezuela durante 1992], p. 331-336. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Preliminary results are presented from an exploratory fishing program with traps undertaken at La Blanquilla and Los Hermanos Islands, northwest of Margarita Island in eastern Venezuela. Twelve monthly surveys were made between January and December 1992, with Antillean traps, at a depth of 37-128 m. Mean fishing effort was 154 trap-day·month⁻¹, and the total catch was 10 t, with a mean catch/effort of 5.6 kg trap⁻¹·day⁻¹. Catches were composed of 18 fish species. Snappers (Lutjanidae) were most abundant during the second half of the year, with an average yield of 5 kg trap⁻¹·day⁻¹, while groupers and hinds (Serranidae) and grunts (Haemulidae) produced low catches during the entire period.

Resumen

La presente contribución reporta los resultados preliminares de un programa de pesca exploratoria con trampas de peces antillanos alrededor de las islas La Blanquilla y Los Hermanos, al noroeste de Isla Margarita, este de Venezuela. Se efectuaron doce campañas entre Enero y Diciembre de 1991, con trampas antillanas colocadas a profundidades de 36.6-128.0 m. El esfuerzo de pesca promedio fué de 154 trampas·día mes⁻¹. La captura total fué de 10 t con un rendimiento medio de 5.65 kg trampa⁻¹·día⁻¹. Las capturas estuvieron compuestas por 18 especies de peces, entre las cuales un grupo de tres tenían interés comercial. Los meses de Enero, Agosto, Octubre y Noviembre, contribuyeron con el 47% de la captura total. Los pargos (Lutjanidae) fueron los mas abundantes durante la segunda mitad del año, con un rendimiento promedio de 5 kg trampa⁻¹·día⁻¹. Los meros y cabrillas (Serranidae) y roncos (Haemulidae) produjeron bajos rendimientos durante todo el período de estudio, sin picos de importancia en su abundancia.

Introduction

Venezuela, as a coastal country in the West Central Atlantic Ocean, has rich fisheries resources, owing to the North Equatorial Current and upwellings along the coast, which induce a high primary productivity, itself supporting important fish, crustacean and molluscan communities (Anon. 1989). Some of these communities have been intensively fished, but others have scarcely been exploited despite their potential importance.

La Blanquilla and Los Hermanos Islands, in eastern Venezuela, hold some of these latter communities. The rocky, coralline or sandy seabeds around these islands make them ideal habitats for commercial fish species. Among the most important fish families found in this area are Lutjanidae, Serranidae and Haemulidae (Ginés 1972). However, their fishing potential has not been properly evaluated.

The aforementioned arguments form the basis for the present study: an exploratory fishing program with traps, with the purpose of describing the demersal fish species of the area, as well as their distribution in space and time and their potential yield.

Study Area

The study area was located around La Blanquilla and Los Hermanos Islands, northwest of Margarita Island, between $11^{\circ}40'N$: $64^{\circ}23'W$ and $11^{\circ}50'N$: $64^{\circ}40'W$ (Fig. 1).

Materials and Methods

The fishing program was conducted between January and December 1992, through 12 monthly cruises on board the FONAIAP's *R/V Golfo de Cariaco*. The fishing gear was the Antillean Z-trap (Munro 1974; Fig. 2).

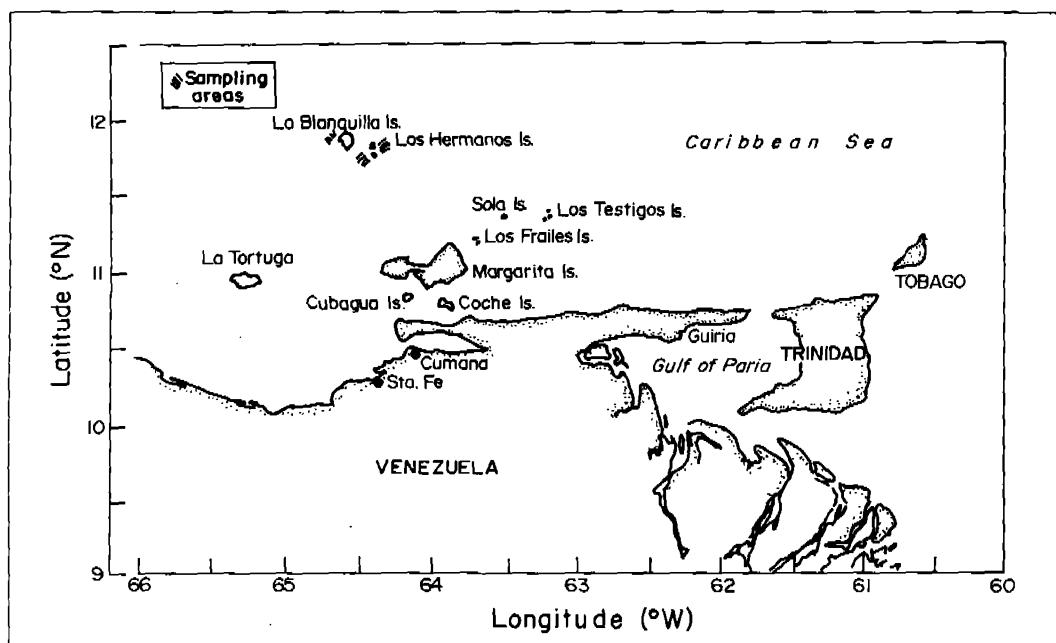


Fig. 1. Location of the sampling areas, showing the position of La Blanquilla and Los Testigos Islands in eastern Venezuela. [Localización de áreas de muestreo indicando la posición de las Islas La Blanquilla y Los Testigos, al este de Venezuela.]

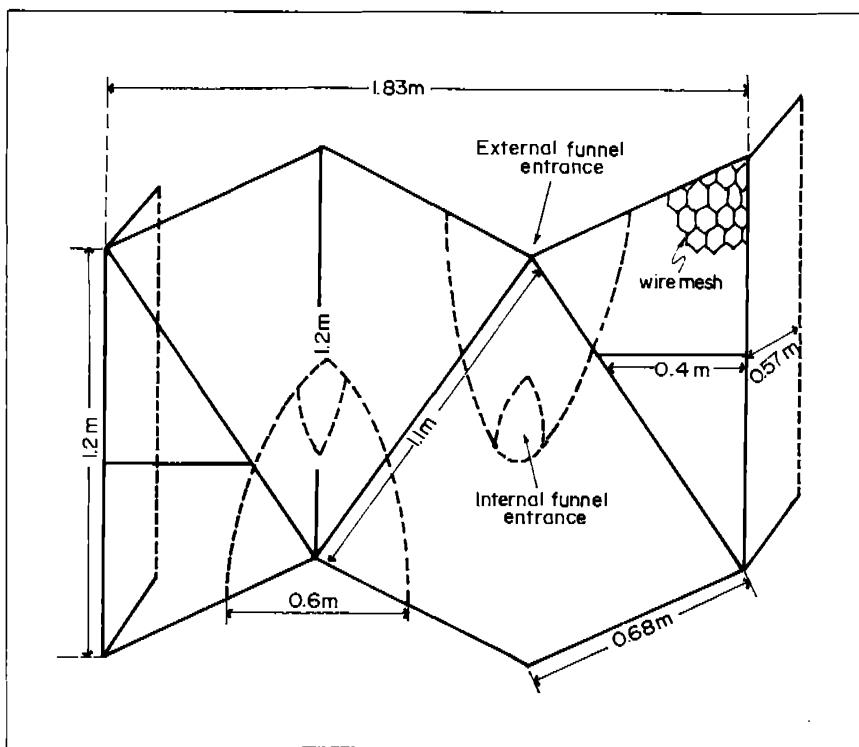


Fig. 2. Diagram of Antillean trap of the Jamaican type (after Munro 1974). [Diagrama de la trampa Antillana del tipo Jamalquino (adaptada de Munro 1974).]

This type of trap is considered to be one of the most efficient of its kind, and better than the ones with a single entrance (Buesa-Mas 1962).

Some 20 to 25 traps were used in every cruise. The traps were placed in groups of 4-5 traps, joined together with polyethylene rope, with an intertrap distance of 64.0-82.3 m, according to depth. The depth of the working area varied between 37 and 128 m. The traps were baited with fresh sardine (*Sardinella aurita*) and were checked every 24 hours. On some occasions, no bait was placed in the traps.

Lifting of the traps started at 0600-0700 hours; groups of traps were taken on board, the fish were removed and the traps rebaited and reset. Species identification, as well as measurements of the fish and evaluation of the sex and sexual maturity stage were then performed.

The data on capture of the main commercial fish species and the fishing effort (no. trap-days·month⁻¹) were used to derive an index of relative abundance, kg trap⁻¹·day⁻¹, by strata of time and space.

Results

Fishing effort varied from 100 to 178 trap-days·month⁻¹, with an average of 154 trap-days·month⁻¹, for a total of 1 848 trap-days during the study period (Table 1). Total catch was 10.4 t, with an average annual yield of 5.63 kg·trap-day⁻¹. The catch consisted of 18 fish species, among which there were two groups of major economic interest, the snappers (family Lutjanidae), and the groupers (family Serranidae), which accounted for 80% of total catch. There was a third group, of less commercial value but with substantial catches, formed by species of the family

Table 1. Distribution of the catch (kg) by species and effort (no. trap-days·month⁻¹), from the exploratory fishing with traps in La Blanquilla and Los Testigos Islands in January-December 1992. [Distribución de la captura (kg) por especies y esfuerzo (no. de trampas·día·mes), de la pesca exploratoria con trampas en las Islas La Blanquilla y Los Testigos, de Enero-Diciembre de 1992.]

Species caught	Month												Total
	J	F	M	A	M	J	J	A	S	O	N	D	
	Catch (kg)												
<i>Lutjanus buccanella</i>	202	117	136	158	166	123	231	211	87	309	262	139	2 141
<i>Lutjanus vivanus</i>	134	95	98	105	111	122	141	140	81	181	167	85	1 460
<i>Rhomboplites aurorubens</i>	569	115	290	99	400	400	281	433	413	324	439	100	3 863
<i>Epinephelus guttatus</i>	35	17	27	73	44	30	12	49	1	32	13	27	360
<i>Epinephelus morio</i>	7	-	4	31	11	13	9	10	-	27	20	16	148
<i>Mycteroperca ciliata</i>	2	5	20	21	21	8	29	52	3	71	46	33	311
<i>Haemulon melanurum</i>	356	66	110	30	95	94	65	19	44	223	205	35	1 342
<i>Holocentrus ascensionis</i>	16	14	32	6	-	19	4	2	-	5	-	4	102
<i>Caranx</i> sp.	-	8	-	-	9	14	3	3	-	2	63	28	130
<i>Rhizoprionodon porosus</i>	30	7	9	1	4	3	-	1	-	4	3	2	64
<i>Gymnothorax</i> sp.	-	6	22	89	12	10	26	80	-	6	-	4	255
<i>Lycodontys</i> sp.	-	-	36	26	9	-	-	4	-	2	-	3	80
<i>Caulolatilus</i> sp.	-	1	3	-	4	-	2	30	-	9	8	2	59
<i>Calamus</i> sp.	-	-	6	-	3	3	-	3	-	3	5	-	23
<i>Balistes</i> sp.	2	-	-	-	4	-	1	-	-	1	-	1	9
<i>Sphyraena barracuda</i>	-	-	-	3	-	1	-	-	-	2	-	-	6
<i>Prionotus</i> sp.	15	20	-	-	1	-	-	-	-	3	-	-	39
<i>Glyptothorax cirratum</i>	6	-	-	-	-	-	-	-	-	-	-	-	6
Total catch	1 374	471	793	642	894	840	804	1 037	629	1 204	1 231	479	10 398
Trap-days·month ⁻¹	198	178	175	121	190	169	136	121	100	155	178	127	1 848
Fishing days	9	8	8	5	8	8	6	6	4	7	7	7	83
Depth (m)	80-102	86-113	66-110	51-110	37-115	73-115	68-104	62-115	82-101	62-121	68-113	49-128	

Haemulidae, which accounted for 13% of the total catch (Table 1).

The snapper catch, the most important group of fish in the sample, consisted of *Rhomboptilus aurorubens* (51%), *Lutjanus buccanella* (29%) and *L. vivanus* (20%) and their monthly catch varied from 471 kg to 1 374 kg, with January, August, October and November producing 47% of the total catch (see Cuellar et al., this vol.).

Snappers were more abundant during the second half of the year, with an average yield of $4.96 \text{ kg trap}^{-1} \cdot \text{day}^{-1}$. Groupers, on the other hand, varied little from 0.1 to $1.0 \text{ kg trap}^{-1} \cdot \text{day}^{-1}$. In the case of the grunts, there were important variations in catch/effort, with a short period (October-November) in which the greatest values were observed.

Among the Lutjanidae, *R. aurorubens* was the most abundant species with an average

annual catch/effort of $2.1 \text{ kg trap}^{-1} \cdot \text{day}^{-1}$, with a maximum from May to November. The average catch/effort for *L. buccanella* and *L. vivanus* were 1.2 and $0.8 \text{ kg trap}^{-1} \cdot \text{day}^{-1}$, respectively, with the greatest abundance during the period July-December for both of these species.

The bathymetric distribution of abundances (Fig. 3) showed that the Lutjanidae were most abundant at depths between 66 m and 91 m, while the Serranidae were most abundant in deeper waters (102-110 m).

Discussion

The number of fish species encountered during the exploratory survey in the La Blanquilla and Los Hermanos Islands was low in comparison with other, similar ecosystems in the Venezuelan Caribbean. Thus,

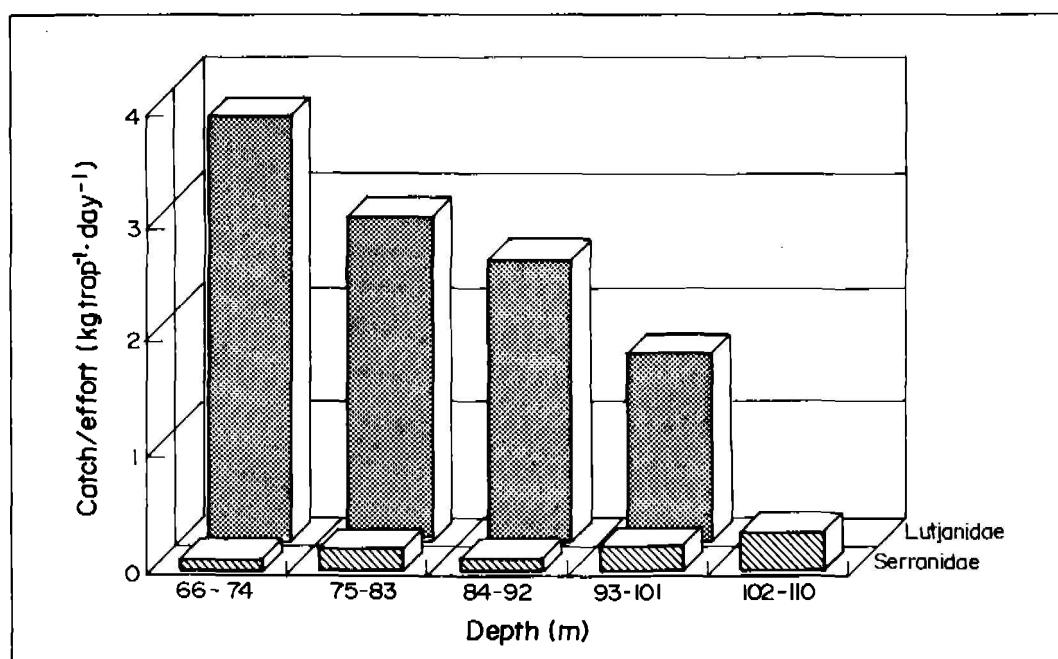


Fig. 3. Bathymetric distribution of the yields ($\text{kg trap}^{-1} \cdot \text{day}^{-1}$), by group of species (familles Lutjanidae and Serranidae), from the exploratory fishing with traps in the La Blanquilla and Los Testigos Islands in January-December 1992. [Distribución bathimétrica de los rendimientos ($\text{kg trampa}^{-1} \cdot \text{día}^{-1}$), por grupo de especies (familias Lutjanidae y Serranidae) de la pesca exploratoria con trampas en las islas La Blanquilla y Los Testigos, de Enero-Diciembre de 1992.]

Cervigón (1982) reported that 76 fish species were captured with traps placed on coralline bottom, at depths from 7.3 m to 64 m in the Los Roques Archipelago.

Ginés (1982) suggested for Los Roques Archipelago, and the La Orchila and Aves Islands, that the observed high fish species diversity was due to high nutrient concentration, as a result of upwellings.

The analysis of the total catch revealed that snappers were the dominant group of fish species caught in our survey contributing 72% in weight. This result matches earlier results of Baez and Plaut (1978), conducted in the same area, and who reported that this group of fish contributed 65% of their total catch.

The snappers show a definite seasonality, with a greater abundance during the second half of the year, at depths between 65.8 m and 91.4 m. Cervigón (1982) also found that snappers were more frequent in catches from May to November elsewhere in the Venezuelan Caribbean. Cervigón (1982) also found a definite bathymetric preference in some species of groupers, some being more abundant between 7.3 m and 64 m. This fact would explain the low yields found for these two families in our study, since most of our samples were taken at a greater depth.

Considering that the study area is important for its commercial fishing potential, and that the exploitation of its resources has begun only recently, it is recommended that studies on the biology, population dynamics and fishery of the major fish species should be promptly undertaken.

Acknowledgements

We thank FONAIAP technicians R. Chacón, R. Marcano, M. Márquez, A. Urbaneja and G. Vizcaíno for their participation in the field and laboratory work; Cachan Gil for the processing of the data, and J. Alió for the revision and translation of the manuscript.

Also, we acknowledge the crew of the *R/V Golfo De Carácaro*, whose will and discipline made this work possible.

References

- Anon. 1989. Prospecciones de recursos de las áreas de la plataforma entre Surinam y Colombia. NORAD/UNDP/FAO Program. Report on surveys with *R/V Fridtjof Nansen*, Institute of Marine Research, Bergen, Norway. 143 p.
- Baez, C. and P. Plaut. 1978. Pesca exploratoria costera. Ensayos de pesca mecanizada aplicable a la pesca artesanal. Prog. CIP-MAC-CONICIT. 18 p.
- Buesa-Mas, R.J. 1962. La nasa antillana. Contrib. Cent. Invest. Pesq., La Habana (15):5-26.
- Cervigón, F. 1982. Especies y rendimiento de peces comerciales capturados con nasas en un área del archipiélago de Los Roques. Inf. MAC, Caracas. 26 p.
- Ginés, H., Editor. 1972. Carta pesquera de Venezuela. I. Areas del nororiente y Guayana. Fund. La Salle de Cienc. Nat., Caracas. Monografía No. 16, 316 p.
- Ginés, H., Editor. 1982. Carta pesquera de Venezuela. II. Areas central y occidental. Fund. La Salle de Cienc. Nat., Caracas. Monografía No. 27, 226 p.
- Munro, J.L. 1974. The mode of operation of Antillean fish traps and the relationship between ingress, escapement, catch and soak. J. Cons. CIEM 35(3):337-350.

ENTERED IN FILE

APR 14 1998

Impact of Variability in Numbers and Size at First Recruitment on the $F_{0.1}$ Reference Point in the US Red Snapper Fisheries of the Gulf of Mexico

N.M. EHRHARDT

C.M. LEGAULT

Division of Marine Biology and Fisheries

Rosenstiel School of Marine and Atmospheric Science

University of Miami

4600 Rickenbacker Causeway

Miami, Florida 33149-1098 USA

EHRHARDT, N.M. and C.M. LEGAULT. 1996. Impact of variability in numbers and size at first recruitment on the $F_{0.1}$ reference point in the US red snapper fisheries of the Gulf of Mexico. [*Impacto de la variabilidad en número y tamaño de primer reclutamiento sobre el parámetro de referencia $F_{0.1}$, en las pesquerías de pargo del Golfo de México de US*], p. 337-349. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) *Biology, fisheries and culture of tropical groupers and snappers*. ICLARM Conf. Proc. 48, 449 p.

Abstract

Red snapper (*Lutjanus campechanus*) is heavily exploited by commercial and recreational fisheries in the US Gulf of Mexico. Additionally, a large number of red snappers are caught as bycatch in the shrimp trawler fishery. The directed fisheries are managed under strict catch quotas, minimum size restrictions, area closures and gear restrictions. However, the ability of these measures to recover the stock may be compromised by the large, and uncertain, nondirected catch. The annual uncertainty in the shrimp trawl bycatch was estimated through a bootstrap procedure and this uncertainty was propagated to the stock assessments. To examine the relationship between the shrimp trawl bycatch and the directed fishery management, stock assessments were carried out under three scenarios: 1) management of directed fisheries considering nondirected catch; 2) management of directed fisheries not considering nondirected catch; and 3) management of directed fisheries under zero discards. Resulting allowable biological catches computed under the biological reference point $F_{0.1}$ show that the shrimp trawl bycatch reduces significantly the amount of biomass available to the directed fishery. The shrimp trawl bycatch also smooths the recruitment of red snapper into the directed fishery thus reducing the variability of the directed catch.

Resumen

*El pargo del Golfo, *Lutjanus campechanus*, es fuertemente explotado por pesquerías comerciales y recreativas en aguas de US del Golfo de México. Adicionalmente, un número importante de pargos del Golfo son capturados como fauna acompañante en la pesquería de arrastre de camarón. Las pesquerías dirigidas son manejadas bajo un sistema estricto de cuotas, restricciones a tamaño mínimo, áreas vedadas y restricciones a las artes de pesca. Sin embargo, la habilidad de estas medidas para lograr la recuperación del stock puede ser comprometida por la gran cantidad, e incertidumbre, de captura no dirigida. La incertidumbre anual de la captura acompañante de los arrastres de camarón fué estimada a*

través de la técnica de "bootstrap", y fué propagada a la evaluación del stock. Para examinar las relaciones entre la captura acompañante de los arrastres camaróneros y el manejo dirigido a la pesquería, la evaluación del stock se llevó a cabo bajo tres escenarios: 1) manejo de la pesquería dirigida considerando la captura no dirigida; 2) manejo de la pesquería dirigida sin considerar la captura no dirigida; y 3) manejo de la pesquería dirigida bajo cero descargas. Las capturas biológicas permisibles resultantes calculadas bajo el punto de referencia biológico F_0 , mostró que las capturas de arrastres de camarón reduce significativamente la cantidad de biomasa disponible para la pesquería dirigida. La captura acompañante de camarón también suaviza el reclutamiento del pargo del Golfo en la pesquería dirigida reduciendo la variabilidad de la captura dirigida.

Introduction

The Gulf of Mexico red snapper (*Lutjanus campechanus*) resources are distributed from Florida to the Yucatan Peninsula (Fig. 1). In the United States' Exclusive Economic Zone the species sustain economically important commercial and recreational fisheries. Landings in the US commercial fishery (Fig. 2) were stabilized at about 3 100 t in 1964-1976. However, a decline in landings occurred during the 1980s and only 990 t

were taken in 1991, mainly as a result of strict quota allocations. A slight increase of commercial landings was observed in 1992 and 1993, resulting from management actions imposed on the fishery. Decreases in landings do not appear to follow similar patterns Gulf-wide. Historically, landings have been more severely reduced in grids 1 to 9 (Fig. 3), corresponding to areas from Florida to Alabama (Fig. 1), than in grids 10 to 21 off Mississippi, Louisiana and Texas. Commercial landings are mostly

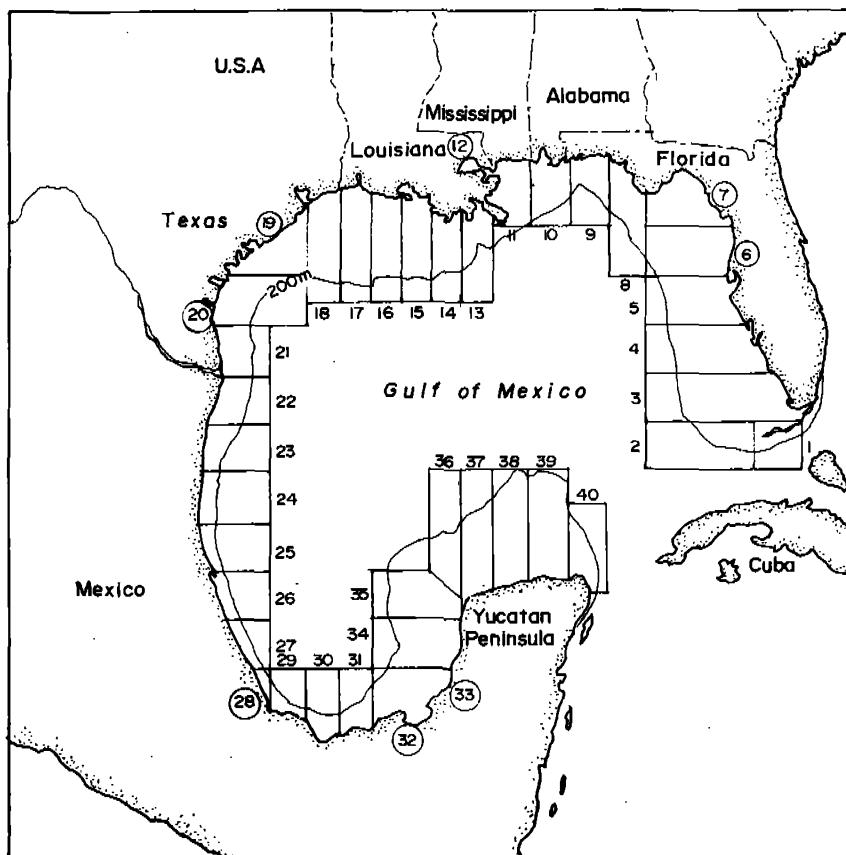


Fig. 1. Gulf of Mexico with National Marine Fisheries Service statistical grids.
[Golfo de México con las áreas estadísticas del Servicio Nacional de Pesquerías Marinas.]

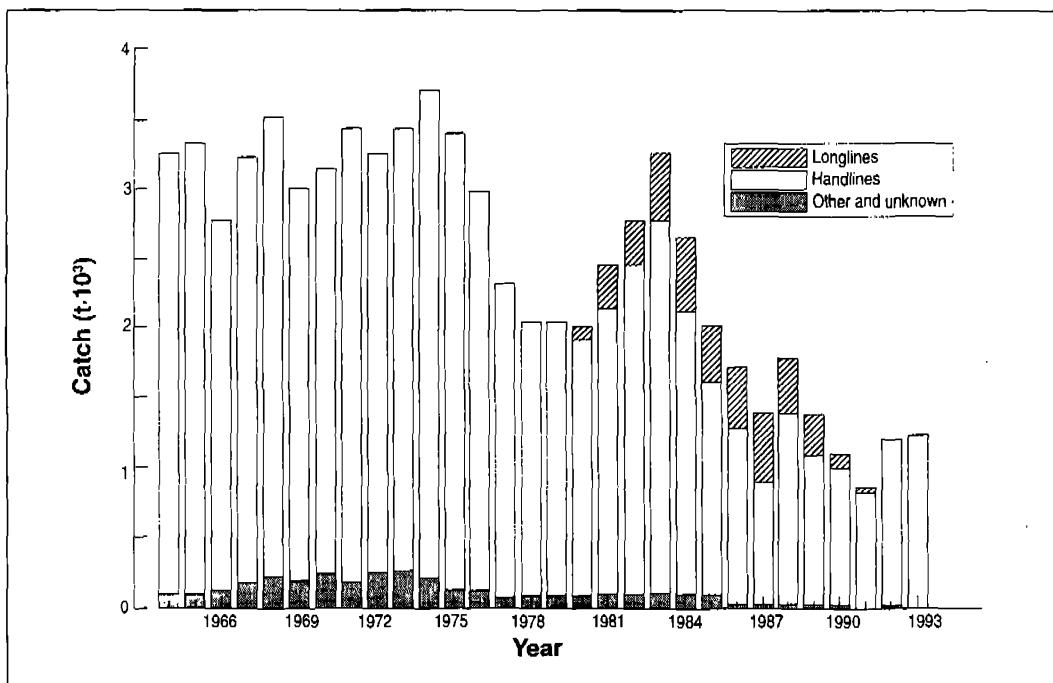


Fig. 2. Red snapper commercial landings by gear and year of the US fleet. [Descargas comerciales del pargo del Golfo por arte de pesca y año de la flota de EU.]

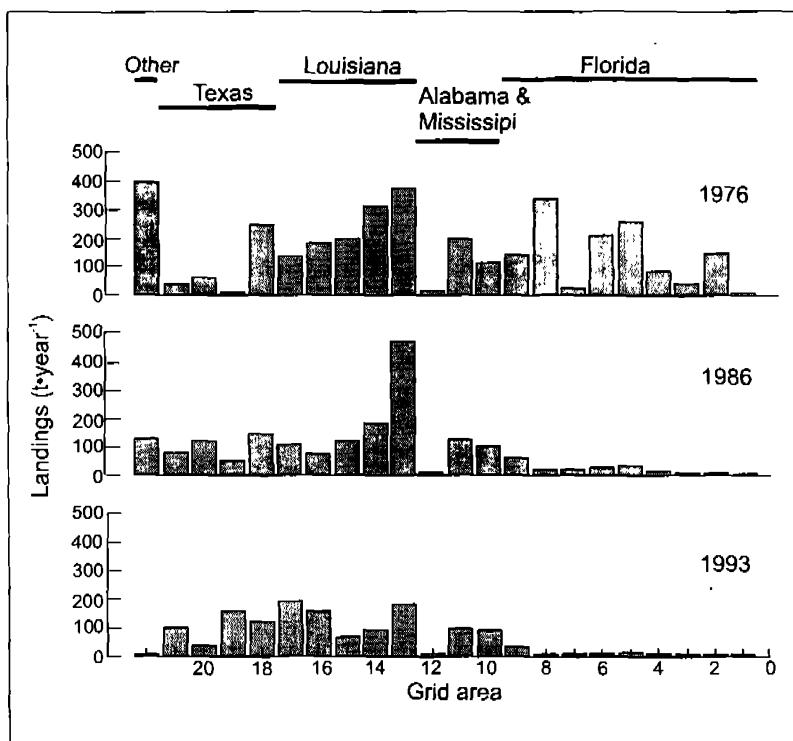


Fig. 3. Commercial landings of red snapper for three years by NMFS statistical grid. [Descargas comerciales del pargo del Golfo para tres años por área estadística del NMFS.]

from fishing operations with handlines, with some catches taken by bottom longlining in the 1980s (Fig. 2).

The US recreational fishery landed about 5 000 t·year⁻¹ during 1979-1981 (Fig. 4). However, a steady decline in recreational landings occurred in the early 1980s which stabilized at an average of 935 t during 1986-1992. The decrease in recreational landings in 1990 was the result of a significant increase in the number of undersized fish released as a consequence of adopting a 33.0 cm (13 inch) minimum size (Fig. 5) and a bag limit of 7 red snappers per person per day. Release mortality in the recreational fishery is unknown; however, a release mortality of 33% per year has been used in stock assessment work (Goodyear 1993).

The red snapper fisheries in the US sector of the Gulf of Mexico are intensively managed as a consequence of increased fishing pressures exerted on the stocks. Management actions include strict catch quotas, minimum size restrictions, area closures and gear restrictions. In spite of these management actions, the stocks have remained at low levels of abundance, with spawning potential ratios at slightly above one percent (Goodyear 1993). However, these extremely low levels of spawning stock biomass are not the consequence of the directed fisheries alone but, more significantly, a result of very high mortalities inflicted indirectly on ages 0 and 1 by the shrimp trawl fishery.

A "Reef Fish Fishery Management Plan" developed by the Gulf of Mexico Fishery Management Council (GMFMC) mandates that a spawning potential ratio for the species should be at least 20% by the year 2007. This goal, however, may not be attainable unless considerable reductions in the discarded shrimp bycatch are considered (GMFMC 1993). In this paper we analyze the effect of discards of red snapper in the shrimp fishery on the traditional biological reference point of $F_{0.1}$ (Gulland and Boerema

1973), commonly used to estimate allowable biological catches (ABCs) (see Scott Denton and Nance, this vol.).

Materials and Methods

Red snappers discarded in the shrimp trawl fishery were estimated by multiplying catch of red snappers per unit of shrimp fishing effort and the total amount of shrimp fishing effort exerted in the different areas of the US sector of the Gulf of Mexico. For this purpose red snapper catch per unit of effort was estimated by a general linear model (GLM) developed by Nichols et al. (1987) and used in a bootstrap algorithm developed by Ehrhardt and Legault (in press). The algorithm applies to a shrimp bycatch database which consists of several data sources collected since 1971 by the National Marine Fisheries Service in the Gulf of Mexico (Nichols et al. 1987, 1990; Nichols and Pellegrin 1992). These data sources were generated during sea turtle excluder device evaluations, a sea turtle incidental catch project, a shrimp bycatch evaluation project and the National Marine Fisheries Service resource survey cruise program in the Gulf of Mexico. Each record in the database corresponds to a single bottom trawl tow and the information consists of date, location, depth, length of tow, catch by species and ancillary information on sea conditions.

The GLM used in the bootstrap algorithm is given as

$$\log(\text{CPUE}+1)_{ijklm} = \text{mean} + \text{data set}_i + \text{year}_j + \text{season}_k + \text{area}_l + \text{depth}_m + \varepsilon_{ijklm}$$

where "CPUE" is the red snapper catch rate in numbers per hour fishing, "mean" is the overall red snapper relative abundance and "data set" is an effect term discriminating shrimp fishing effort from research survey fishing effort in the database. The terms "year", "season", "area" and

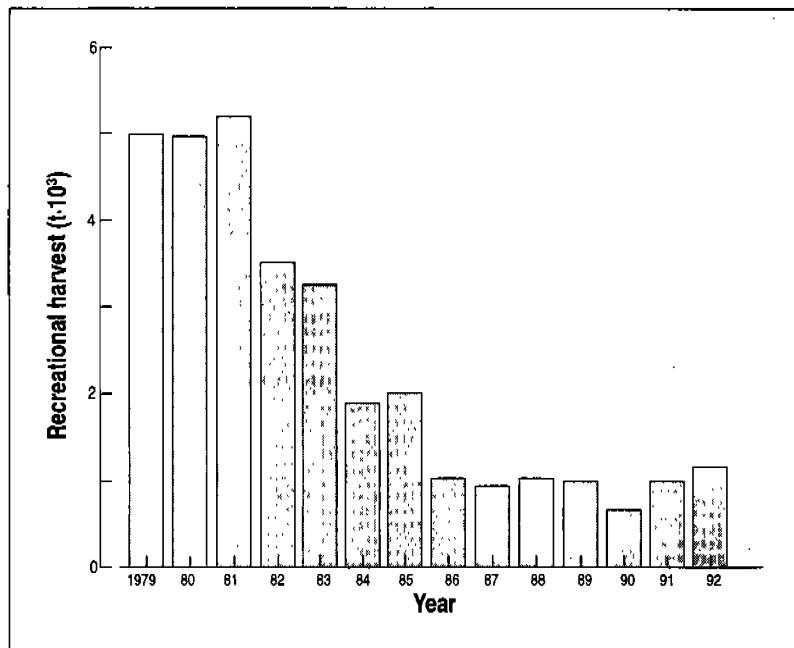


Fig. 4. Red snapper recreational harvest by year in the US Gulf of Mexico. [Captura de pesca recreativa por año en el Golfo de México de EU.]

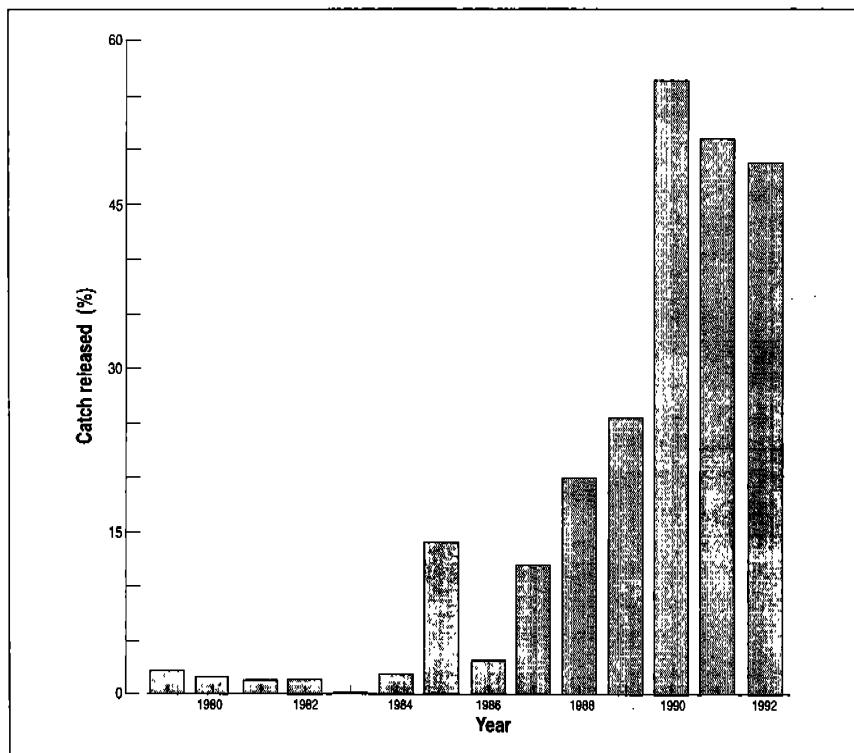


Fig. 5. Marine Recreational Fisheries Statistical Survey estimates of recreational release of red snapper in the US Gulf of Mexico. [Estimaciones de liberación de pargo del Golfo en la pesca deportiva del Golfo de México de US, de las estadísticas de cruceros de las Pesquerías Marinas Recreativas.]

"depth" are effects terms for the spatial and temporal breakdown and "ε" are error terms assumed to be independently and normally distributed.

Discard estimates are subjected to significant levels of uncertainty derived from the estimation procedure. Therefore, a variance for the annual estimates was obtained by resampling, with replacement, tow records at random from the database. A total of 250 bootstrap samples were generated through this procedure and estimates of red snapper catch-per-unit-of-fishing-effort were obtained for each sample using the GLM.

Shrimp fishing effort estimates were derived from data collected by the dealer canvas/vessel interview system conducted by port agents for the National Marine Fisheries Service, Southeast Fisheries Center. Effort estimates for each month/area/depth cell were calculated by dividing total reported shrimp catch (ignoring species) by average shrimp catch per effort from the interview data (Nichols et al. 1987).

Discard estimates were distributed among ages 0 and 1 in a 58:42 ratio according to red snapper catch-at-age information available at the National Marine Fisheries Service, Miami Laboratory.

Values of $F_{0,1}$ were estimated as those values of instantaneous fishing mortality rate, F , corresponding to a point in the catch curve where the slope of the curve is 10% of that in the origin. The Beverton and Holt (1957) equilibrium catch curve equations were not used to estimate $F_{0,1}$; rather, nonequilibrium catch curves were generated for a range of fishing mortality rates based on the estimated population age structure present in the fishery and a gear selectivity at age vector as

$$\text{Catch} = \sum(s_j F / (s_j F + M)) (1 - e^{-(s_j F + M)}) N_j W_j$$

where s_j is selectivity at age j , M is the instantaneous natural mortality rate, N_j and

W_j correspond to numbers and average weight at age, respectively, and the sum is over all ages.

Cohort abundances, N_i , in a given year were estimated by the traditional sequential population analysis (SPA) technique of Gulland (1965). Initial fishing mortality rates used as a parameter required in SPA were obtained from separable SPA techniques developed by Pope and Shepherd (1982) and then used as input in a CPUE-calibrated SPA which adjusted the initial F values to minimize the difference between expected and observed CPUEs. The calibration technique consists of a nonlinear least squares procedure developed by Gavaris (1988) and included in an expanded FORTRAN algorithm developed by V. Restrepo (University of Miami, pers. comm.).

A catch-at-age matrix required for SPA was obtained from Goodyear (1993) and integrated with discard estimates for ages 0 and 1 obtained by the GLM algorithm. Because discards were estimated by a bootstrap GLM procedure (Ehrhardt and Legault, in press), several discard estimates were thus available for each year in the matrix. Consequently, SPAs were run as many times as matrices were available to estimate N_s .

Natural mortality rates required in the SPA procedure are not well known for red snapper. However, Nelson and Manooch (1982) have estimated natural mortality rates of 0.18-0.20 year⁻¹ for the species using the approximation of Pauly (1980). Standard red snapper stock assessment work performed by the US National Marine Fisheries Service (Goodyear 1993) currently use a natural mortality rate of 0.20 year⁻¹. Therefore, a similar rate was adopted in this study.

ABCs for any year i were estimated from Baranov's catch equation corresponding to a given $F_{0,1}$ and exploited population biomass, B_i , according to

$$\text{ABC}_i = \sum(F_{0,1} / (F_{0,1} + M)) (1 - e^{-(F_{0,1} + M)}) B_i$$

where:

$$B_i = N_{ij} W_i$$

N_{ij} = numbers of age j in year i estimated from SPA

W_i = average weight of a fish of age j .

Analyses of the fishery under the assumption of zero discards in the shrimp fishery were accomplished by adding the discard estimates to the recruitment in the directed fishery, discounted by the natural mortality rate that might have acted upon the individuals if they had not been discarded. With these values, a matrix of expected catch at age was constructed using the fishing mortality rates previously estimated by SPA applied to the directed fishery only. The resulting matrices were used in other SPAs to calculate abundance matrices and the values of abundance at age were used to estimate new $F_{0.1}$ s and ABCs in year i .

Results and Discussion

A total of 250 bootstrapped GLMs were run with the discard database corresponding to the period 1972 to 1991. The resulting values for 1982 to 1991 are given in Fig. 6. Two facts are immediately evident from the figure: 1) red snapper discards in the shrimp fishery are extremely large and 2) annual discard estimates have very different levels of variability. Years with the highest number of discards are 1990 and 1991 when on average between 40 and 50 million fish were discarded. There are six other years when discards are the lowest, ranging from 15 to 25 million fish, although the shrimp fishing effort varied from 17 to 25 thousand days fished during these years (Fig. 7).

The catch-at-age matrix resulting from the directed and nondirected fisheries corresponded to the period 1984 to 1991. Therefore, results of SPA are estimated 1992 numbers-at-age. Cohort abundances for this year and their corresponding confidence intervals are given in Fig. 8. It is evident

from this figure that the effect of discards in the shrimp fishery overwhelms the population to the point that population abundance available for the directed fisheries is so low that any management restriction imposed on the directed fisheries would not generate any meaningful result in terms of recuperation of this fishery from severe overexploitation. This situation contrasts dramatically with cohort abundances obtained under the condition of zero bycatch in the shrimp fishery (Fig. 8). This situation is in agreement with the findings of the GMFMC (1991) when it concluded that unless the shrimp fishery reduces the shrimp bycatch, the red snapper fishery would not recuperate from overexploitation by the 2007 target date.

The comparison of bycatch and no bycatch cases in Fig. 8 also shows the effect of bycatch smoothing recruitment to the directed fishery. The no bycatch population abundance at age 2 has a much larger confidence interval than the bycatch case, thus another source of uncertainty arises when the variability in bycatch is removed. The high level of discard mortality in the shrimp fishery appears to act as a smoothing process whereby both high and low biological recruitment years will result in similar recruitment to the directed fishery. The relative importance of these two sources of uncertainty in recruitment to the directed fishery deserves more attention in the future.

In order to measure the effect of discards variability on $F_{0.1}$ and the resulting effect on ABCs, SPAs were run with all other parameters constant (i.e., point estimates of natural mortality, CPUE series used in calibrations and catch at age matrix of directed fishery were assumed with no error). Three scenarios were prepared with the results: 1) management of directed fisheries considering nondirected catch in ABC estimates; 2) management of directed fisheries not considering nondirected catch in ABC estimates; and 3) management of directed fisheries under zero bycatch.

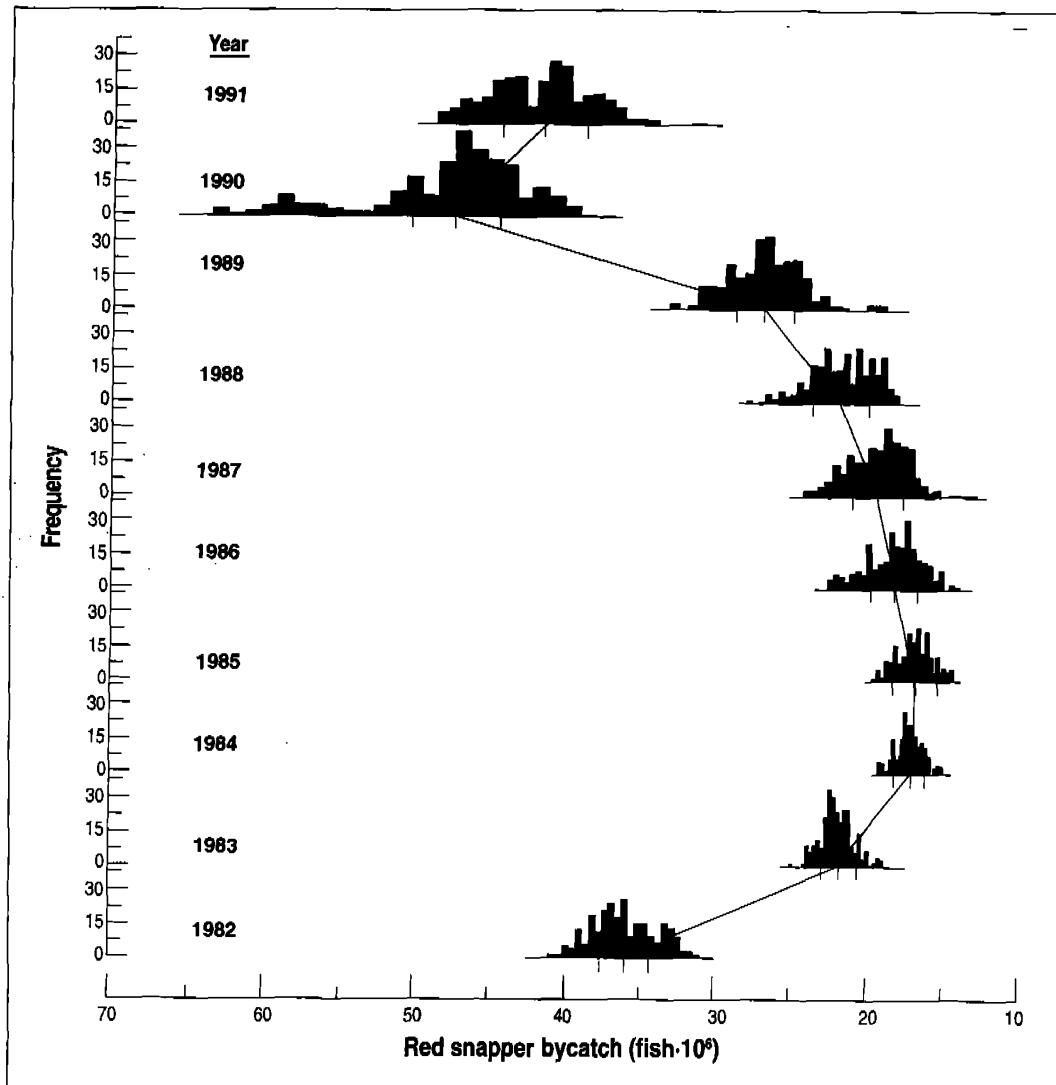


Fig. 6. Annual bycatch of red snappers in the shrimp fishery for years 1982 to 1991. The histograms are the results of 250 bootstraps of the original data as described in the text. The solid line connecting the histograms denotes the mean estimate of annual bycatch from Nichols and Pellegrin (1992) and the ticks below the histograms are the 90% confidence Intervals estimated by Nichols and Pellegrin (1992) using the delta method. Note the bycatch axis increases to the left. [Captura incidental anual del pargo del Golfo en la pesquería de camarón para los años 1982 a 1991. Los histogramas son el resultado de 250 iteraciones siguiendo la técnica "bootstrap" de los datos originales como es descrito en el texto. La línea continua que conecta los histogramas indica la estimación media anual de la pesca incidental según Nichols y Pellegrin (1992), y las líneas apuntando abajo del histograma corresponden al 90% del Intervalo de confianza estimado por Nichols y Pellegrin (1992) usando el método delta. Note que el eje de pesca incidental aumenta hacia la izquierda.]

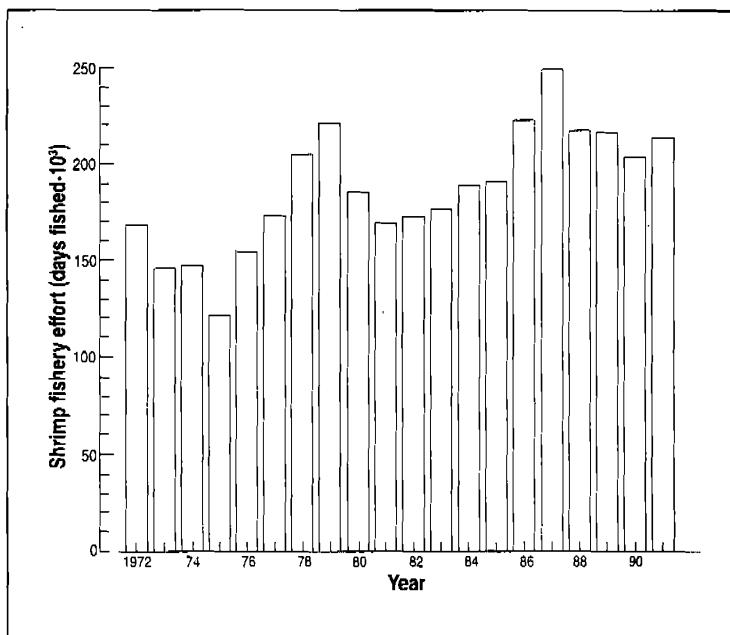


Fig. 7. Estimated number of days fished annually in the shrimp fishery of the US Gulf of Mexico. [Número estimado de días de pesca al año en la pesquería de camarón del Golfo de México de EU.]

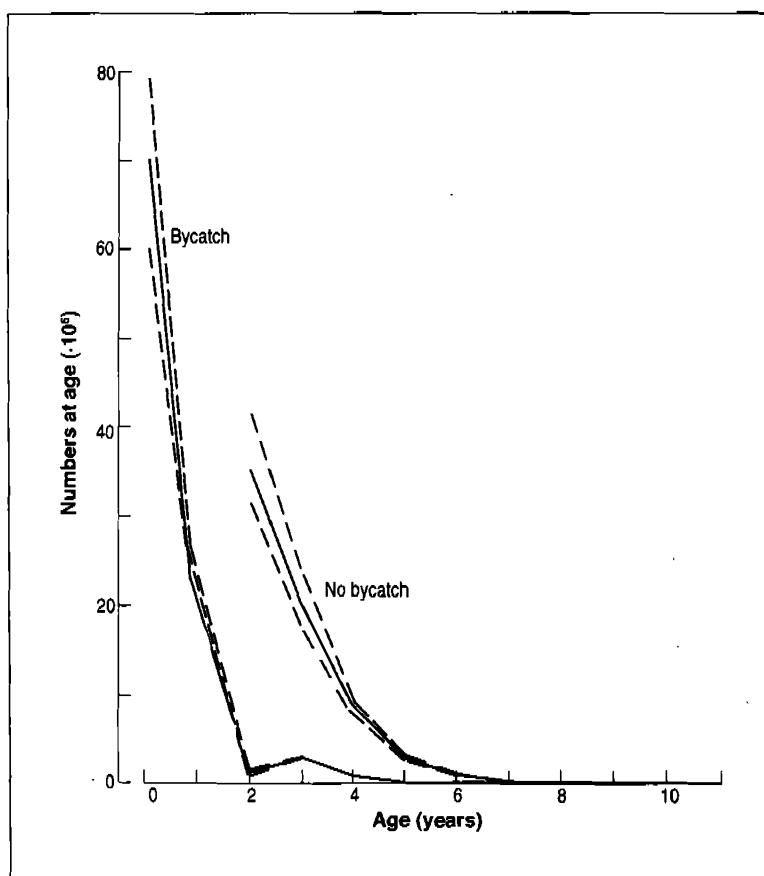


Fig. 8. Estimated 1992 population abundance at age for bycatch and no bycatch cases described in the text, each with 95% confidence intervals. [Abundancia por edad estimada para la población de 1992 por pesca incidental o sin ella descritas en las pruebas, cada uno con intervalos de confianza al 95%.]

Fig. 9 gives the mean yield curve for scenario 1, bycatch considered as part of the ABC, with the $F_{0.1}$ and associated yield points superimposed on the curve. Each of the 250 annual bycatch bootstraps would have its own yield curve, but all the curves are not presented for the sake of clarity. The mean bycatch vector produced an $F_{0.1}$ of 2.2 year^{-1} with an associated yield of 9 290 t. The uncertainty in the bycatch produced a range in $F_{0.1}$ of approximately 2.1 to $2.4 \cdot \text{year}^{-1}$ for the 250 bootstraps, as shown in the lower histogram of Fig. 9. This small range in the management parameter $F_{0.1}$ produced a very large range in the associated yield though,

from 7 500 t to 12 000 t (Fig. 9 upper histogram). Managers in this situation would be faced with the problem of a small change in the biological reference point causing a major change in ABC, especially since each of the bootstrapped points on the curve are equally likely but the risk of overfishing or foregoing yield varies greatly over the range of ABCs.

If only the directed fishery is managed, even though the shrimp fishery is causing discard mortality (scenario 2), the total yield decreases and the $F_{0.1}$ values increase relative to scenario 1 (Fig. 10). The mean bycatch increases the $F_{0.1}$ to $3.29 \cdot \text{year}^{-1}$ with an associated yield of 6 790 t. This shift down

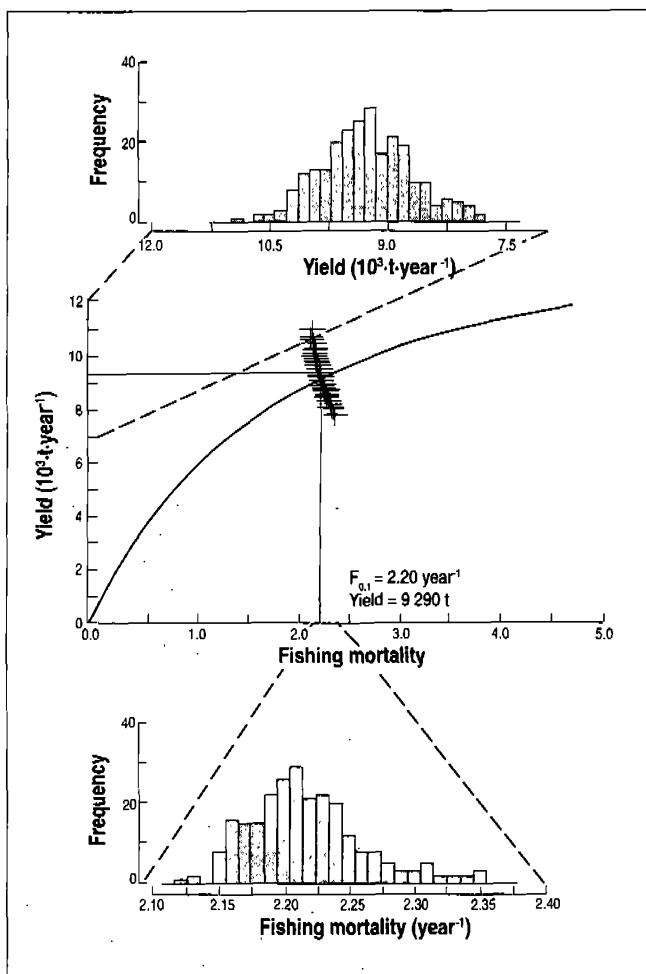


Fig. 9. Red snapper yield curve with $F_{0.1}$ and associated yield for the 250 bootstrapped annual bycatch estimates for scenario one. The yield curve is for the mean bycatch values given by Nichols and Pellegrin (1992). The distributions of the $F_{0.1}$ and associated yields are shown in the lower and upper histograms, respectively. [Curva de rendimiento del pargo del Golfo con $F_{0.1}$, y rendimiento asociado para las capturas incidentales estimadas para el escenario uno a partir de 250 iteraciones del método bootstrap. La curva de rendimiento es para los valores medios de captura incidental dados por Nichols y Pellegrin (1992). Las distribuciones de $F_{0.1}$ y rendimientos asociados son mostradas en los histogramas inferiores y superiores, respectivamente.]

and to the right in the yield vs. fishing mortality plots is due to fewer available age classes in the fishery requiring a higher effort to reach $F_{0,1}$, while producing a lower yield. As in scenario 1, a small range in the biological reference point $F_{0,1}$ causes a large range of ABCs (Fig. 10 histograms). The approximate 3 000 t difference between scenarios 1 and 2 for fishing mortalities at either biological reference point corresponds to the biomass of red snapper that is caught by the shrimp fishery and never landed.

If the red snapper discarded by the shrimp fishery had only experienced natural mortality (scenario 3), the expected yield to the directed fishery would be an order of magnitude greater (Fig. 11). The yield curve shown in Fig. 11 corresponds to the mean bycatch being introduced into the numbers-at-age matrix and the 250 $F_{0,1}$ and associated yield points correspond to the 250 bycatch bootstraps being introduced into the numbers at age matrix. The mean $F_{0,1}$ of $3.21 \cdot \text{year}^{-1}$ is similar to scenario 2 because the directed fishery does not catch

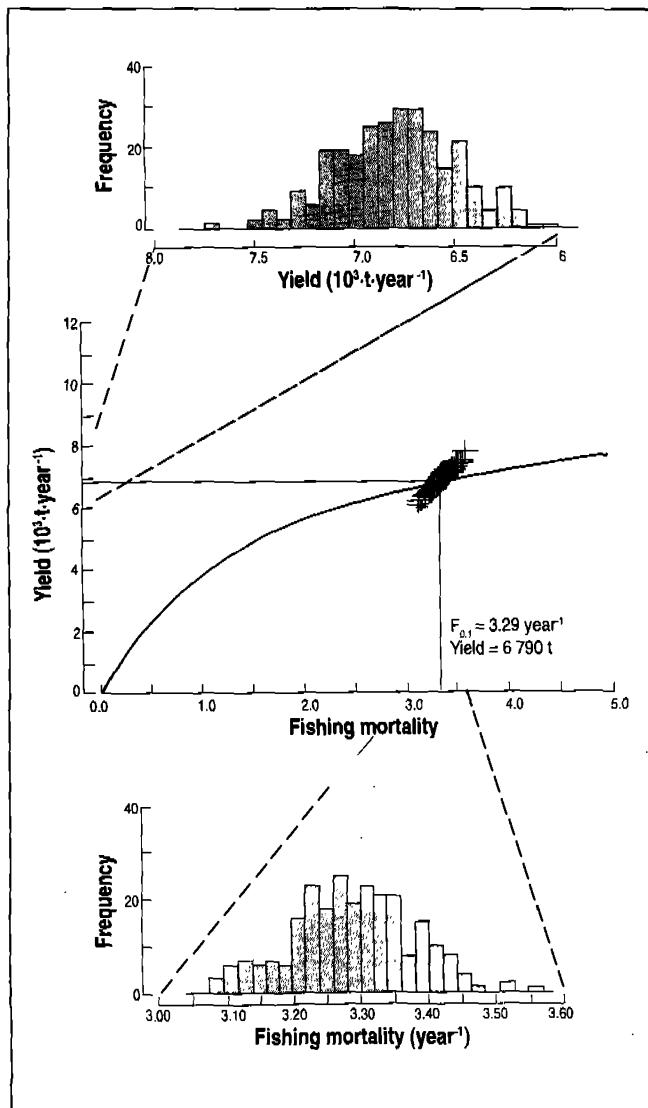


Fig. 10. Red snapper yield curve with $F_{0,1}$ and associated yield for the 250 bootstrapped annual bycatch estimates for scenario two. The yield curve is for the mean bycatch values given by Nichols and Pellegrin (1992). The distributions of the $F_{0,1}$ and associated yields are shown in the lower and upper histograms, respectively. [Curva de rendimiento del pargo del Golfo con $F_{0,1}$, y el rendimiento asociado para las capturas incidentales estimadas para el escenario dos a partir de 250 iteraciones del método bootstrap. La curva de rendimiento es para los valores medios de captura incidental dados por Nichols y Pellegrin (1992). Las distribuciones de $F_{0,1}$ y rendimientos asociados son mostrados en los histogramas inferiores y superiores, respectivamente.]

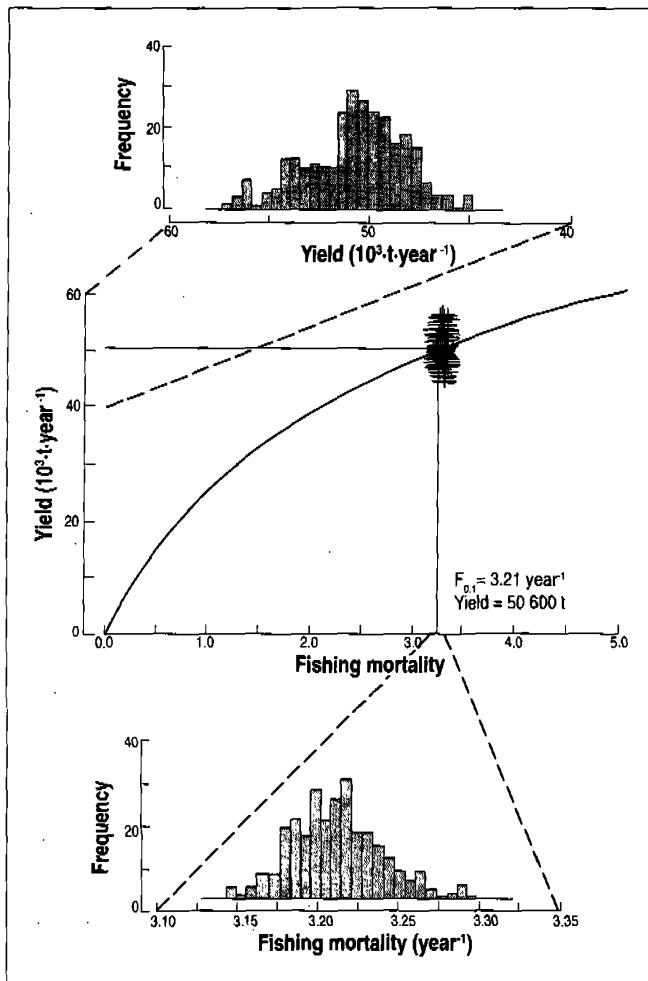


Fig 11. Red snapper yield curve with $F_{0,1}$ and associated yield for the 250 bootstrapped annual bycatch estimates for scenario three. The yield curve is for the mean bycatch values given by Nichols and Pellegrin (1992). The distributions of the $F_{0,1}$ and associated yields are shown in the lower and upper histograms, respectively. Note the change in scale for the yield axis relative to Figs. 9 and 10. [Curva de rendimiento del pargo del Golfo con $F_{0,1}$ y el rendimiento asociado para las capturas incidentales estimadas para el escenario tres a partir de 250 iteraciones del método bootstrap. La curva de rendimiento es para los valores medios de captura incidental dados por Nichols y Pellegrin (1992). Las distribuciones de $F_{0,1}$ y rendimientos asociados son mostrados en los histogramas inferiores y superiores, respectivamente. Note el cambio en la escala para el eje de rendimiento en relación a las Figs. 9 y 10.]

age 0 and age 1 fish, but the associated yield is much higher because much more biomass is available to the directed fishery. Even though the numbers-at-age vectors used to compute the yield curves are much more uncertain than those used for scenarios 1 and 2 (see Fig. 8), the range of $F_{0,1}$ for scenario 3 is still quite small, 3.1 to $3.3 \cdot \text{year}^{-1}$. As before, this small range in $F_{0,1}$ produces a large range in the associated yield, 45 000-57 000 t. Comparison of scenarios 1 and 3 shows the increase in yield from the red snapper population that could occur if mortality created by shrimp fishing was prevented.

Conclusions

The management of the directed red snapper fishery in the US Gulf of Mexico is reduced in importance due to the nondirected effects of the shrimp fishery. Similar to the discard problem caused by the shrimp industry, release mortality also occurs in the recreational fishery for red snapper; especially since there are minimum size and bag limit regulations in effect and the red snapper is only one part of a multispecies complex targeted by recreational fishers. Discard uncertainty causes some variability in the management parameter $F_{0,1}$, but this

small range causes high variability in the associated yield, which is the ABC that management must set. This relationship in the variability of $F_{0.1}$ and associated yield is a direct consequence of the curvature of the catch model at the reference point. Managers presented with a range of ABCs such as these must weigh the risks of overfishing and foregoing yield along with the socioeconomic impacts to determine a quota.

The effects of discards of red snappers in the US sector of the Gulf of Mexico shrimp fishery on managing the red snapper directed fishery may be common to other snapper fisheries of the world. As such, research leading to sound scientific advice for managing this resource should emphasize the significance of understanding cryptic mortality sources in nondirected fisheries.

References

- Beverton, R.J.H. and S.J. Holt. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. 2, Vol. 19. UK Ministry of Agriculture and Fisheries, London.
- Ehrhardt, N.M. and C.M. Legault. The role of uncertainty in fish stock assessment and management: a case study of the Spanish mackerel, *Scomberomorus maculatus*, in the U.S. Gulf of Mexico. Fish. Res. (In press).
- Gavaris, S. 1988. An adaptive framework for the estimation of population size. Canadian Atlantic Fishery Scientific Advisory Commission. Research Document 88/29.
- Goodyear, C.P. 1993. Red snapper in US waters of the Gulf of Mexico: 1992 assessment update. Contribution MIA 92/93-76. National Marine Fisheries Service, Southeast Fisheries Center, Miami Laboratory. 125 p.
- GMFMC. 1991. Reef Fish Stock Assessment Panel Report, 1991. Gulf of Mexico Fisheries Management Council, Sarasota, Florida. 10 p.
- GMFMC. 1993. Reef Fish Stock Assessment Panel Report, 1993. Gulf of Mexico Fisheries Management Council, Sarasota, Florida. 9 p.
- Gulland, J.A. 1965. Estimation of mortality rates. Annex to Arctic Fisheries Working Group Report. ICES CM 1965, Doc No. 3, 9 p. (mimeo).
- Gulland, J.A. and L.K. Boerema. 1973. Scientific advice on catch levels. Fish. Bull. 71(2):325-335.
- Nelson, R.S. and C.S. Manooch III. 1982. Growth and mortality of red snappers in the West-Central Atlantic Ocean and northern Gulf of Mexico. Trans. Am. Fish. Soc. 111:465-475.
- Nichols, S., A. Shah, G.J. Pellegrin, Jr. and K. Mullin. 1987. Estimates of annual shrimp fleet bycatch for thirteen finfish species in the offshore waters of the Gulf of Mexico. Report to the Gulf of Mexico Fishery Management Council.
- Nichols, S., A. Shah, G.J. Pellegrin, Jr. and K. Mullin. 1990. Updated estimates of shrimp bycatch in the offshore waters of the Gulf of Mexico, 1972-1989. Report to the Gulf of Mexico Fishery Management Council.
- Nichols, S. and G.J. Pellegrin, Jr. 1992. Revision and update of estimates of shrimp fleet bycatch, 1972-1991. Report to the Gulf of Mexico Fishery Management Council.
- ✓ Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. J. CIEM 39(3):175-192.
- Pope, J.G. and J.G. Shepherd. 1982. Simple method for the consistent interpretation of catch-at-age data. J. CIEM 40:176-184.

ENTERED IN NAGA

APR 14 1998

Analyses of Catch-per-Effort Data for Red Snapper on Campeche Bank in 1992

M. DEL CARMEN MONROY-GARCÍA^a

R. BURGOS ROSAS^a

M.E. GONZÁLEZ Y DE LA ROSA^b

M. GARDUÑO-ANDRADE^a

^a*Centro Regional de Investigaciones Pesqueras de Yucalpetén
Apdo. Postal 73, Progreso
97320 Yucatan, México*

^b*Centro Regional de Investigaciones Pesqueras de Lerma
Km 5 carretera Campeche-Lerma
24000, Campeche, México*

MONROY-GARCÍA, M.D.C., R. BURGOS ROSAS, M.E. GONZÁLEZ DELA ROSA and M. GARDUÑO-ANDRADE. 1996. Analyses of catch-per-effort data for red snapper on Campeche Bank in 1992 [*Analisis de la captura-por-unidad de esfuerzo de la pesquería del huachinango del golfo en el Banco de Campeche en 1992*], p. 350-354. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.)] Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

This paper analyzes the catch, effort, and catch-per-unit-effort (CPUE) of red snappers in the Complejo Industrial Pesquero del Mayab fleet (CPI fleet). There are three different areas: Area I (western side of the Campeche Bank) gave the highest average CPUE, with $82.7 \text{ kg} \cdot \text{day}^{-1}$ (± 37.2 ; CV=0.44). Area II (northeastern part between the Arenas Key, Alacranes Reef and the North Keys) gave an average CPUE of $57.1 \text{ kg} \cdot \text{day}^{-1}$ (± 59.4 ; CV= 1.04). Area III (eastern part of the Bank) had the lowest average with $22.4 \text{ kg} \cdot \text{day}^{-1}$ (± 22.0 ; CV=0.98). Effort varied monthly between 10 and 47 fishing trips-month $^{-1}$. Area I and Area II yielded a high CPUE in January to May and in November-December.

Resumen

En este trabajo se analiza la información de la captura, el esfuerzo y la captura por unidad de esfuerzo (CPUE) del pargo del Golfo proveniente de la flota (CPI) del complejo industrial pesquero del Mayab. Se definen tres áreas diferentes: Área I (al oeste del Banco de Campeche) donde se registró la CPUE promedio más alta, con 82.7 kg dia^{-1} (± 37.2 , CV=0.44). Área II (región noreste, entre Cayo Arenas, Arrecife Alacranes y los Cayos del Norte), con valores promedio de CPUE de 57.1 kg dia^{-1} (± 59.4 , CV=1.04). Área III (región oriental del Banco) que presentó los menores valores promedio de CPUE con 22.4 kg dia^{-1} (± 22.0 , CV=0.98). El esfuerzo varió mensualmente entre 10 y 47 viajes de pesca por mes. En las Áreas I y II se registraron altos valores de CPUE de Enero a Mayo y en Noviembre-Diciembre.

Introduction

Red snapper (*Lutjanus campechanus*) fisheries are important in Yucatan State, Mexico, this species being of high quality (see Render and Wilson; Ehrhardt and Legault, this vol.). It is exported to the USA, providing foreign exchange while also generating employment. Between 1990 and 1992, red snappers contributed from 2.2% to 19.4% of the total monthly catch recorded by the Progreso Fisheries Office (Secretaría de Pesca), which covers 90% of Yucatan State.

In fisheries stock assessment, two important factors are the spatial distribution and seasonal changes (Hilborn and Walters 1992).

The objective of this study was to analyze the effort, catch and catch-per-unit-effort (CPUE) applied to red snapper for different areas of Campeche Bank, for a standard fleet.

Materials and Methods

Data were collected from the Complejo Industrial Pesquero del Mayab (CPI fleet), whose target species is red snapper. This fleet is quite standardized: the vessels are 12.2 m (40 ft) long, each equipped with three line haulers with a pulley and 4 or 5 #7 or #8 hooks. There are three fishers per vessel. Fishing depth is 36-146 m (20-80 fathoms).

Effort and catch data for each fishing trip were recorded in a logbook by the vessel's captain. Records cover the effective catch days, fishing grid number, red snapper catch and total catch by weight. Campeche Bank is divided by a grid of one degree longitude by latitude.

The logbook catches were matched with the catch records from the Progreso Fisheries Office (Secretaría de Pesca). Logbooks without matching records were not considered.

Effective catch days are the total time less the travel time. The t-student statistic

was used to compare spatial (grids) and monthly differences in effort and CPUE. Averages, standard deviations and the coefficients of variation ($CV = \bar{x}/s.d.$) were calculated.

Results

Data from 379 fishing trips were used, corresponding to 3 911 effective fishing days by the CPI fleet during 1992. Table 1 shows the effort and its distribution on the Campeche Bank grid.

The red snapper catch rates show that there are three different areas (t-student <0.05):

Area 1, corresponding to grid squares 8, 14 and 15 gave the highest average CPUE, with $82.7 \text{ kg} \cdot \text{day}^{-1}$ (± 37.2 ; $CV=0.44$); this area is on the western side of the Campeche Bank off Celestún (between $20^{\circ}-24^{\circ}\text{N}$ and $91^{\circ}-93^{\circ}\text{W}$) (Fig. 1).

Table 1. Number of fishing trips and effective catch days by grid square, for the CPI fleet on Campeche Bank during 1992. [Número de viajes de pesca y días efectivos de pesca aplicados a los diferentes cuadrantes en el Banco de Campeche durante 1992.]

Grid square	Fishing trips	Effective days
1	33	333
2	46	446
3	32	337
4	44	432
5	21	211
6	16	148
7	3	23
8	73	780
9	3	30
10	5	46
11	0	0
12	2	24
13	5	54
14	45	515
15	51	532

Area II includes grid squares 2, 3, 4 and 5, in the north and in the northeastern part of Campeche Bank between the Arenas Key, Alacranes Reef and the North Keys (between 23-24°N and 88-91°W). This area produced a medium CPUE of red snapper averaging $57.05 \text{ kg} \cdot \text{day}^{-1}$ (± 59.42 ; CV= 1.04).

Area III had the lowest average CPUE of red snapper, $22.39 \text{ kg} \cdot \text{day}^{-1}$ (± 22.03 ; CV= 0.98); including grid squares 9, 10, 11 and 12 along the coastal zone (21-22°N and 87-92°W) and grid squares 1, 6, 7 and 13, along the eastern part of Campeche Bank.

Nominal effort ranged from 10 to 47 fishing trips·month⁻¹ (Table 2). Area I and Area II yielded high catch rates of red snapper from January to May and in November/December. The summer months, June to September, yielded low catch rates (student t, p< 0.05). In the high season there were 174 fishing trips corresponding to 1 735 effective days, with an average of

$79 \text{ kg} \cdot \text{day}^{-1}$ (± 51). The low season had 138 fishing days, corresponding to 1 518 effective days, with an average of $57 \text{ kg} \cdot \text{day}^{-1}$ (± 52).

Discussion

In stock assessment it is customary to attempt to use CPUE data as index of fish abundance. There are three types of relationships between CPUE and true abundance; "hyperstability," "proportionality" and "hyperdepletion". Hyperstability, the most dangerous of these relationships, occurs when CPUE remains stable while abundance drops rapidly, i.e., CPUE only declines when the abundance is very low and the fishery has collapsed. The relationship between CPUE, effort and abundance is dictated by the spatial pattern (aggregations) and fish abundance. When the fishes have big aggregations and there is an efficient search system, the CPUE will remain high

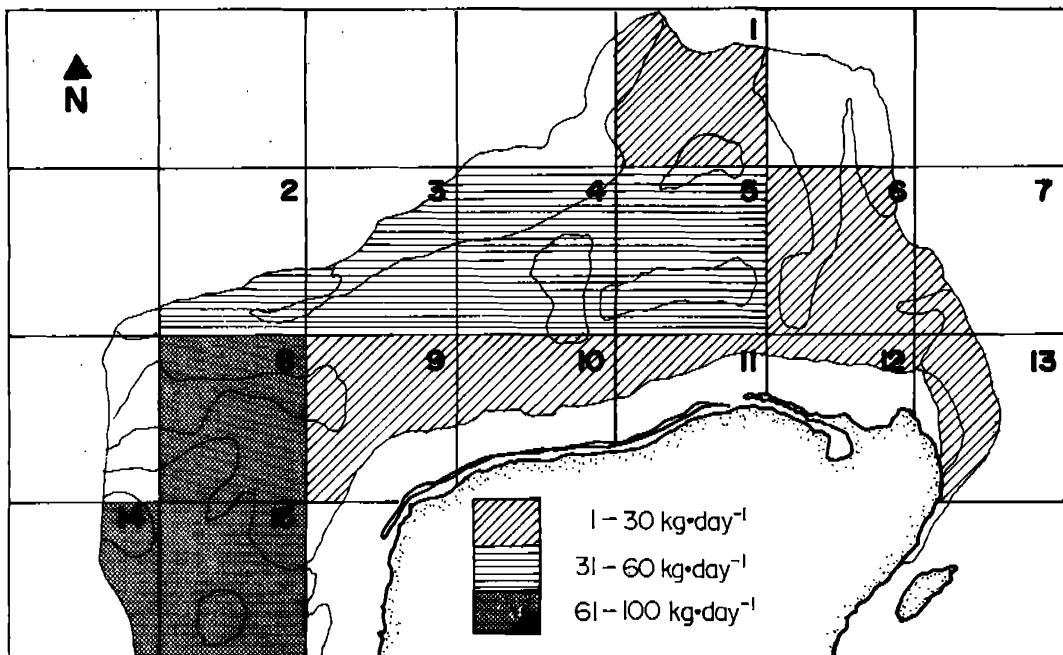


Fig. 1. CPUE of red snapper on Campeche Bank, by statistical square, in 1992 (see Table 2 for the corresponding effort levels). [Distribución de la captura por unidad de esfuerzo en las diferentes zonas de la plataforma durante 1992.]

Table 2. Number of fishing trips and effective catch days during 1992 by the CPI fleet on Campeche Bank. [Número de viajes de pesca y días efectivos por mes durante 1992 por la flota CPI del Banco de Campeche.]

Month	Fishing trips	Effective days
January	10	76
February	23	217
March	30	326
April	24	240
May	29	323
June	30	345
July	38	397
August	35	389
September	39	421
October	41	427
November	33	293
December	47	457

until the stock is badly depleted (Hilborn and Walters 1992).

In terms of the weather, the worst period in Yucatan is the winter, with strong winds from the North. In this season except December, the fishing effort is low and CPUE reaches high values. The spawning season of red snapper is between June and September (Grimes 1987). At this time, fishing effort is high but CPUE is lowest; it seems that during the spawning season, red snappers have a low catchability and the fishers switch to other species, such as the red grouper, which is easy to catch but is less profitable.

December is the month with the highest number of fishing trips and January that with the lowest number (Fig. 2). Due to social and economic factors, the fishers probably make an extra effort around Christmas to increase their earnings and in January,

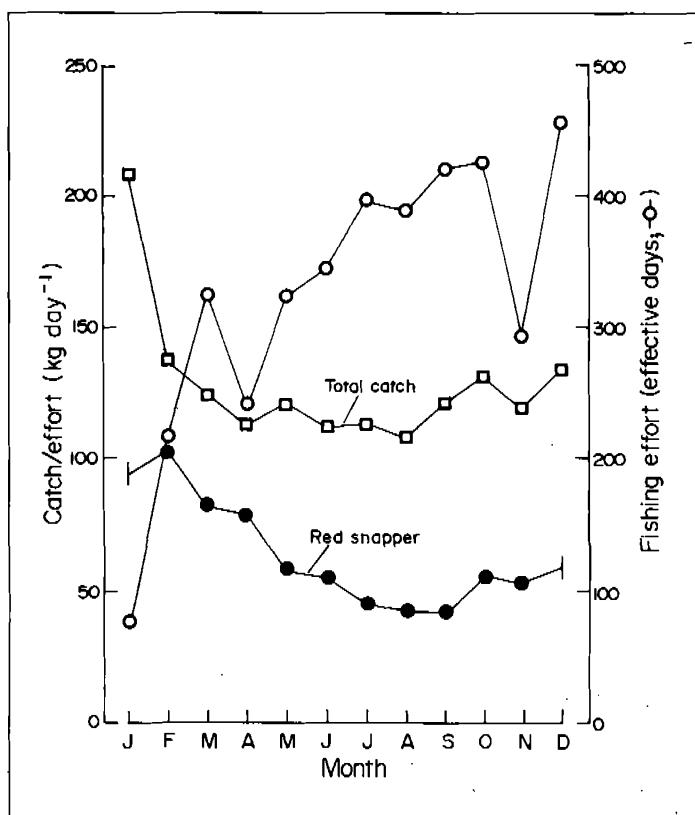


Fig. 2. Total red snapper catch by month (of 1992), and fleet effort and catch/effort. [Captura total del pargo del Golfo, esfuerzo y captura/efuerzo de la flota por mes en 1992.]

when climatic conditions are poor, they replant their crops and dry dock the vessels.

The grid squares with the highest CPUE and the lowest CV are the grid squares with the highest number of fishing trips. A major problem with using commercial catch-and-effort data to estimate stock distribution and abundance is that fishers go where the fish are. Fishing effort is normally concentrated on the highest density fish and attempts to assess the range, or total abundance of fish from commercial catch-and-effort data can be expected to be biased.

References

- Grimes, C.B. 1987. Reproductive biology of the Lutjanidae: a review, p. 239-294. In J.J. Polovina and S. Ralston (eds.) Tropical snappers and groupers: biology and fisheries management. Westview Press, Boulder.
- Hilborn, R.Y and C.J. Walters. 1992. Quantitative fisheries stock assessment. Choice, dynamics and uncertainty. Chapman & Hall, New York.

ENTERED IN FILE
APR 14 1998

Time Series Analysis and Multivariate Methods Applied to the Red Grouper Fishery on Campeche Bank, Mexico

J. POL
S. MORENO

Flota del Golfo

C. García 111, Regla, C. Habana, Cuba

POL, J. and S. MORENO. 1996. Time series analysis and multivariate methods applied to the red grouper fishery on Campeche Bank, Mexico [Series de tiempo y métodos multivariados aplicados a la pesquería de mero americano del Banco de Campeche, México], p. 355-359. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.). Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Time series analysis was applied to monthly yield data of the red grouper (*Epinephelus morio*) commercial fishery from the Campeche Bank, in the Gulf of Mexico, during 1973 to 1991. A single exponential smoothing technique was used to fit the data, resulting in a series characterized by small changes of individual values with respect to the mean, without a specific trend. The forecast mean value was 3.56 kg/100 hooks. Principal component analyses showed that total abundance of fish is significantly related to variables such as depth, fishing ground and red grouper abundance.

Resumen

Se presentan los resultados del análisis de series de tiempo aplicado a los valores mensuales de CPUE total de la pesquería comercial con palangre de fondo del mero americano (*Epinephelus morio*) en el Banco de Campeche de 1973-1991. El mejor ajuste se logra con el método de suavizamiento exponencial simple con un error del 18.6%. La serie se caracteriza por pequeños cambios en los valores respecto a la media, sin tendencia definida. El valor medio del pronóstico fué de 3.56 kg/100 anz. El análisis de componentes principales sugiere que la abundancia total de peces está relacionada de forma significativa con otras variables como son la profundidad, zona de pesca y las variaciones de la abundancia de mero americano.

Introduction

The structure of demersal fish communities in a given area is related to the type and characteristics of the sea bed, the depth and the local oceanographic dynamics (Caddy and Sharp 1988). Thus, environmental changes promote fluctuations in abundance of fish populations. Fishing grounds of the Campeche Bank visited by the Cuban fleet

are characterized by a coralline sea floor where serranids and lutjanids dominate commercial catches (see Arreguín-Sánchez et al., this vol.). This region is also characterized by east-west currents and a seasonal upwelling on the northeastern continental shelf of the Peninsula of Yucatan (Elizarov and Machado 1971).

Sharp and Csirke (1983) emphasize that prognoses must not ignore environmental

influence. For the Campeche Bank, García et al. (1980) developed a prognostic based on a system of equations which relate the effect of atmospheric pressure, Gulf Stream flow and upwelling, the last effect being related to low temperatures. These changes also promote high abundance of some species such as grunts (Haemulidae) (Oleachea 1975). However, the red grouper (*Epinephelus morio*) tends to move away from low temperatures, which have therefore been interpreted as a major cause of the east-west red grouper population movements.

Currently, studies developed in the Campeche Bank relate temperature and fish density. This contribution aims to analyze relationships among some environmental variables and the abundance of the fish populations for forecasting purposes.

Materials and Methods

Time series of catch/effort data (U , kg/100 hooks) were used to analyze changes in population abundance for the most important species caught by the red grouper hook-and-line fishery of the Campeche Bank, Mexico. For the analysis, 161 samples were used, taken from 15 surveys undertaken from 1986 to 1991. An exponential smoothing procedure was used to derive a main trend through the equation:

$$U_f(t+1) = \alpha U(t) + (1 - \alpha) U_f(t)$$

where

U = observed value of catch/effort (kg/100 hooks), as a measure of abundance;

U_f = forecast abundance;

t = time, in months;

α = smoothing constant, with $0 \leq \alpha \leq 1$.

The variables used for environmental characterization were: time, fishing ground, mean depth, population abundance for the main species (red grouper [*Epinephelus morio*], black grouper [*Mycteroperca bonaci*],

snappers [*Lutjanus campechanus*], *L. analis*, porgies [*Calamus* spp.], yellowtail snapper [*Ocyurus chrysurus*]) and total abundance (U_t).

Factorial analysis of these variables was developed through the Principal Component Analysis (PCA) technique in order to identify main interrelationships with a minimum loss of information (Linares 1990).

Results and Discussion

The monthly trends of catch/effort shown in Fig. 1 do not exhibit a clear pattern. The percentage of error estimated after single exponential smoothing (SES), with a value for $\alpha = 0.1$ was 18.6%. This analysis was considered adequate for time series where changes are small with respect to the mean value.

The monthly trend exhibits two periods of low yields, 1980-1982 and 1990-1991, which coincide with low temperatures. These conditions occur more frequently during summer (García 1980), but their intensity and duration remain ill-defined. High values of fish abundance during October - December 1988 were an effect of hurricane Gilbert, which occurred the previous September.

The SES permits a prognosis of the weighted average (3.56 kg/100 hooks), which, unfortunately is strongly affected by values at the beginning of the time series (Zerguera 1988). However, the prognosis is not dependent on the older values; rather, it depends on the most recent abundance records.

Cansado (1970) suggests that adequate predictions are given by the average values in time series such as used in this analysis, where no cyclical processes are involved. In practice, this average value did vary as a consequence of environmental variables such as temperature, which has a very important effect on many species and their fisheries in the Campeche Bank.

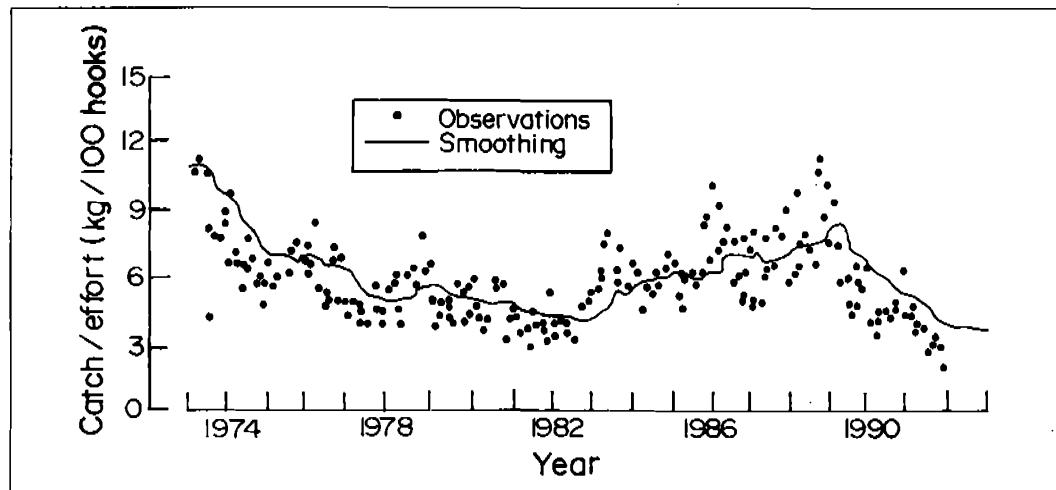


Fig. 1. Time series of monthly yields by the Cuban fleet on Campeche Bank. [Serie de tiempo de los rendimientos mensuales de la flota Cubana en el Banco de Campeche.]

García (1974) indicates that 43% of the variance of red grouper abundance is explained by temperature. Conversely, Cervigón (1972) suggested that complexity of coral reef ecosystems is a result of their environmental stability; notably their stable temperatures.

Although the red grouper constitutes 80% of the total fish caught, other species appear to be of importance for forecasting purposes. The most important are other species of serranids (13.4%), lutjanids (5.3%) and sparids (1.3%).

To analyze the results from the PCA, those values for correlation coefficients higher than 0.4 were taken to be significant. This criterion was applied to the first to fourth components because they explain 71% of the total variance (Table 1). A high association was observed between population abundance and depth (Table 2). Differences among species related with their depth distribution indicate that higher total abundance was found in the range of 27 m to 45 m.

The second component of the PCA suggests a relationship between some spatial variables, such as fishing ground and depth, with total abundance; and specifically that

of red and black groupers. This association is clearly observed on the eastern region of the Campeche Bank, where the Cuban fleet operates most frequently. This particular result is a consequence of the fishing strategy, because the Cuban fleet operates on targeted fishing grounds where, in this particular case, the black grouper

Table 1. PCA analysis of catch/effort data by the Cuban fleet on Campeche Bank; eigenvalues and variation for each component. [Valores propios y varabilidad aplicada para cada componente.]

Eigenvalues	Explained variance (%)	Cummulated variance (%)
2.436	24.36	24.36
2.119	21.19	45.55
1.365	13.65	59.19
1.182	11.83	71.02
0.909	9.01	80.03
0.690	6.90	86.93
0.511	5.11	92.03
0.466	4.66	96.69
0.316	3.16	99.85
0.015	0.15	100.00

Table 2. Correlation coefficients for significant variables within each component, U = catch/effort. [Coeficientes de correlación para las variables primarias en cada componente. U = captura por unidad de esfuerzo.]

Item	Factor 1	Factor 2	Factor 3	Factor 4
month	-	-	-	-
fishing ground	-	0.53	-0.53	-
mean depth	-0.47	-0.49	-	-
fishing effort	-	-	0.44	0.48
U_{Total}	-0.73	0.53	-	-
$U_{\text{red grouper}}$	-0.45	0.75	-	-
$U_{\text{black grouper}}$	-0.74	-0.42	-	-
U_{snappers}	-0.58	-	-	-
U_{porgies}	-0.59	-	-	0.61
$U_{\text{yellowtail snapper}}$	-	0.58	-0.45	0.55

have larger sizes and weights than the other species with a significant influence on the total abundance.

Yellowtail snapper is a schooling demersal fish most frequently found at a depth of about 27 m in exploited areas of the western part of Campeche Bank. However, the economic value of this species is relatively low, and is not a primary target species. This species was considered significant for the third component of the PCA.

There is little difference among the different seasonal indices of abundance for

each month; all tend to have lower values during early summer, just when the upwelling impact occurs (Fig. 2); however, during winter and early spring, relative abundance is much higher, probably because of the reproductive aggregation of the red grouper, which is well known to fishers (Arreguín-Sánchez 1992; Arreguín-Sánchez et al., this vol.).

We conclude by noting that the best representation of our catch/effort time series was obtained by the single exponential smoothing, with an error of 18.6%, and

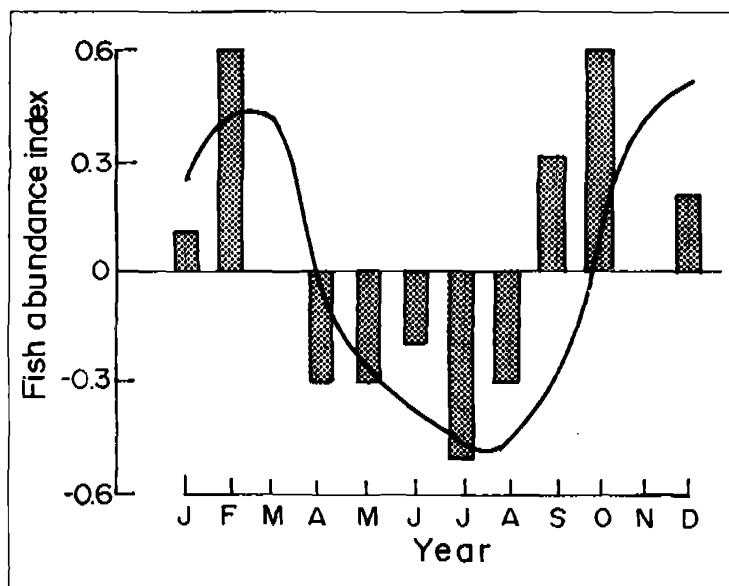


Fig. 2. Monthly fish abundance indices. [Indices mensuales de abundancia de peces.]

characterized by small changes with respect to the mean value.

For the red grouper fishery it is not recommended to use time series analysis without consideration of interacting factors, such as fishing ground, depth and species-specific abundances.

References

- Arreguin-Sánchez, F. 1992. An approach to the study of the catchability coefficient with application to the red grouper (*Epinephelus morio*) fishery from the continental shelf of Yucatan, Mexico. Centro de Investigación y de Estudios Avanzados del IPN, Unidad Mérida, México. Doctoral thesis.
- Caddy, J.E. and G.D. Sharp. 1988. Un marco ecológico para la investigación pesquera. FAO Doc. Téc. Pesca (283). 153 p.
- Cansado, E. 1970. Curso de estadística general. Inst. del Libro. 662 p.
- Cervigón, F. 1972. Los peces, p. 308-355. En H. Ginés y R. Margalef (eds.) Ecología marina. Fund. La Salle de Cienc. Nat., Dossat S.A. Caracas.
- Elizarov, A.A. and I. Machado. 1971. Variabilidad de la corriente de Yucatán y tipos de circulación en dicho estrecho en relación a la concentración de organismos comerciales en el Banco de Campeche. Invest. Pesq. Sov. Cub. Fascículo 3:130-141.
- García, C. 1974. Influencia de la temperatura en el comportamiento de la cherna americana (*E. morio*) en el B. de Campeche. 1er Simp. Cienc. Pesq. 4 p.
- García, C. 1980. Caracterización general del Banco de Campeche. Rev. Cub. Invest. Pesq. 5(2):1-10.
- García, C., M.H. Obregón and M.E. de León. 1980. Relaciones oceanográfico-pesqueras. Rev. Cub. Invest. Pesq. 5(3):22-31.
- Linares, G. 1990. Análisis de datos. Universidad de la Habana. ENPES. 590 p.
- Oleachea, A. 1975. Distribución y abundancia de peces demersales y su relación con las temperaturas de las aguas de fondo. Rev. Invest. Pesq.(2):161.
- Sharp, G. and J. Csirke, Editors. 1983. Proceedings of the Expert Consultation to Examine Changes in Abundance and Species of Neritic Fish Resources. FAO Fish. Rep. (291) Vol. 2:552-1224.
- Zerguera, P. 1988. Introducción a la dirección científica de los inventarios. CEDISATEMA. 174 p.

ENTERED IN MAGA

APR 1 1998

Shrimp Trawl Bycatch Research in the US Gulf of Mexico and Southeastern Atlantic

E. SCOTT-DENTON

J. NANCE

National Marine Fisheries Service
Southeast Fisheries Science Center

Galveston Laboratory
4700 Avenue U

Galveston, Texas 77551, USA

SCOTT-DENTON, E. and J. NANCE. 1996. Shrimp trawl bycatch research in the US Gulf of Mexico and southeastern Atlantic [*Investigaciones sobre captura acompañante de arrastres camaroneseros en aguas de US del Golfo de México y Atlántico Suroriental*], p. 360-362. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

A brief description is given of a project initiated in 1992 by the National Marine Fisheries Service, designed to assess the status of fish caught as bycatch in the shrimp fishery of southeastern Atlantic and Gulf of Mexico coast of the USA. Some preliminary results are presented.

Resumen

Se presenta una breve descripción de un proyecto iniciado en 1992 por el Servicio Nacional de Pesquerías Marinas y diseñado para evaluar el estado de los peces capturados como fauna acompañante de la pesquería de camarón del Atlántico suroriental y en aguas de USA en el Golfo de México. Se presentan algunos resultados preliminares.

Introduction

As elsewhere in the world, shrimp trawling in the US Gulf of Mexico and southeastern Atlantic has been identified as a contributing factor for the declining stocks of demersal finfishes (Alverson et al. 1994). A reduction in red snapper landings in the 1980s brought considerable attention to shrimp trawl bycatch as being the primary cause of juvenile red snapper mortality (see also Ehrhardt and Legault; Monroy-Garcia et al., this vol.). As a result of the 1990

amendments to the Magnuson Act, a three-year research plan was established to assess bycatch from the commercial shrimp fishery operating in the southeast region. Since April 1992, scientists at the Southeast Fisheries Science Center Galveston Laboratory of the National Marine Fisheries Service (NMFS) have been collecting bycatch data onboard shrimp vessels in the US Gulf of Mexico and southeastern Atlantic, in the context of a project that is briefly presented below, along with some preliminary results.

Goals and Objectives

The goals of this project were to update and expand bycatch estimates temporally and spatially in the offshore, nearshore and inshore waters of the Gulf of Mexico and the southeastern US Atlantic and to evaluate various devices to reduce shrimp trawl bycatch. Bycatch data were used to determine what species are impacted during shrimping activity. Catch-per-unit effort estimates for various species were available for inclusion into stock assessment models.

Materials and Methods

This research project follows the guidelines in the *Research Plan Addressing Finfish Bycatch in the Gulf of Mexico and South Atlantic Shrimp Fisheries*, prepared by the Gulf and South Atlantic Fishery Development Foundation under the direction of a Steering Committee composed of individuals representing industry, environmental, State and Federal interests in the United States. The intent of the sampling design is to survey the commercial shrimp fishery in operation and not to simply establish a research survey study of the bycatch or the finfish populations. The sampling universe in this case consists of all tows from all vessels shrimping in the Gulf of Mexico and along the Atlantic coast of the southeastern United States. Parameters of interest are the catch totals and size distributions of species of finfish and invertebrates incidentally taken by the shrimp fleet.

The quantity and type of bycatch change with fishing location, season and depth. Stratification by these variables will help to minimize the variances of catch estimates. Forty-five analysis strata were identified using season (January through April, May through August, and September through December), location (Statistical zones 1-9, 10-12, 13-17, 18-21, and the US Atlantic coast),

and depth (inshore, nearshore and offshore). The statistical sample unit within each stratum consists of a single subsample from a trawl haul.

NMFS-trained observers collect the trawl haul subsamples and record the data following the established *NMFS Bycatch Characterization Protocol* published with the Bycatch Research Plan. A 13-kg per tow hour subsample is obtained from one randomly selected net after each tow. The data collected consist of total tow weight, subsample weight, species composition, abundance, weight and miscellaneous data from which life history information can be derived.

The actual number of sea days at the end of the project will greatly depend on co-operating shrimp vessels. Since the purpose of the research is to characterize total bycatch by the shrimp fleet, allocation of samples is based only on intensity of shrimping effort and not on abundance levels of selected finfish species.

Preliminary Results

A total of 750 sea days of observations on shrimp vessels has been conducted in the Gulf of Mexico and along the east coast of the United States between May 1992 and September 1993. However, only data through April 1993 for the Gulf of Mexico were available for summary analysis. All other data are in various stages of analysis.

As of late 1993, a total of 282 species of finfish, 72 species of crustaceans, and 47 species of invertebrates were identified from the 440 trawl samples (401 different species). Most of the species were taken only on rare occasion, with about sixteen species being found in more than 50% of the sampled trawls. Overall, Atlantic croaker (*Micropogonias undulatus*) and longspine porgy (*Stenotomus caprinus*) were the dominant bycatch species in terms of both biomass (38%) and numbers (37%). The other

eight biomass dominant bycatch were hardhead catfish (*Arius felis*), Gulf menhaden (*Brevoortia patronus*), inshore lizardfish (*Synodus foetens*), Gulf butterfish (*Peprius burti*), spot (*Leiostomus xanthurus*), sand seatrout (*Cynoscion arenarius*), cutlass fish (*Trichiurus lepturus*) and lesser blue crab (*Callinectes similis*), while the other eight numerical dominants included seabob shrimp (*Xiphopenaeus kroyeri*), sugar shrimp (*Trachypenaeusspp.*), longspine swimming crab (*Portunus spinicarpus*), lesser blue crab, iridescent swimming crab (*Portunus gibbesii*), mantis shrimp (*Squilliaspp.*), Gulf butterfish, and hardhead catfish. On a seasonal basis, Atlantic croaker and longspine porgy were the biomass and numerical dominants during the May 1992 through December 1992 period, while during the January 1993 through April 1993 period the biomass dominants were the inshore lizardfish and the longspine porgy, and the numerical dominants were the sugar shrimp and the Gulf butterfish. With regard to the Florida area, pinfish and inshore lizardfish were the biomass dominants, while sugar shrimp and mantis shrimp were the dominant bycatch by number. In the Mississippi/Alabama area, Atlantic croaker and sand seatrout were

dominant by biomass, and Atlantic croaker and mantis shrimp were the numerical dominant bycatch. In the Louisiana and Texas areas, Atlantic croaker and longspine porgy were the biomass and numerical dominant bycatch. Red snapper (*Lutjanus campechanus*) accounted for less than 1% in terms of biomass for the entire Northern Gulf of Mexico coast. The highest percent biomass (2.7%) of red snapper occurred off the Texas coast in offshore waters during September 1992 through December 1992 (based on 25 trawl samples). Numerical abundance (number/hour) of red snapper ranged from zero off the Florida coast to 16 off the Texas coast from May 1992 though April 1993, while biomasses (kg·hour⁻¹) ranged from zero to 0.5 kg·hour⁻¹ for these same areas. Median length (FL) of red snapper for the same time period ranged from 7.5 cm to 17.4 cm.

Reference

- Alverson, D.L., M.H. Freeberg, S.A. Murawski and J.G. Pope. 1994. A global assessment of fishery bycatch and discards. FAO Fish. Tech. Pap. 339, 233 p.

PART V: AQUACULTURE AND CONTROLLED REPRODUCTION

ENTERED IN NAGC

APR 14 1998

Nassau Grouper Aquaculture

J.W. TUCKER, JR.
P.N. WOODWARD

Harbor Branch Oceanographic Institution
5600 North U.S. Highway 1
Fort Pierce, Florida 34946
USA

TUCKER, J.W., Jr. and P.N. WOODWARD. 1996. Nassau grouper aquaculture [Acuacultura de la cherna criolla], p. 363-377. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Nassau grouper (*Epinephelus striatus*), which ranges throughout the tropical western Atlantic, is highly valued commercially and has been severely depleted in many areas. We have studied the reproduction and culture of this species since 1987. Short-term captive wild fish produced eggs in four ways: (1) induced ovulation with human chorionic gonadotropin followed by artificial fertilization; (2) induced ovulation followed by fertilization by males in the holding tank; (3) natural ovulation followed by artificial fertilization; and (4) natural ovulation followed by fertilization in the holding tank. Long-term captive fish also have spawned; (5) unexpected voluntary spawning in a cage in a related project; and (6) planned voluntary spawning in a concrete raceway. In 1990, larvae were fed mainly enriched rotifers and *Artemia* metanauplii, with some *Artemia* nauplii. In 1994, oyster trochophores and copepods were also used. The best survival rates in three trials were 25% from fertilization to 15 days, 59% during 10-75 days, and 5% from fertilization to 98 days. After weaning at transformation, the groupers were fed a series of dry pelleted feeds developed at Harbor Branch Oceanographic Institution for marine fish. Under less than optimal conditions, medium-sized groupers reached a mean weight of 1.5 kg at 23 months after fertilization (with feed conversion ratio (FCR) rising from 0.9 to 1.3), and 2.0 kg in 28 months (FCR up to 1.8). When the pelleted diet was supplemented with live and frozen food, growth rate was slightly better. Improved water systems with temperature control (22-30°C) would allow production of 600-g groupers within 12 months, one-kg groupers within 18 months, and two-kg groupers within 24 months.

Resumen

La cherna criolla (*Epinephelus striatus*), la cual se distribuye a lo largo del Atlántico occidental tropical, tiene un alto valor comercial y su abundancia ha decrecido severamente en muchas áreas. Peces silvestres en cautiverio produjeron huevos por cinco vías diferentes: (1) ovulación inducida con gonadotropina coriónica humana seguida por fertilización artificial; (2) ovulación inducida seguida por desoves en estanques; (3) ovulación natural seguida por fertilización artificial. Peces cautivos por períodos de tiempo largos también desovaron; (4) ovulación natural seguida por desove en estanques; (5) desove voluntario en una jaula; y (6) Desoves voluntarios planeados en un canal de concreto. Las larvas fueron alimentadas con metanauplios de *Artemia* enriquecido con rotíferos y algunas nauplio de *Artemia*. Después de completada la transformación de las larvas, los peces fueron alimentados con una serie de alimento artificial ("pellets") desarrollados en HBOI, para peces marinos. Bajo poco menos que

las condiciones óptimas, las chernas criollas medianas alcanzaron un peso promedio de 1.5 kg en 23 meses, después de la fertilización (con una conversión alimenticia de 0.9 a 1.3), y 2.0 kg en 28 meses. Cuando la dieta artificial fué complementada con alimento vivo y congelado, la tasa de crecimiento fué ligeramente mejorada. Los sistemas de agua implementados con control de temperatura (22-30°C) podrían permitir la producción de cherna criolla de 600 g dentro de los primeros 12 meses; meros de 1 kg dentro de los 18 meses y chernas de 2 kg dentro de los 24 meses.

Introduction

The Nassau grouper (*Epinephelus striatus*, family Serranidae) ranges from Brazil to South Carolina and Bermuda, including the Caribbean Sea and Gulf of Mexico (see also Sullivan and Sluka, this vol.). It is an important food fish and has been severely depleted in many areas, usually as a result of overfishing of spawning aggregations (Bohnsack 1989; Carter 1989; Fine 1990; Butler et al. 1993; Sadovy 1993; Sadovy, in press). In January 1987, we began a research program to investigate aspects of the biology and culture of this species (see Bush et al., this vol.), and to evaluate the feasibility of its culture for commercial farming or for stock enhancement. This paper reviews the work completed through early 1994.

Methods

Spawning

Nassau grouper eggs were routinely obtained by inducing ovulation in wild fish with injections of human chorionic gonadotropin, or HCG (Tucker et al. 1991). Spawning normally occurs at about 26°C (Tucker et al. 1993). Four types of spawning by short-term (days to weeks) captive fish have occurred: (1) hormone-induced ovulation followed by artificial fertilization; (2) hormone-induced ovulation followed by fertilization by males in the holding tank; (3) natural ovulation followed by artificial fertilization; (4) natural ovulation followed by fertilization in the tank. Voluntary spawning of long-term (months) captive fish occurred (5) in a cage and (6) in a concrete raceway.

Culture conditions

Several preliminary larval rearing trials were conducted. Adult groupers were raised from five spawns to the juvenile stage at Harbor Branch Oceanographic Institution (HBOI). The first and the most recent trials are described here.

12 February 1990 spawn (4.9-kg female): These were HCG-induced, artificially spawned eggs from a pair of wild adults caught at Grand Cayman. Larvae and early juveniles were raised in 3.5-m³ fiberglass tanks. At 48 days after hatching (dah), a white polyethylene milk crate (34.5 cm x 38 cm x 28 cm) was anchored (opening sideways) just below the water surface in each tank to provide cover for newly transformed juveniles. Older juveniles were raised in the 3.5-m³ tanks, a pair of 10-m³ (3.3 m x 2.6 m x 1.2 m deep) concrete tanks, and a 37-m³ (12.2 m x 3.4 m x 0.9 m deep) concrete raceway. Seawater at 27-38 ppt and 23-30°C was provided by a flow-through system with slow gravel filter and rapid sand filter (plus 5 µm polyester cartridge filters for 3.5-m³ tanks). In the hatchery phase, water exchange rate was gradually increased to 300%/day during 5-70 dah. For older fish in the 3.5-m³ tanks, exchange rate was 300-500%/day. In the 37-m³ tank, it was 5-10%/day. The 10-m³ tanks had water recirculated through a biofilter, with 5-10%/day exchange.

26 January 1994 spawn (2.8-kg female): These were naturally ovulated, artificially-spawned eggs from a pair of wild adults caught in the Berry Islands, Bahamas. Larvae were reared in a 7-m³ fiberglass tank supplied with biofiltered well water at 30-31 ppt and 22-26°C. Greenwater

conditions (static until 12 dah) were maintained throughout larval rearing to 75 dah. During 13-41 dah, water exchange averaged 6.8% per day, and during 42-75 dah it was 15% per day.

Growth studies

1990. About 1 000 eggs were stocked in each of four 3.5-m³ round fiberglass tanks. At 98 dah, juveniles were removed, counted, measured (total length, TL), and weighed. In growth trials with older fish, survival, TL, weight, feed conversion ratio and daily ration were determined.

1994. About 9 000 eggs were stocked in a 7-m³ round fiberglass tank. At 75 dah, the fish were removed, counted, measured and weighed.

Feeding

1990. Reared groupers were fed rotifers (*Brachionus plicatilis*), *Artemia* sp., minced penaeid shrimp, an experimental starter feed, two experimental grower feeds, and two experimental broodstock feeds. Rotifers and *Artemia* in continuous cultures were fed *Nannochloropsis oculata* and Tahitian *Isochrysis*. These were chosen because they contain significant amounts of fatty acids that are essential in the diet of marine fish (EPA and DHA, see review in Tucker 1992a). During 0-25 dah, 1-2 l of each alga from mature cultures (i.e., nutrients mostly used up) were added to larval rearing tanks each day to feed rotifers and *Artemia* and to take up ammonia. Grouper larvae were fed rotifers and 1-5 day-old brine shrimp enriched for 2-3 hours with Frippak Booster microcapsules, and occasionally with Roti-Rich, a yeast- and algae-based rotifer food. Newly hatched *Artemia* were given to larvae during 11-60 dah in decreasing amounts

but were not digested well, at least initially. Crumbled starter pellets were offered to the fish once a day during 42-60 dah and twice a day during 61-66 dah; older fish received one meal a day. Weaning from live food to pellets was accomplished, using minced penaeid shrimp as an appetizer, during 56-61 dah when most larvae were transforming (range 46-70 dah, 32-50 mm TL). After weaning, the only food given (except for tagged and released fish) was a series of dry pelleted feeds developed at HBOI for marine fish.

For a 128-day tagging study (Roberts et al. 1995) the pelleted feed was partly replaced with live and frozen food to accustom the fish to a more natural diet. During the study, pellets were fed 84 times. Live food consisted of 1 218 goldfish (*Carassius auratus*, 12 times), 50 minnows (Cyprinidae, once), 718 live pink shrimp (*Penaeus duorarum*, 6 times), and 160 fiddler crabs (*Uca* sp., twice). Frozen food consisted of fish (tuna, tilefish, Spanish mackerel, dolphin, gag, 16 times), queen conch (*Strombus gigas*, 12 times), penaeid shrimp (9 times), and scallops (twice).

1994. During the entire period (0-75 dah), 0.4-1 l each of *Nannochloropsis*, *Isochrysis*, and *Tetraselmis suecica* was added to the tank each day. Both small strain rotifers and large strain rotifers were used. Cryopreserved Pacific oyster (*Crassostrea gigas*) trochophore larvae (50 µm width) were given as a supplemental food, initially to ensure enough small prey, then up to 18 dah to help slow-growing larvae and as an extra source of essential fatty acids. Copepods (*Tigriopus japonicus*) also were fed. Rotifers and *Artemia* were enriched with Microfeast Booster (Provesta Corporation). To delay buildup of an oil film, rotifer enrichment was started late (11 dah). Minced shrimp was offered during 41-74 dah and crumbled pellets during 44-75 dah. Weaning was accomplished during 54-75 dah.

Results and Discussion

Spawning

Wild females containing fully-yolked oocytes were induced to ovulate with two injections of 700 IU HCG/kg body weight spaced 24 hours apart, with ovulation occurring about 2 days after the first injection (Tucker et al. 1991). Females whose oocytes had begun to hydrate required only one injection, and ovulation occurred sooner. Despite some problems with the broodstock holding systems, eggs were obtained from seven of 12 females injected with HCG at Grand Cayman (Tucker et al. 1991) during four seasons (1987-1990). Broodstock treatment was then standardized as follows. Immediately after capture, fish that are overinflated from gas bladder expansion are deflated with a large bore (18-20 gauge) hypodermic needle, or equivalent (see Render and Wilson, this vol.). They are handled gently but decisively with wet hands, soft nylon nets, or clear polyethylene bags. Anesthesia with tricaine methanesulfonate is used for weighing and measuring reared fish, but has never been necessary when processing, injecting or spawning broodfish, if they are handled without hesitation. Females are injected soon after they reach the laboratory, but this has been as long as 4 days (once >14 days) after capture. Running ripe males will stay that way for several days and have never needed injections. Two 4.4 kg males transported from Nassau to Florida in December 1992 and held in a 6 m³ nylon net cage remained running ripe at least until April 1993. In a limited trial with two other running ripe males, milt volume was increased 24 hours after a single half dose of 350 IU/kg BW. As in many groupers, hydration of oocytes is indicated by swelling of the abdomen, and ovulation by protrusion of the egg mass through the genital opening. The female does not swim smoothly, rests on the

bottom more often, and sometimes turns pale relative to its tankmates. Bicoloration (top dark, bottom pale) occurs more often in both males and females as spawning becomes imminent. When the eggs are protruding, the membrane holding them in is stretched thinly, and biopsies are very easy to take with 1-140 µm inside diameter polyethylene tubing. Before that time, biopsies tend to injure the fish and should be avoided.

Wet fertilization was used during 1987-1990, but in 1992-1994 the dry method was found to be more convenient and just as reliable. One milliliter of milt was more than enough to fertilize 300 000 eggs. High quality eggs were consistently obtained during the 1992-1993 and 1993-1994 seasons (Table 1). Eggs were obtained from 11 wild females that naturally ovulated and 19 that were induced to ovulate with injections of 700 IU HCG/kg (Table 2). During December, January and February 1992-1994, we observed that many wild females held in cages and tanks in Nassau ovulated naturally from two days before until seven days after the full moon. In a few cases, eggs were released in the holding tank before the female was removed for stripping. Each time, fertilization in the tank was near 100%. Intentional fertilization was not observed, but the males were very ripe and probably were constantly leaking enough milt. Only stripped eggs were used for culture purposes, because they are cleaner and already concentrated. Also, when under stress, females sometimes retain ovulated eggs until they overripen. Voluntary spawning of long-term captive groupers in ponds, cages or tanks has occurred with at least 22 species (Tucker 1994), including Nassau groupers in a large aquarium (Guitart Manday and Juarez Fernandez 1966), in a 26-m³ cage (P.G. Bush, personal observation, in Tucker et al. 1993), and in a 37-m³ concrete raceway (Tucker and Woodward 1996).

Table 1. Spawning of wild Nassau groupers purchased from live fish dealers at Nassau during the 1992-1993 and 1993-1994 seasons. The dry fertilization method was used. [Desoves de cherna criolla silvestre obtenidos de distribuidores de peces vivos durante la temporada 1992-1993. Se utilizó el método de Fertilización en seco.]

No.	Spawning date	Spawning time (std)	Time after first ovulation injection (h)	Type of ovulation	Female weight (kg)	Male weight (kg)	Number of eggs (1,000's)	Fertilization rate (%)	Hatching rate (%)
Full moon during night of 9 Dec 1992, 24-25°C in tanks									
0	9 Dec	1630		Natural	5.2	3.3	>590	98	~100
1	10 Dec	1300	25	Induced	2.8	4.0	>470	96	~100
1	10 Dec	1730	30	Induced	3.2	3.9	>470	98	~100
1	10 Dec	1830	31	Induced	4.9	5.2	>770	99	~100
1	10 Dec	0600	18	Aborted	4.1				
Full moon during morning of 8 Jan 1993, 23-25°C in tanks									
0	6 Jan	1600		Natural	5.0	5.0	>710	99	~100
0	6 Jan	1700		Natural	5.0	7.6	>710	99	~100
1	7 Jan	1330	20	Induced	4.7	4.2	>470	97	~100
1	7 Jan	1500	24	Induced	5.4	3.5	>470	92	~100
0	7 Jan	1615		Natural	8.9	4.8	>1180	100	~100
0	7 Jan	1745		Natural	8.8	4.8	>1180	100	~100
1	7 Jan	1900	29	Induced	6.1	4.8	>470	96	~100
1	7 Jan	1715	27	Induced	5.8	3.5	>350	99	~100
Full moon during night of 6 Feb 1993, 23-25°C in tanks									
2	7 Feb	0930	45	Induced	6.6 ^a	6.7 ^a	>940	10	~100
2	7 Feb	1400	49	Induced	5.6 ^a	6.7 ^a	>830	35	~100
1	8 Feb	1330	25	Induced	5.0	5.9	>1770	99	~100
2	8 Feb	1345	43	Induced	5.6	6.8	>1770	99	~100
2	8 Feb	1415	43	Induced	5.8	5.4 ^a	>1060	99	~100
1	8 Feb	1530	27	Induced	1.9	6.8	>240	94	~100
2	8 Feb	1545	45	Induced	7.7	6.7 ^a	>470	65	~100
1	8 Feb	1930	31	Induced	5.0	5.4 ^a	>590	99	~100
2	8 Feb	1630	76	None	7.5 ^a				
Full moon during morning of 29 Nov 1993, 25°C in tanks									
2	10 Dec	0655	37	Induced	6.3	5.4	>1220	99	~100
2	10 Dec	0710	38	Induced	6.1	7.2	>1240	97	~100
2	10 Dec	0730	38	Induced	5.7	4.8	>650	99	~100
2	10 Dec	0930	40	Induced	8.1	4.3	>1930	88	~100
Full moon during night of 28 Dec 1993, 23°C In tanks									
0	28 Dec	1700		Natural	6.7	4.2	>590	100	~100
0	28 Dec	1720		Natural	5.4	3.4	>550	99	~100
0	28 Dec	2010		Natural	5.0	4.4	>440	78	~90 ^b
Full moon during morning of 27 Jan 1994, 24°C in tanks									
0	26 Jan	1645		Natural	4.4	3.0	>97	100	~100
0	26 Jan	1715		Natural	2.8	3.2	>125	100	~100
0	26 Jan	1850		Natural	4.2	4.6	>112	100	~100

^aFish that had been held in vendors' cages without food for more than 14 days. Other fish were obtained within 2-4 days after capture.

^bEggs were partly overripe.

Table 3. Development of Nassau groupers to early juveniles at about 26°C and to adults at variable temperatures. Sizes correspond with events, and not necessarily with ages. [Desarrollo de la cherna criolla a juveniles tempranos a cerca de 26°C, y a adultos a temperaturas variables. Las tallas corresponden a eventos y no necesariamente a edades.]

Event	Days after hatching	Total length (mm)
Hatching	0	1.9
First feeding	2.5-3.5	2.6
Exhaustion of yolk & oil	5-6	3
First feeding on <i>Artemia</i> nauplii	10-12	5
Transformation	46-75	32-50
First feeding on dry feed	56-59	40-60
Maturation	4-5 (\bullet 365)	<500-600

occurred over a longer period in 1994, partly because of lower temperatures. Many of the juveniles used openings of the milk crates as perches until they outgrew the spaces. Egg and larval development is described in Powell and Tucker (1992).

Culture conditions

Table 4 summarizes details of culture conditions.

Temperature. The range tolerated by eggs and larvae was 19-28°C. Sudden temperature changes (e.g., from thermal stratification or too much sunlight) can result in sudden high mortality of early larvae. Older fish survived in a temperature range of 11-33°C, but food intake was minimal below 18°C and growth was best at 22-30°C.

Water quality. Bacterial counts indicated zero *Vibrio* in incoming hatchery water and rotifer cultures.

In 1994, ammonia peaked at about 13 dah when rotifer density was high (150 ppb total ammonia nitrogen (TAN)) and nitrite at about 20 dah (300 ppb NO₂-nitrogen, zero ammonia). At 35 dah, ammonia was zero, nitrite 20 ppb and nitrate (NO₃-nitrogen) 1.1 ppm. Dissolved oxygen was relatively constant at 4.9-5.2 ppm.

In early trials, when TAN reached 100 ppb, weak larvae died within 12 hours. In

1994, strong larvae (13 dah) tolerated 150 ppb TAN for 12 hours. At 100-300 ppb TAN, juveniles and adults were stressed and some died within 48 hours. When incoming water from pipelines was contaminated with ammonia, low but possibly toxic levels of hydrogen sulfide might also have been present, but H₂S analysis was not possible.

Larvae seemed to be alternately sluggish and agitated when nitrite nitrogen reached 300 ppb, and these signs stopped when it dropped to 150 ppb; however, no cause and effect were proven.

Although juveniles tolerated salinity as low as 15 ppt for a few days, they seemed stressed and ate less.

Surface films. In some cases, naturally occurring sticky substances (probably from decaying seaweeds) in the water supply formed a surface film that trapped early larvae like flypaper, usually killing all the fish in a tank. Sticky films must be avoided by reliable water treatment. Inevitably, surface oil films will occur in the rearing tanks and these must be kept thin. Sources of the oil are the oil globules of dead eggs and early larvae, added phytoplankton and zooplankton, and enrichment mixtures added with zooplankton, either stuck to it or in the water added with it. With grouper larvae, compressed-air skimmers could not be used

Table 4. Environmental ranges and constraints for rearing Nassau groupers.
[Intervalos ambientales y restricciones para la cría de la cherna criolla.]

Factor	Comments
Larvae	
Temperature	19-28°C was tolerated 24-27°C probably is best
Salinity	27-38 ppt was tolerated 30-37 ppt probably is best
Total ammonia nitrogen	100 ppb was lethal to weak larvae within 12 h 150 ppb was tolerated by strong larvae for 12 h 0 ppb is best
Nitrite nitrogen	300 ppb apparently stressed strong larvae 150 ppb apparently was tolerated by strong larvae
PVC cement	Contamination of water—from mild stress to total mortality
Sticky surface film	Possible complete mortality of early larvae
Oily surface film	If thin, tolerated by strong larvae, no gas bladder problem
Light	5% natural light increases food and water quality by supporting algal growth (avoid radiant heat)
Juveniles and adults	
Temperature	11-33°C was tolerated 22-30°C probably is best
Salinity	15-37 ppt was tolerated 25-37 ppt probably is best
Total ammonia nitrogen	100-300 ppb was lethal within 48 h 0 ppb is best
Light	Some natural light helps water quality

to remove sticky films because the turbulence usually caused high mortality. When larvae are strong enough to avoid being trapped, such devices could be used for oil/algae/debris films that will move but are less effective with thick or very viscous films. Even late larvae are relatively passive drifters and can be carried into a skimmer

or down the drain by a weak current. For small tanks, we have at times used a peristaltic vacuum pump with Pasteur pipette attached to manually remove the oil film. Disturbance to larvae is minimal with this method, but it is laborious and slow and thus impractical. When larvae are not at the surface, clean, non-shredding, paper towels

have been used to blot up sections of the film. The towels must be free of toxicants and they must be removed promptly before they trap larvae or sink.

Light. About 5% natural sunlight transmitted through the hatchery roof supported a light bloom of microalgae at first, then macroalgae on tank walls beginning within 10 days after stocking. Because Nassau grouper larvae are very sensitive to ammonia and early larvae are very sensitive to water changes, removal of ammonia by algae was considered a critical factor in larval survival. A very reliable recirculating system is an alternative; however, algae in the tank take up ammonia very quickly. Unevenly distributed intense light caused larvae to bunch up, sometimes interfering with feeding or causing localized oxygen depletion.

Aeration. Water movement is important to ensure oxygenation, to prevent thermal stratification and to disperse food. Too much movement might keep larvae from feeding, make them struggle and waste energy, or cause gas bladder overexpansion by a rapid upward excursion. Early Nassau grouper larvae are very sensitive to turbulence. At first, very light or no aeration is best. Circulation can be improved by directing water flow from diffuser pipes, by having constant air currents blow across the water surface or sprinkling water on the surface. Added water must be well-aerated before it enters the hatchery tanks. In 1994, aeration was provided by one airstone inside a screened airlift tube during 0-39 dah, one uncovered airstone on the tank bottom beginning 38 dah, and two on the bottom from 60 dah onward.

Feeding

Idealized feeding and weaning schedules for groupers are given in Tucker (1992a). Table 5 summarizes actual feeding schedules. Although *Nannochloropsis oculata*

provides EPA and Tahitian *Isochrysis* provides DHA to the food organisms, enrichment was done mainly as a precaution against essential fatty acid deficiencies. Although weaning was accomplished during 56-61 dah in 1990, minced shrimp was given three more times to help the slow learners.

The tagged juvenile groupers showed no hesitation in eating any of the new foods when first presented, except for live shrimp, which in the beginning were eaten gradually over several hours, and later as fast as they were added to the tank. Live fish and crabs were easier for the groupers to handle and, from the beginning, were usually eaten within 20 minutes.

Nassau groupers are more flexible than some other fish in their feeding habits. Reared groupers will eat pellets and frozen food either combined or alternately. Wild juveniles (averaging about 250 mm TL) ate pellets in 1-m³ fiberglass tanks within 2 hours after being captured in a trap. We also have trained several small to medium wild adults (500-700 mm TL) to eat pellets, as well as frozen food. Reared juvenile and adult Nassau groupers often ate well within 3 hours after being transferred to different tanks, if handled gently.

Survival

1990. Mortality peaks occurred during three phases. At first feeding (2.5-3.0 dah) some larvae apparently were too weak to continue or were adversely affected by temperature changes. At EYS (end of yolk sac, 5 dah), a larger number died, probably because they were not feeding effectively. Most mortality occurred over several days when larvae were mainly eating newly hatched *Artemia* nauplii, especially near 20 dah. Survival from eggs to 98-day old juveniles (129 fish) in the four 3.5-m³ tanks was 1%, 2.4%, 4.5%, and 5.0%. After weaning, mortality was negligible. Between 98 dah and 1 year, only two runts were lost.

Table 5. Feeding schedule used for Nassau groupers. [Calendario de alimentación usado para la cherna criolla.]

Days after hatching	Total length (mm)	Food
Larvae (in 1990)		
0-25	1.9-8	<i>Nannochloropsis</i> & <i>Isochrysis</i> to feed prey
3-22	2.6-6	Enriched rotifers (40-200 µm)
11-60	5-60	<i>Artemia</i> nauplii (just hatched) ^a
21-60	6-60	Enriched <i>Artemia</i> (1-5 dah)
23-49	7-40	Enriched rotifers (118-200 µm)
Transforming (in 1990)		
56-61,63,66,69		Minced penaeid shrimp
Larvae (in 1994)		
0-75	1.9-70	<i>Nannochloropsis</i> , <i>Isochrysis</i> , & <i>Tetraselmis</i> to feed prey
4-18	2.7-6	Oyster trochophores
4-20	2.7-6	Small strain rotifers (fed <i>Nannochloropsis</i> & <i>Isochrysis</i>)
7-40	2.8-35	Large strain rotifers (fed <i>Nannochloropsis</i> & <i>Isochrysis</i>)
11-20	5-6	Small strain rotifers (enriched)
11-32	5-20	Large strain rotifers (enriched)
14-64	5-60	<i>Artemia</i> (1-5 dah, enriched)
16-75	6-70	<i>Artemia</i> (1-5 dah, fed <i>Nannochloropsis</i> & <i>Isochrysis</i>)
18-67	6-60	Copepods
18-74	6-70	<i>Artemia</i> nauplii
Transforming (in 1994)		
54-74		Minced penaeid shrimp
Juvenile to adult (all years)		
56-97	40-90	1.6 mm pellets (HB9110)
	80-140	2.4 mm pellets (HB9120 or HB9220)
	140-250	4.0 mm pellets (HB9120 or HB9220)
	250-600	9.5 mm pellets (HB9120, HB9220, HB9261, or HB9262)
	600-	12.7 mm pellets (HB9120, HB9220, HB9261, or HB9262)

^a *Artemia* are probably more digestible after their own digestive systems are open (about 12 hours after hatching).

Later, some fish were lost from ammonia contamination of the water supply.

1994. Only the second mortality peak was important. High egg quality and better temperature control helped eliminate the first peak, and the diverse diet helped eliminate the third. During 0-5 dah, survival was near 100%. Because of high mortality

during 7-9 dah, survival at 10 dah was only 1.2%. During 10-75 dah, survival was 59%. Overall survival was 0.71%, mainly because of the 7-9 dah losses.

In a preliminary trial, survival at 15 dah was 25% (200/800) in a 120-l glass aquarium. Based on that result and 59% survival during 10-75 dah in 1994, 15% overall survival

seems possible. Earlier enrichment of rotifers (before 11 dah) and earlier feeding of copepods (before 18 dah) might improve early survival.

Growth and feed conversion

1990. Medium-sized groupers grew and utilized food well (Tables 6 and 7). Mean weight was 0.5 kg in 12 months, 1.5 kg in 23 months and 2.0 kg in 28 months (Fig. 1). Feed costs would be low for commercially raising Nassau groupers to a market size of 2 kg. In trials 3, 4 and 6, feeding and growth were reduced during periods of low temperature (<22°C). Improvement of early growth rates (particularly by diet and temperature control) will allow production of 2 kg groupers within 24 months.

Rearing units

Round fiberglass tanks. Larvae, juveniles and adults grew well and remained healthy in fiberglass tanks as long as water quality was maintained. Based on rearing experience with 35 marine species, a tank containing 1 m³ of water probably is the minimum practical size required for grouper larval rearing. A 3.5-m³ tank is better and is convenient to manage. The 7-m³ tank worked very well, except the bottom was hard to clean. Increasing tank size (moving toward extensive rearing with lower fish density) has a moderating effect on water quality fluctuations and allows more larvae to be reared in each tank, but sometimes increases management difficulties.

Rectangular concrete tanks. Nassau groupers can be grown out in smooth concrete tanks. Slight fin and body abrasion was caused by bare concrete walls and concrete blocks but not by concrete covered with macroalgae.

Rectangular cages. Plastic or plastic-coated wire cages probably are suitable for growing out Nassau groupers. Wild Nassau groupers usually do not live long (<1 day) if left in wire traps after capture, but survive for weeks on boats in live-wells lined with plastic-coated wire if motion is minimal. Some Asian groupers are raised in flexible polyethylene net cages. Nassau groupers might be more aggressive than some other species, but probably would do reasonably well in such cages. When 27 tagged, reared groupers (never before kept in a cage) fish were suddenly transferred to a chicken wire cage (4 m x 1.2 m x 1.2 m high) and held there for 2 weeks, eight developed eye injuries from early escape attempts. Adult groupers kept in a rigid polyethylene cage (2.4 m dia. x 1.8 m deep) in Grand Cayman for a year remained healthy (P.G. Bush, pers. comm.).

Tagging and release study

Thirty-two medium-sized groupers were tagged with 76-mm orange dart tags, held in a raceway and alternately fed pellets, frozen seafood, and live fish, shrimp or crabs for three months (Roberts et al. 1995). Despite their benthic habits, at the end of this evaluation period, 22 of the groupers had retained their tags. The others were retagged and 27 of them (0.6-1.1 kg) were held in a transitional cage for two weeks at a small reef-fringed island off St. Thomas (U.S. Virgin Islands) and then were released. The fish immediately began instinctive wild behavior, such as allowing gobies and shrimp to clean them and hunting with an octopus. Diving teams monitored behavior and dispersal of the tagged fish for several months. Most of them remained near the release area for at least a month. At least two of the fish stayed in the area for 200-297 days. One of the fish was seen in the area 16 months after release.

Table 6. Compositions of six experimental diets (dry pellets) developed at Harbor Branch Oceanographic Institution for Nassau groupers. All values except protein:energy are in percent. Except for moisture, proximate analysis values are moisture free. [Composición de seis dietas experimentales ("pellets" secos) desarrollados por Harbor Branch Oceanographic Institution para la cherna criolla. Todos los valores excepto proteína:energía están dados en porcentaje. Excepto la proporción para mezcla, todos los análisisproximales son libres de mezcla.]

Component	Feed HB9010	Feed HB9020	Feed HB9120	Feed HB9261	Feed HB9110	Feed HB9220	Feed HB9262
Type Status	Starter used	Grower used	Grower used	Broodfish used	Starter revised	Grower revised	Broodfish revised & used
Moisture (% of air dry weight)	8.0	7.6	7.8	7.9	8.0	6.5	8.4
Formulation							
Low temperature							
herring meal	60.4	45.4	45.5	40.5	60.5	30.0	40.5
Shrimp meal	—	—	—	10.0	—	—	—
Krill meal	—	—	—	—	—	—	10.0
Poultry meal	—	—	—	8.0	—	15.0	8.0
Meat meal	—	—	—	8.0	—	15.0	8.0
Blood meal	3.5	3.5	3.5	—	3.5	—	—
Feather meal	5.0	10.0	10.0	—	5.0	—	—
Textured vegetable							
protein	8.0	13.0	13.0	10.0	8.0	20.0	10.0
Corn gluten-meal	5.0	5.0	5.0	5.0	5.0	—	5.0
High gluten wheat flour	4.9	13.9	15.7	12.2	6.7	12.7	10.2
Brewer's yeast	1.0	1.0	1.0	1.0	1.0	—	1.0
Bone meal	2.0	2.0	—	—	—	—	—
Menhaden oil	7.5	3.5	3.5	2.5	7.5	4.5	4.5
Lecithin	1.0	1.0	1.0	1.0	1.0	1.0	1.0
Microingredients ^a	1.7	1.7	1.8	1.8	1.8	1.8	1.8
Proximate analysis (vacuum dry)							
Crude protein (Kjeldahl)	60.1	59.7	59.9	58.6	60.3	53.4	58.2
Crude fat (ether extract)	16.2	10.3	10.3	11.8	16.2	13.3	13.8
Carbohydrate (difference)	9.6	17.2	18.7	16.7	11.1	20.1	14.0
Fiber (acid detergent)	0.3	0.9	0.9	1.7	0.3	0.9	1.9
Ash (600°C for 4 h)	13.8	11.9	10.2	11.2	12.1	12.3	12.1
Total fish oil	13.4	7.7	7.7	6.2	13.4	7.4	8.2
Total crustacean oil	—	—	—	1.5	—	—	1.5
EPA ^b	1.3	0.7	0.7	0.8	1.3	0.7	1.0
DHA ^b	1.4	0.8	0.8	0.8	1.4	0.8	0.9
Protein:energy (mg P/kcal DE)	151	160	158	155	149	140	151
Protein:energy (mg P/kJ DE)	36.0	38.3	37.9	37.0	35.7	33.6	36.1

^a Microingredients in the formulas are given below.

Feeds HB9010 and HB9020 contained, in mg/kg diet: iodine (potassium iodide) 4, zinc (oxide) 60, iron (ferrous sulfate) 50, manganese (oxide) 5, chromium (chromium potassium sulfate) 1, thiamin (mononitrate) 40, riboflavin 60, pyridoxine 40, pantothenic acid (d-calcium pantothenate) 200, niacin 300, biotin 2, folacin 20, cyanocobalamin 0.2, choline 4 800, inositol 900, APP (L-ascorbyl-2-polyphosphate) 300 mg/kg ascorbic acid equivalent, ethoxyquin 150; in IU/kg diet: retinol 20 000, cholecalciferol 3 000, tocopherol 500, menadione 50.

Feeds HB9110 and HB9120 contained the same as A except: (1) zinc was increased to 90 mg/kg, (2) iron was deleted, (3) manganese was increased to 40 mg/kg, (4) copper (sulfate) was added at 3 mg/kg, (5) L-ascorbyl-2-polyphosphate was increased to 400 mg/kg AAE.

Feeds HB9220, HB9261, and HB9262 contained the same as B except: (1) copper was deleted.

^b Contents of eicosapentaenoic and docosahexaenoic acids were calculated using average values for herring, menhaden and shrimp oils from Lovell (1989) and krill oil from Sargent et al. (1989).

^c For comparison, digestible energy was estimated using the values 4 kcal/g protein, 8 kcal/g fat, 3 kcal/g carbohydrate.

Table 7. Results of nine growth trials with medium-sized Nassau groupers reared from eggs. Feed formulas are given in Table 4. Daily growth = specific growth rate. Fish were held in 3.5-m³ round fiberglass, 10-m³, 20-m³ or 37-m³ rectangular concrete tanks. Feed conversion ratio = weight of dry feed that produced a unit weight of wet fish. Data from the first trial are means for four tanks, the rest for single tanks. [Resultado de ocho experimentos con cherna criolla de tamaño medio criados desde huevo. Las fórmulas del alimento son dadas en la tabla 4. Crecimiento diario = tasa de crecimiento específica. Los peces fueron mantenidos en tanques de fibra de vidrio circulares de 3.5 m³, 10 m³, 20 m³, o tanques rectangulares de concreto de 37 m³. La proporción de conversión alimenticia = peso de alimento seco que produce una unidad de peso húmedo de pez. Los datos del primer experimento corresponden al promedio de cuatro tanques, el resto para un solo tanque.]

Trial no.	Feed no.	Tank size (m ³)	Time (days)	Mean temp. (°C)	Temp. range (°C)	Number of fish	Survival (%)	Initial length (TL, mm)	Final length (TL, mm)	Initial weight (g)	Final weight (g)	Mean growth (g/d)	Daily growth (%)	Daily ration (%)	Feed conv. ratio
1	HB9010 ^a	3.5	96	26.5	23-30	129	-3	2.5	72	0.1	6.1	0.06	4.28	-	-
2	HB9020	3.5	145	28.7	24-33	25	100	77	162	7	71	0.44	1.57	1.41	0.90
3	HB9120	37	227	26.8	19-30	38	100	182	280	95	448	1.56	2.01	2.04	1.02
4	HB9120	3.5	138	27.3	18-33	5	100	233	305	210	594	2.78	0.75	0.77	1.02
5	HB9120 ^b	37	128	28.4	23-32	32	100	294	350	483	928	3.46	0.51	-	-
6	HB9120	37	140	23.1	17-29	24	100	307	354	598	906	2.20	0.30	0.39	1.32
7	HB9120	10	410	27.0	22-31	6	100	221	396	174	1490	3.21	0.52	0.73	1.41
8	HB9261 ^c	20	158	27.3	24-32	5	100	403	443	1396	2030	4.01	0.24	-	-
9	HB9261	3.5	42	27.2	24-30	5	100	437	449	1682	1870	4.48	0.25	0.45	1.80

^a Fed rotifers and *Artemia* during 3-60 dah and starter feed during 56-98 dah.

^b Because pellets were supplemented with live and frozen food, DR and FCR were not determined.

^c Because a larger wild male was in the tank, DR and FCR could not be determined.

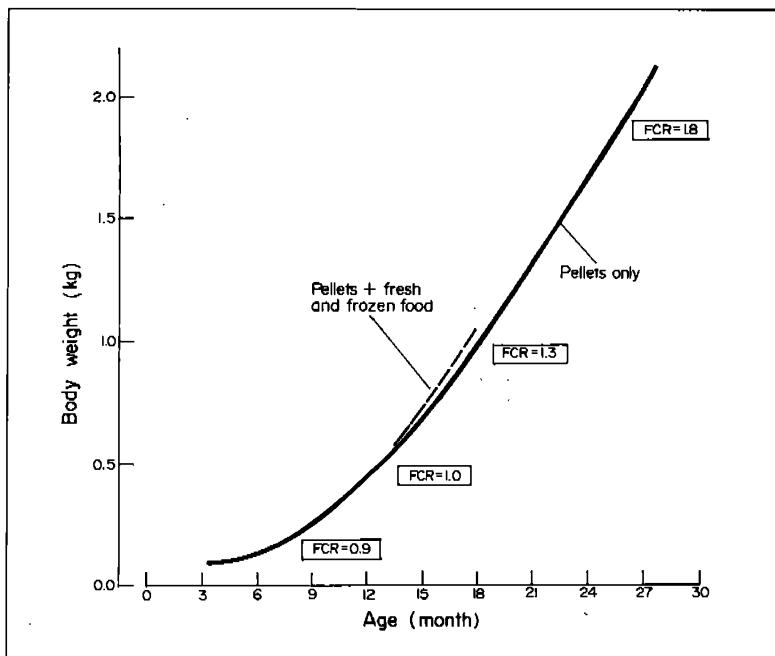


Fig. 1. Growth curve and feed conversion ratios of Nassau groupers (*Epinephelus striatus*). Solid line: pellets only; dashed line: tagged fish fed both pellets and whole foods in trial 5. [Curvas de crecimiento y proporción de conversión alimenticia para la cherna criolla (*Epinephelus striatus*) alimentada sólo con "pellets" (línea continua). La línea discontinua representa los peces marcados y alimentados con ambos, "pellets" y alimento entero en el experimento 5.]

Conclusions

Nassau grouper aquaculture is not yet close to commercialization; however, the species has potential. Obtaining large numbers of viable eggs is relatively easy. Although Nassau groupers endure a long and sensitive larval period, we believe that survival from egg to juvenile can be improved from 5% to 15% or more by better management of temperature, water quality and food. Juveniles and adults are robust. Barring accidents, nearly 100% survival after transformation can be expected. Temperature control and improved early diets can result in growth to 2 kg within 24 months. Hatchery-reared Nassau groupers have the potential to survive if carefully released in

suitable habitats. In special cases, depleted spawning populations could be replenished with large juveniles or adults (as long as genetic diversity is maintained).

Acknowledgements

We thank the personnel of the Bahamas Department of Fisheries, Cayman Islands Natural Resources Laboratory, Cayman Islands Turtle Farm, and HBOI Aquaculture Division for providing technical assistance; and Allen Johnson, HBOI, the U.S. Department of the Interior in cooperation with the National Sea Grant Office, and the University of Puerto Rico Sea Grant College Program for funding. This is HBOI Contribution No. 1030.

References

- Bohnsack, J.A. 1989. Protection of grouper spawning aggregations. NOAA/NMFS Coastal Resources Division Contribution CRD-88/89-06.
- Butler, J.N., J. Burnett-Herkes, J.A. Barnes and J. Ward. 1993. The Bermuda fisheries: a tragedy of the commons averted? Environment 35:6-15, 25-33.
- Carter, J. 1989. Grouper sex in Belize. Natural History 98:61-68.
- Colin, P.L. 1992. Reproduction of the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae) and its relationship to environmental conditions. Env. Biol. Fishes 34:357-377.
- Colin, P.L., D.Y. Shapiro and D. Weiler. 1987. Aspects of the reproduction of two groupers, *Epinephelus guttatus* and *E. striatus* in the West Indies. Bull. Mar. Sci. 40:220-230.
- Fine, J.C. 1990. Groupers in love: spawning aggregations off Honduras. Sea Frontiers 36:42-45.
- Guitart Manday, D. and M. Juarez Fernandez. 1966. Desarrollo embrionario y primeros estadios larvales de la cherna criolla, *Epinephelus striatus* (Bloch) (Perciformes: Serranidae). Academia de Ciencias de Cuba, Instituto de Oceanologia Estudios, Havana 1:35-45.
- Lovell, T. 1989. Nutrition and feeding of fish. Van Nostrand, New York.
- Powell, A.B. and J.W. Tucker, Jr. 1992. Egg and larval development of laboratory-reared Nassau grouper, *Epinephelus striatus* (Pisces, Serranidae). Bull. Mar. Sci. 50:171-185.
- Roberts, C.M., N. Quinn, J.W. Tucker, Jr. and P.N. Woodward. 1995. Introduction of hatchery-reared Nassau grouper to a coral reef environment. North American J. Fish. Manage. 15:159-164.
- Sadovy, Y. 1993. The Nassau grouper, endangered or just unlucky? Reef Encounter 13:10-12.
- Sadovy, Y. The case of the disappearing grouper *Epinephelus striatus*, the Nassau grouper, in the Caribbean and western Atlantic. Proc. Gulf Caribb. Fish. Inst. 45. (In press).
- Sargent, J., R.J. Henderson and D.R. Tocher. 1989. The lipids, p. 153-218. In J.E. Halver (ed.) Fish nutrition. Academic Press, San Diego.
- Tucker, J.W., Jr. 1992a. Feeding intensively-cultured marine fish larvae, p. 129-146. In G.L. Allan and W. Dall (eds.) Proceedings, Aquaculture Nutrition Workshop, Salamander Bay, 15-17 April 1991. New South Wales Fisheries, Brackish Water Fish Culture Research Station, Salamander Bay, Australia.
- Tucker, J.W., Jr. 1992b. Marine fish nutrition, p. 25-40. In G.L. Allan and W. Dall (eds.) Proceedings, Aquaculture Nutrition Workshop, Salamander Bay, 15-17 April 1991. New South Wales Fisheries, Brackish Water Fish Culture Research Station, Salamander Bay, Australia.
- Tucker, J.W., Jr. 1994. Spawning by captive serranid fishes: a review. J. World Aquacult. Soc. 25:345-359.
- Tucker, J.W., Jr. and P.N. Woodward. 1996. Voluntary spawning by captive Nassau groupers (*Epinephelus striatus*) in a concrete raceway. J. World Aquacult. Soc. 27:373-383.
- Tucker, J.W., Jr., J.E. Parsons, G.C. Ebanks and P.G. Bush. 1991. Induced spawning of Nassau grouper *Epinephelus striatus*. J. World Aquacult. Soc. 22:187-191.
- Tucker, J.W., Jr., P.G. Bush and S.T. Slaybaugh. 1993. Reproductive patterns of Cayman Islands Nassau grouper (*Epinephelus striatus*) populations. Bull. Mar. Sci. 52:961-969.

ENTERED IN NAGA

APR 14 1998

Maturation and Induced Spawning of the Mangrove Red Snapper (*Lutjanus argentimaculatus*) Reared in a Floating Net Cage in the Philippines

A.C. EMATA

Aquaculture Department

Southeast Asian Fisheries Development Center (SEAFDEC/AQD)
Tigbauan, Iloilo, Philippines

EMATA, A.C. 1996. Maturation and induced spawning of the mangrove red snapper, *Lutjanus argentimaculatus*, reared in a floating net cage in the Philippines [Maduración y desove inducido del pargo de manglar, *Lutjanus argentimaculatus*, criado en cajas de red flotantes en Filipinas], p. 378-384. In F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Wild-caught mangrove red snapper (*Lutjanus argentimaculatus*) were reared in a floating net cage at SEAFDEC/AQD's Igang Marine Substation at Guimaras Island, Central Philippines. In 1993, monthly samplings and induced spawning trials were conducted as part of a project on seed production. Gonadal development began in February for males and April for females, reached a peak in September and declined in December. Males and females had ripe gonads for up to 5-6 consecutive months. Spawning occurred in the evening (2000-2300 hours), 32-36 hours after a single intramuscular injection of 1 500 IU human chorionic gonadotropin kg⁻¹ body weight (BW). About 0.53-2.14 million eggs were collected per female (2.5-4.4 kg BW) with fertilization rates of 21-97% and hatching rates of 42-80% resulting in 30-85% normal larvae (straight and without deformities). The results strongly suggest the feasibility of breeding mangrove red snapper in floating net cages.

Resumen

*Pargos de manglar silvestres (*Lutjanus argentimaculatus*) fueron capturados y criados en cajas de red flotantes en SEAFDEC/AQD de la Subestación Marina de Igang en la Isla Guimaras, al centro de Filipinas. En 1993, muestras mensuales y experimentos de desoves inducidos fueron efectuados como parte de un proyecto sobre producción de semilla de pargo de manglar. El desarrollo de las gónadas empezó en Febrero para los machos, y en Abril para las hembras, alcanzando un máximo en Septiembre y declinando en Diciembre. Machos y hembras estuvieron sexualmente maduros por 5-6 meses consecutivos. El desove ocurrió durante la noche (2000-2300), 32-36 horas después de una simple inyección intramuscular de 1 500 IU de gonadotropina coriónica humana por cada kg de peso corporal húmedo. Cerca de 0.53 a 2.14 millones de huevos fueron colectados por cada hembra (2.5-4.4 kg peso húmedo), con tasas de fertilización de 21-97%, tasa de incubación de 42-80%, y 30-85% de larvas normales (derechas y sin deformidades). Los resultados sugieren fuertemente la factibilidad de criar pargos de manglar en cajas de red flotantes.*

Introduction

Many snappers belonging to the family Lutjanidae have long been recognized to have mariculture potential. In Southeast Asia, the mangrove red snapper (*Lutjanus argentimaculatus*) command a relatively high market price (FAO 1990) and are cultured in cages and brackishwater ponds (Cheong 1988; A. Maravilla, pers. comm.; N.J. Ogburn, pers. comm.). However, in the Philippines, the fry (2-3 cm total length, TL) needed to stock ponds still come exclusively from the wild where they are mostly collected near river mouths together with grouper fry. Thus, broodstock development was initiated at the Aquaculture Department of the Southeast Asian Fisheries Development Center (SEAFDEC/AQD) as part of a project on seed production to supplement the natural fry supply.

Materials and Methods

Mangrove red snappers were collected in 1991 and 1992 from fish corrals along the southwestern coast of Guimaras Island, Central Philippines. These were kept in a 5 x 5 x 3 m deep floating net cage located at SEAFDEC/AQD's Igang Marine Substation at Guimaras Island. Fish were fed trash fish every other day at 5% body weight (BW). Seawater temperature and salinity ranges were 27-32°C and 30-36 ppt respectively, during 1991-1993.

Fish were sampled monthly, beginning on 17 February 1993 to assess their gonadal development based on biopsied material. During sampling, fish were anesthetized in 250 ppm 2-phenoxy-ethanol (Merck, Germany) and BW and TL of each fish was measured. Gonadal biopsy for females was conducted by inserting polyethylene tubing (PE 100, Clay Adams, New Jersey) into the genital pore followed by gentle aspiration of ovarian oocytes. The oocytes were fixed in 5% buffered formalin. Diameters of 20 oocytes were measured to the nearest

0.05 mm using an ocular micrometer. The mean oocyte diameter was later used to select females for induced spawning trials. Mature males were identified by the presence of milt following gentle massage to the abdomen. Fish with no cannulated oocytes or milt were considered unidentified (UD). Each fish was then marked with a numbered opercular tag as described by Garcia and Gapasin (1988).

Induced spawning trials were conducted as soon as adequate number of females possessing vitellogenic oocytes and males with copious amount of milt were obtained during sampling. Females and males were then given a single intramuscular injection of 1 500 IU human chorionic gonadotropin (hCG, Argent Chemicals, Philippines) kg⁻¹ BW or 100 mg des Gly¹⁰(D-Ala⁶)-luteinizing hormone-releasing hormone ethylamide (LHRHa, Lam Hua Dragon Trading Co., Hongkong) kg⁻¹ BW. Injected fish were then placed in 2 x 2 x 2 m deep fine mesh (0.6-0.8 mm) net cage at 1:1 to 1:3 female to male ratio and allowed to spawn spontaneously.

Spawning, which occurred during the night, was monitored by checking for the presence of eggs in the water column of the spawning cages each morning. As soon as spawning was confirmed, the spawners were removed from the spawning cage. By lifting the cage and splashing the sides of the net with seawater, eggs were concentrated at the cage bottom and collected and incubated in 500-l fiberglass tanks containing gently aerated filtered seawater of ambient temperature and salinity. Eggs were transported to the hatchery in double-lined plastic bags containing 300 000 eggs in 12 l of filtered seawater saturated with oxygen. The total number of eggs and fertilization rate were determined from three 700 ml aliquots. Likewise, hatching rates and percent of normal larvae were determined from three 700 ml aliquots obtained the day after spawning.

Table 1. Gonadal development of mangrove red snapper (*Lutjanus argentimaculatus*) broodstock reared in floating net cages in the Philippines in 1993. Zero (0) or plus (+) indicates presence or absence of cannulated oocytes or free-running milt. Oocyte diameters are means \pm S.E.M. (mm). [Desarrollo gonádico del pargo de manglar (*Lutjanus argentimaculatus*) criado en cajas de red flotantes en Filipinas en 1993. Cero (0) o mas (+) indican ausencia o presencia de oocitos canulados o fecundados libremente. El diámetro de los oocitos fueron medidas \pm s.e.m. (mm).]

Fish No.	Body weight (kg)	Total length (cm)	17 Feb	21 Apr	18 May	7 Jul	17 Aug	29 Sep	27 Oct	7 Dec
Females										
4 469	2.6	51.0	0	0	0.46 \pm 0.025	0.34 \pm 0.020	0	0.25 \pm 0.016	0	0
4 895	2.5	51.5	0*	0	0	0	0.46 \pm 0.001 ^b	0.41 \pm 0.020	0	0
4 892	3.5	54.5	0	0	0	0.38 \pm 0.010	0.46 \pm 0.007	0.36 \pm 0.012	0.38 \pm 0.014	0
4 890	3.5	55.5	0	0	0	0	0.46 \pm 0.010	0.42 \pm 0.006	0.46 \pm 0.008	0
4 898	4.0	60.0	0	0.49 \pm 0.006	0	0.42 \pm 0.010	0.50 \pm 0.006	0.40 \pm 0.006	0.41 \pm 0.010	0
4 851	4.4	61.5	0	0	0.46 \pm 0.004	0.42 \pm 0.003	0.45 \pm 0.020	0.35 \pm 0.014	0.44 \pm 0.008	0
2 960	3.4	57.0	0	0.46 \pm 0.004	0.41 \pm 0.005	0.41 \pm 0.004	0.45 \pm 0.020	x*	x	x
Males										
4 894	1.8	45.0	0	0	0	0	+b	+	+	+
4 891	1.9	44.5	0	0	0	0	0	+	+	0
4 900	2.5	50.0	0	+	0	0	+	+	+	+
4 896	2.5	49.5	0	0	+	+	+	+	+	+
4 471	2.6	50.5	0	0	0	+	+	+	+	0
4 899	2.5	49.5	0	0	+	+	+	+	+	0
4 893	3.0	53.5	+	0	+	+	+	+	+	0
2 683	3.3	55.5	0	0	+	+	+	+	+	+
4 897	3.6	57.5	+	+	0	+	+	+	+	+
4 541	4.0	58.0	0	0	+	+	+	+	+	0
4 889	4.5	61.5	0	0	+	+	+	+	+	+
Unidentified										
4 543	3.3	55.5	0	0	0	0	0	0	0	0
3 994	3.5	55.5	0	0	0	0	0	0	0	0
535	3.9	57.5	0	0	0	0	0	0	0	0
4 538	4.0	58.0	0	0	0	0	0	0	0	0

* Mortality

^b Presence of viscous milt

Results

Monthly samplings conducted between 17 February and 7 December 1993 showed that the *L. argentimaculatus* broodstock consisted of seven females (2.5-4.4 kg BW, 51.0-62.0 cm TL), 11 males (1.8-4.5 kg BW, 44.5-61.5 cm TL), and four UD (3.3-4.0 kg BW, 55.5-58.0 cm TL) (Table 1). Ripe females were observed from April to October, with a peak of ripeness in September, and were sexually inactive in February and December (Fig. 1). A single female (fish no. 4851) possessed mature oocytes for up to five consecutive months even when induced to spawn in the previous months. Spermiating males were observed from February to December. But, as in females, sexual activity reached a peak in September when almost all fish were

ripe. Males (fish no. 2683 and 4896) were spermiating for up to 6 consecutive months even when used for induced spawning trials. None of the unidentified fish matured during 1993.

Preliminary results of induced spawning trials are shown in Table 2. A single intramuscular injection of 1 000 IU hCG kg⁻¹ BW resulted in successful spawning 32-36 hours post-injection in six out of eight trials. In one instance of unsuccessful spawning, a female ovulated but died at 48 hours post-injection with a bulging abdomen as overripe eggs could not be released. Females that spawned had initial mean oocyte diameters of 0.35-0.46 mm. About 0.53-2.14 million eggs were collected per female, with fertilization rates of 21-97%. Hatching rates and percentages of normal larvae were from 42-80% and 30-85%,

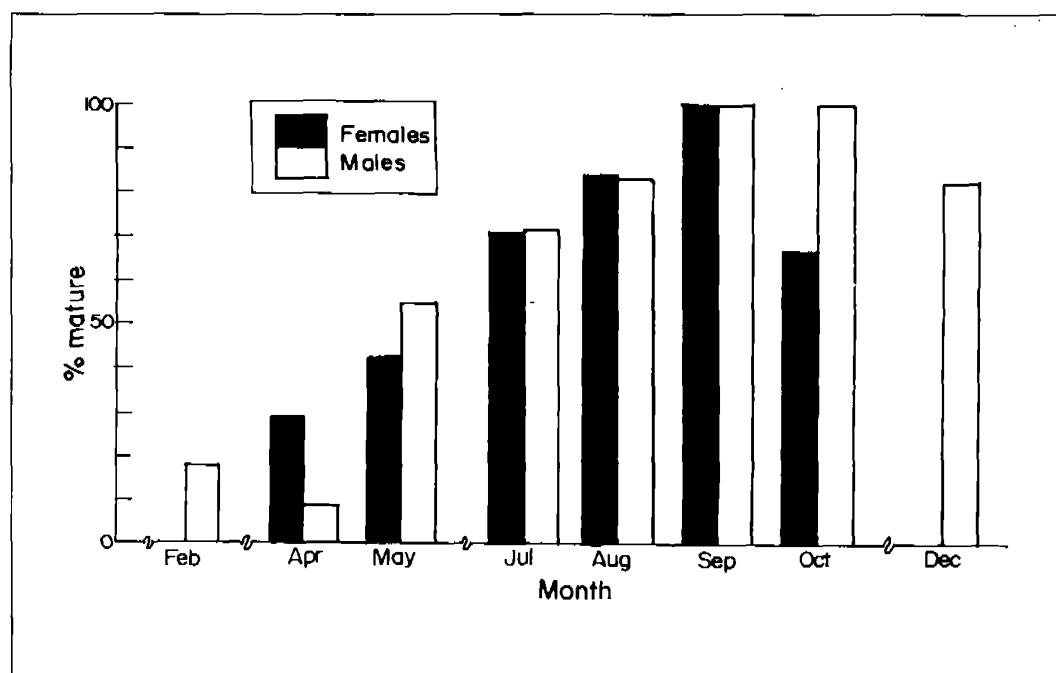


Fig. 1. Reproductive state of mangrove red snapper (*Lutjanus argentimaculatus*) reared in a floating cage in the Philippines in 1993. [Tasa de reproducción del pargo de manglar, *Lutjanus argentimaculatus*, criados en cajas de red flotantes en Filipinas en 1993.]

Table 2. Summary of induced spawning trials on mangrove red snapper (*Lutjanus argentimaculatus*) reared in floating net cages in the Philippines in 1993. [Resumen de desoves inducidos experimentalmente en pargos de manglar (*Lutjanus argentimaculatus*) criados en cajas de red flotantes en Filipinas en 1993.]

Date weight (kg)	Fish no.	Body (mm)	OD (mg/kg)	Hormone (F:M)	Dosage (h)	Ratio of eggs	Latency rate	Total number rate	Fertilization larvae	Hatch %	Normal
18 May	2 960	4.7	0.41±0.005	LHRHa	1 000	1:1	No spawning	-	-	-	-
	4 851	4.4	0.46±0.004	LHRHa	100	1:1	No spawning	-	-	-	-
	4 469	2.6	0.46±0.004	LHRHa	100	1:1	No spawning	-	-	-	-
17 Aug	4 890	3.5	0.46±0.010	hCG	1 000	1:1	32	528 800	71	50	98
	2 960	3.5	0.46±0.007	hCG	1 000	1:1	Fish died	-	-	-	-
	4 895	2.5	0.46±0.010	None	-	-	None	None	-	-	-
	4 898	4.0	0.50±0.006	hCG	1 000	1:2	36	2 137 950	87	68	79
	4 851	4.4	0.45±0.020	hCG	1 000	1:2	36	628 816	97	53	85
29 Sep	4 895	-	0.41±0.020	LHRHa	100	1:3	No spawning	-	-	-	-
	4 890	-	0.42±0.006	hCG	1 000	1:2	32	1 162 240	21	42	34
	4 892	-	0.36±0.012	LHRHa	100	1:2	No spawning	-	-	-	-
	4 898	-	0.40±0.006	hCG	1 000	1:2	No spawning	-	-	-	-
	4 851	-	0.36±0.014	hCG	1 000	1:2	36	992 000	21	53	30
27 Oct	4 851	-	0.44±0.008	hCG	-	1:3	34	1 413 920	76	80	65
	4 898	-	0.41±0.010	LHRHa	-	1:3	No spawning	-	-	-	-
	4 890	-	0.46±0.008	LHRHa	-	1:4	No spawning	-	-	-	-

respectively. A single intramuscular injection of 100 µg LHRHa kg⁻¹ BW failed to induce spawning in seven trials. An uninjected female failed to spawn during the trial on 17 August 1993.

Discussion

Wild-caught *L. argentimaculatus* reared in a floating net cage spontaneously matured and rematured for up to 5 consecutive months. These results strongly support the feasibility of breeding these snappers in floating net cages in the Philippines as observed in Thailand (Singhagrawan and Doi 1993), Malaysia (Ostrowski, pers. comm.) and Singapore (Chao Tien Mee, pers. comm.).

Captive *L. argentimaculatus* exhibited a defined seasonal cycle of reproductive activity in the Philippines. Spermiating males were observed as early as February and females possessed vitellogenic oocytes by April. Sexual maturation reached a peak in September. Although spermiating males were still obtained in December no females with vitellogenic oocytes were sampled indicating the end of the spawning season. A similar pattern of seasonal reproductive activity was observed for this species, cage-reared in Thailand (Singhagrawan and Doi 1993). Lutjanids exhibit a seasonal reproductive cycle although the season varied depending on geographic location (review in Grimes 1987).

Seed production of *L. argentimaculatus* entails a reliable breeding program that must be adaptable to the fish farmers. The availability of mature male and female mangrove red snapper for up to 5-6 consecutive months provide spawners for induced spawning. Furthermore, the use of hCG is a reliable protocol for production of quality eggs. The results from induced spawning trials using hCG in this paper are similar to those reported by

Singhagrawan and Doi (1993) for this species. The authors reported about a million eggs spawned per female with fertilization rates of 0 to 86.4%, although a lower hCG dose (300-600 IU/fish) was used. Other species of lutjanids have successfully spawned following injection of hCG (Minton et al. 1983; Lim et al. 1985) using lower doses. Thus, the minimum effective dose of hCG will have to be determined in the future. Furthermore, spawning trials using LHRHa at lower doses also will be continued as LHRHa is cheaper than hCG. These studies, together with those that will determine the relationships of fertilization rates and egg production to initial oocyte diameters are needed to fully attain a reliable spawning technique that can provide eggs when required by the industry.

A number of lutjanids have been reported to spawn serially or in batches (Grimes 1987), including cage-reared *L. argentimaculatus* in Thailand (Singhagrawan and Doi 1993). In all successful trials conducted in the present paper, serial spawning of individual *L. argentimaculatus* was never observed even though spawners were returned to the spawning cage following egg collection. Optimum conditions for serial spawning will be determined further, as well as those of natural spawning which was only observed once in 1993.

Acknowledgements

I am extremely grateful to B. Eullaran and the staff of Igang Marine Substation for the assistance in sampling and egg collection and transport.

References

- Cheong, L. 1988. Aquaculture development in Singapore, p. 117-128. In J.V. Juario and L.V. Benitez (eds.) Perspectives in aquaculture development in Southeast Asia and Japan. SEAFDEC Aquaculture Department, Tigbauan, Iloilo, Philippines.

- FAO. 1990. Regional seafarming resource atlas. RAS/86/024, 60 p. FAO/UNDP Regional Seafarming Development and Demonstration Project, Network of Aquaculture Centres in Asia and the Pacific c/o National Inland Fisheries Institute, Kasetsart University Campus, Bangkhen, Bangkok, Thailand.
- Garcia, L.M.B. and R.S.J. Gapasin. 1988. An inexpensive tag for short-term studies in milkfish (*Chanos chanos* Forsskål) and in sea bass (*Lates calcarifer* Bloch). *J. Appl. Ichthyol.* 4:101-104.
- Grimes, C.B. 1987. Reproductive biology of the Lutjanidae: a review, p. 239-294. In J.J. Polovina and S. Ralston (eds.) *Tropical snappers and groupers: biology and fisheries management*. Westview Press, Boulder.
- Lim, L.C., L. Cheong, H.B. Lee and H.H. Heng. 1985. Induced breeding studies of the John's snapper, *Lutjanus johni* (Bloch), in Singapore. *Singapore J. Pri. Ind.* 13:70-83.
- Minton, R.V., J.P. Hawke and W.M. Tatum. 1983. Hormone-induced spawning of red snapper, *Lutjanus campechanus*. *Aquaculture* 30:363-368.
- Singhagrawan, T. and M. Doi. 1993. Induced spawning and larval rearing of red snapper, *Lutjanus argentimaculatus* at the Eastern Marine Fisheries Development Center. *Thai Mar. Fish. Res. Bull.* 4:45-57.

ENTERED IN NAGA

APR 14 1998

Ultrastructural Study of Lymphocystis in Kelp Bass (*Epinephelus moara*; Serranidae)

Z. YONGJIA

W. ZEYANG

C. KANGRONG

Department of Agriculture
Zhanjiang Fisheries College
China 524025

YONGJIA, Z., W. ZEYANG and C. KANGRONG. 1996. Ultrastructural study of lymphocystis in kelp bass (*Epinephelus moara*; Serranidae) [Estudio ultraestructural en linfocitos de la cabrilla alguera (*Epinephelus moara*; Serranidae)], p. 385-398. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Spontaneous and experimentally infected lymphocystis disease of kelp bass (*Epinephelus moara*, Temminck et Schlegel) cultured in marine net cages in Huanan Farm, Guandong, China, was studied under an electron microscope. Examination of the lymphocystis cells revealed no difference between spontaneous and experimentally infected lymphocystis of kelp bass. In the derma of the lymphocystis fish subcutaneously injected with nodule homogenate, the fibroblast cells changed morphologically, attesting to their transformation into lymphocystis cells. An immunological response occurred which involved macrophage lymphocyte associations before the rupture stage of the nodules. Pathological lesions of the heart, liver, spleen, kidney and intestine suggested that lymphocystis virus infection can damage several types of susceptible cells. The significance of the cellular responses is discussed.

Resumen

Se estudiaron bajo microscopio electrónico infecciones espontáneas y experimentales causadas por linfocistis en la cabrilla alguera (*Epinephelus moara*, Temminck et Schlegel) cultivados en cajas de red, en la granja Huanan, Guandong, China. El examen de las células que presentan linfocistis muestran que no hay diferencias entre infecciones espontáneas e inducidas experimentalmente. En la piel del pez inyectado a nivel subcutáneo con un nódulo homogenizado, los fibroblastos mostraron cambios morfológicos hacia su transformación a células con linfocistis. Una respuesta inmunológica se presentó asociada a linfocitos macrófagos antes de la ruptura de los nódulos. Lesiones patológicas en corazón, hígado, bazo, riñón e intestino sugieren que la infección viral causante de linfocistis puede dañar varios tipos de células susceptibles. Se discute la significancia de la respuesta celular.

Introduction

Fish lymphocystis disease (FLD) with proven viral etiology occurs in groupers (*Epinephelus moara*, *E. malabaricus*, *E. chlorostigma*), and snappers (*Lutjanus russelli*, *L. argentimaculatus*) cultured in marine net cages in China (Yongjia 1992) and Southeast Asia (Chong and Chao 1986). The fish lymphocystis disease virus (FLDV) belongs to the Iridovidae family and has been classified by D.B. Williams as a separate genus of this family with the name of *Cystivirus* (Flugel 1985). The infection is a common, chronic, worldwide disease, and causes high mortality rate of fingerlings. The research works of many authors usually concentrate on the morphology and classification of the virus, and many have reported cases of wild and cultured fish infected with FLD. Experimental transmission has been successful using implantation, injection and application to traumatized skin. Also it was found that the disease could be transmitted by feeding, injection, application of traumatized skin and cohabitation among groupers (*E. moara*, *E. malabaricus*, *E. chlorostigma*) and also from kelp bass to snappers (*L. russelli* and *L. argentimaculatus*) but not to seabass (*Lates calcalifer*) (Yongjia and Zeyang 1993). The present study describes our ultrastructural observations on the cellular response of kelp bass to FLDV.

Materials and Methods

Source of fish and experimental transmission

The fish used for the present work were kelp bass cultured in floating net cages at Huanan Farm, Guangdong, China. The infection was caused by subcutaneous injection of a 20% homogenate of black nodules in

a balanced salt solution buffered to maintain pH 7.2. Ten injected fishes, with a mean length of 13 cm and a mean weight of 32 g, were cultured in a net cage to observe the process of the disease. The experiment was conducted from 20 October 1989 to 20 July 1990. Spontaneously infected fish were obtained from Techeng Farms, Zhanjiang, China.

Preparation for EM

Fish were killed by decapitation on day 1, 3, 7, 14, 21, and month 1, 2 and 5 after injection. Blocks of tissue, namely skin with nodules (if present), heart, liver, spleen, kidney and intestine were dissected, and fixed with 2.5% glutaraldehyde-2% paraformaldehyde mixture in cacodylate buffer before being fixed with 1% osmium tetroxide (OsO_4) for 1 hour at 4°C. After fixation, the specimens were rinsed with cacodylate buffer again and treated with uranyl acetate and dehydrated through progressive grades of ethyl alcohols ending with dry, absolute alcohol. The specimens were then infiltrated with Epoxy 618, and transferred to a gelatin capsule containing fresh resin. The resin with the specimens was then allowed to polymerize for 48 hours at 60°C. The sections were cut by LKB-V ultratome and finally stained on grids with lead acetate and examined under a JEM 100-CXII electron microscope (working voltage 80 kv).

Results

Skin with nodules (if present)

After one month, the thin sections of the fish injected with the homogenate showed the epithelial cells of the skin with a normal structure containing usually a few tonofibrils and microtubules, mitochondria and free ribosomes, and were surrounded

by a small intercellular space. The nuclei were dense with heterochromatin, especially in the peripheral areas. Indentations of the nuclei were occasionally seen (Fig. 1a).

Beneath the epidermis, the subcutaneous tissue is made up of loose connective tissue, containing collagenous fibers and many fibroblasts which are susceptible to FLDV. Within a few days of the initial infection, the fibroblasts had a varied morphology, depending on the cellular response to FLDV. This response was a progressive process, and three types of fibroblasts--besides normal fibroblasts--were observed. Virus particles were occasionally seen attached to the first type of fibroblast. The membrane of the fibroblast to which the virus particle had attached appeared on 1 to 3 electron-dense plates or plaques. One of these was incorporated by a virus particle (Fig. 1b). These cells were similar to other normal fibroblasts in ultrastructure and with the exception of the plates, they were characterized by possessing an ovoid nucleus with fine chromatin and evident nucleolus, abundant granular endoplasmic reticulum, mitochondria and Golgi apparatus. The second type of fibroblast was not changed in size, but in structure. The fibroblasts were characterized by a larger spongy nucleus with dense chromatin, and indentations of the nucleus were usually seen. A target-like lamellar body or paranucleus was occasionally observed in their cytoplasm. Otherwise there were few cellular inclusions, such as vacuoles, mitochondria and granular endoplasmic reticulum. The third type of fibroblast exhibited a swollen and round shape, with a spongy rounded nucleus containing dense chromatin, especially in peripheral areas; also, indentations of the nucleus were found. The cytoplasm of the fibroblast was usually separated by a channeled vesicle into perinuclear and outer areas. In the former, cellular inclusions consisted of no more than a few vesicles; but in the latter microfilaments, numerous vesicles or transversely cut

tubules, measuring approximately 20 nanometers (nm) in diameter, and a few mitochondria were seen. The cytomembrane was not clear. Virus particle inclusion bodies were not seen in the cytoplasm except in the above three types of fibroblasts (Fig. 1c).

After two weeks, the infected fish exhibited the characteristic sign of lymphocystis on fin and skin areas. The nodule consisted of masses of tremendously hypertrophied cells, so-called lymphocystis cells (approximately 20-600 mm in diameter), which were apparently terminal cells. Some fibroblasts were also present. These lymphocystis cells were enclosed in a collagenous sheath of the surrounding dermal connective tissue. No distinct plasma membrane between the sheath and the cytoplasm of lymphocystis cell was visible under the light microscope, but a 8-15 mm thick hyaline and homogeneous wall could be seen, consisting of two layers: a hyaline wall with a fine granular consistency and an outer area consisting of collagenous fibers and few fibrocytes (Fig. 2a). The nucleus was large with nucleoli containing mainly nucleolar filaments and granules. The chromatin appeared in the form of granules, or flakes, irregularly dispersed within the nucleoplasm. The nuclear envelope had a double-layered texture, with distinct nuclear pores (Fig. 2b). Within the cytoplasm of the lymphocystis cell, many inclusion bodies, distributed in the form of a network, were usually observed. The network showed an aggregation of electron-dense granules. The cytoplasm outside the network was densely packed with virus particles; inside the meshes of the network, virus particles were occasionally seen (Fig. 2c). The virus particles were mainly hexagonal in profile and occasionally, pentagonal or decagonal in shape. The diameters, measured from 20 rectangular hexagonal size virus particles, were 190 nm between opposite sides and 235 nm between opposite vertices. The capsid of the virus measured about 15 nm in thickness and was a double-layered

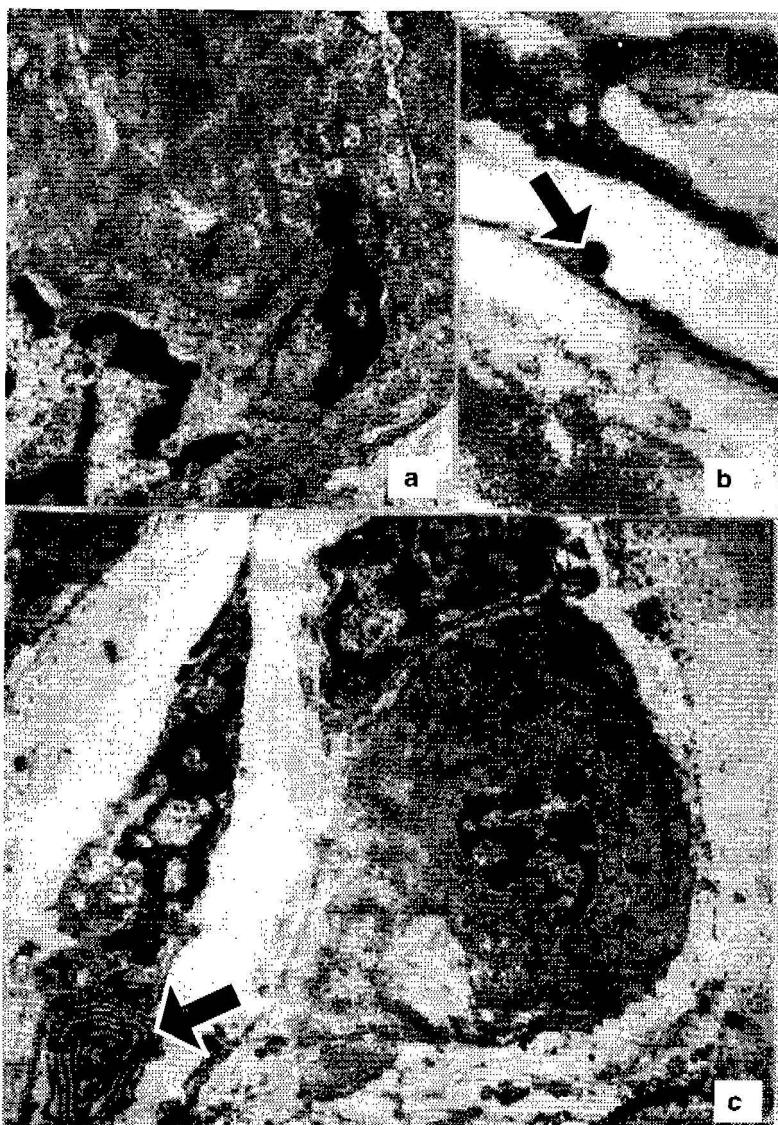


Fig. 1. (a) Enlarged epithelial cells of the kelp bass skin, covering the nodules. x6 000. (b) Fibroblast in dermal connective tissue. Arrow shows a virus particle in the membrane which appears as a thickened plate. x20 000. (c) After one week of infection, three transforming fibroblasts in dermal connective tissue show various stages of metamorphoses. Arrow shows a target-like lamellar body. x10 600. [(a) Células del epitelio germinativo de la piel de la cabrilla algüera cubriendo los nódulos. x 6 000; (b) Fibroblastos en tejido conectivo dérmico. Las flechas muestran una partícula de virus en la membrana, el cual aparece como una placa espesa. x 20 000; (c) Despues de una semana de Infección, tres fibroblastos transformados, en el tejido conectivo dérmico, muestran varios estados de metamorfosis. Las flechas muestran un cuerpo lamelar. x 10 600.]

structure. Outside the capsid there was a fuzzy halo of electron-dense filaments, 50-75 nm in thickness. Within the peripheral area of the cytoplasm, virus particles were only few; there were usually no more than a few vacuoles, mitochondria and endoplasmic reticulum. In mature lymphocystis cells (usually within 1 or 2 months after infection), mitochondria showed degrees of collapse and degradation and some of them had already lost their characteristic cristae. After two or three months of infection, their cytoplasm contained numerous spherical or oval electron-dense myelinated particulate features, measuring 50-70 nm in diameter, and frequently forming an aggregation enclosed in a membranous vesicle (Fig. 2d). In the superficial layer of the cytoplasm, representing the hyaline wall under LM, no mitochondria or defined endoplasmic reticulum was usually observed, but numerous small vesicles were common (Fig. 2a). In the dermal tissue, there were a few macrophages and lymphocytes adjacent to the lymphocystis cells. Macrophages contained abundant mitochondria and lysosomes. Lymphocyte and macrophage were occasionally observed establishing cytoplasmic contact; this took the form of a complete fusion of the membranes of the two cells, which acquired a finely granular consistency (Fig. 3a).

Heart

In most specimens, the heart was grossly edematous and necrotic. Examination of the histopathological specimens revealed the appearance of myocarditis. Muscle fibers showed loss of striation and granulation. The I, A bands and M line of the fibers were difficult to distinguish, and mitochondria

had also lost their cristae or were in various stages of degeneration (Fig. 3b).

Liver

Within three days of infection, hepatocytes showed predominating smooth endoplasmic reticulum with content of medium electron-dense granules and virus-like figures. Giant mitochondria with loss of cristae were generally observed to be surrounded by multilamellate endoplasmic reticulum (Fig. 3c). The nuclear envelope with pores revealed extended into internuclear spaces. There was abundant heterochromatin within the nucleoplasm. Interchromatin granules were usually observed (Fig. 3d). Plasma cell infiltration was pronounced. The plasma cells were characterized by a typically eccentric nucleus and a well-developed reticular system with vesicular cisternae fringed with ribosomes. The cisternae displayed a dilated appearance. The nucleus assumed compact, coarse, flaky chromatin, which showed an expanded perinuclear space connected to the endoplasmic reticulum outside the nucleus (Fig. 4a).

In the stage of late infection, the cytoplasm of the hepatocytes usually showed appearance of necrosis and was reduced to an electron-lucent matrix with degenerated mitochondria and membranous residues (Fig. 4b). A few Kupffer cells exhibited abundant vacuoles and peroxisomes, but few lysosomes (Fig. 5a). Some of these contained protrusions and showed signs of activity. Small lymphocytes were usually seen; they are always smaller (4 - 5 μm in diameter) than neighboring cells and though of varying shape, were characterized by a large nucleus and only a small cytoplasmic rim, with many protrusions of macrophages. A fusion of

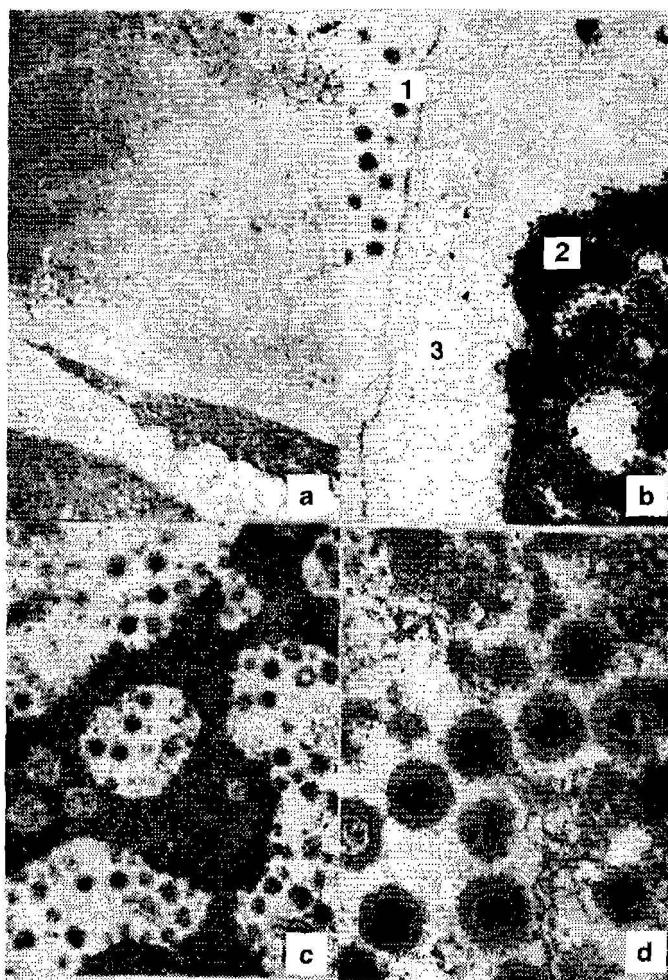


Fig. 2. (a) Hyaline wall of the lymphocystis cell shows a finely granular consistency of medium electron-density inner area and a collagenous outer area with fibrocyte. x4 000; (b) Within two weeks, a part of nucleus of lymphocystis cell. 1: virus particles in the cytoplasm; 2: nucleoli; 3: euchromatin. x 7 000; (c) An inclusion body in the cytoplasm of lymphocystis cell. x8 000; (d) Lymphocystis virus particles in the cytoplasm of lymphocystis cell. x20 000. [*(a) Pared hialina de las células con linfoctis mostrando una consistencia granular de densidad electrónica media dentro del área, y un área externa colágena con fibrocito. x 4 000; (b) Dentro de las dos semanas, una parte del núcleo de la célula con linfoctis: 1: partícula de virus en citoplasma; 2: nucleolo, y 3: eucromatina. x 7 000; (c) Uncuerpo Incluido en el citoplasma de una célula con linfoctis. x 8 000; (d) Partículas de virus de linfoctis en el citoplasma de una célula Infectada. x 20 000.*]

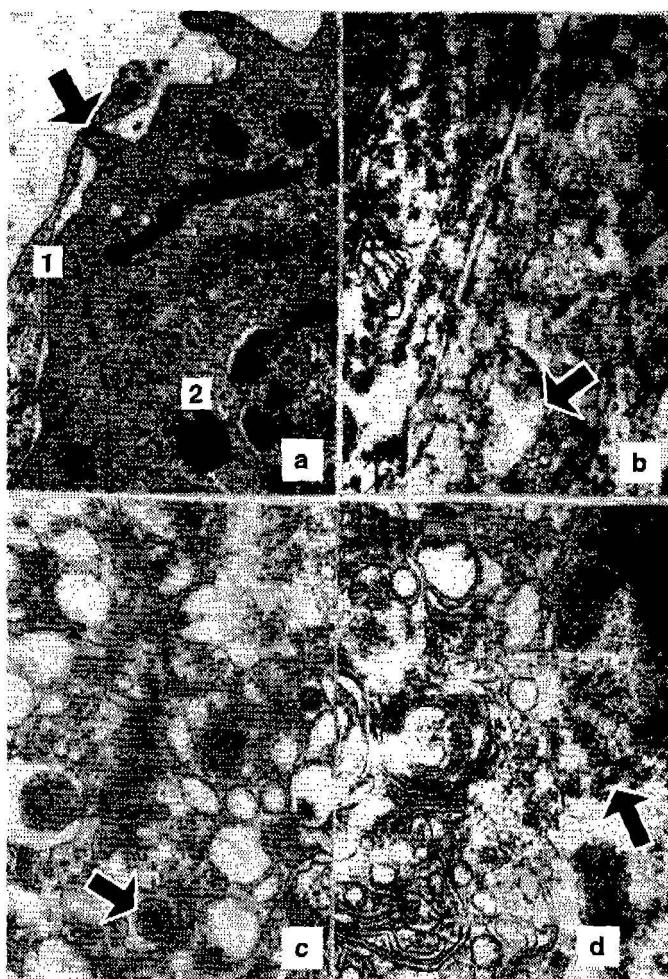


Fig. 3. (a) Lymphocyte-macrophyte association in dermal connective tissue. Observe a cytoplasmic contact between macrophage and lymphocyte on their protrusions. 1: lymphocyte protrusion; 2: macrophage. x 20 000; (b) Myocardial fibers show loss of striation and granulation. Arrow indicates that mitochondria had lost its cristae. x 10 000; (c) Part of cytoplasm of lymphocystis cell within three days of infection. Arrow shows virus-like figure. x 16 000; (d) Part of nucleus of lymphocystis cell within three days of infection. Observe that nucleus contains interchromatin and that multendoplasmic appear in the cytoplasm. x 16 000. [(a) Asociación linfocito-macrófago en tejido conectivo dérmico. Se observa un contacto citoplásмico entre macrófago y linfocito sobre sus protuberancias. 1: protrusión del linfocito, 2: macrófago. x 20 000; (b) Fibras miocárdicas mostrando pérdida de estriación y granulación. Las flechas indican que la mitocondria tuvo pérdida de sus crestas. x 10 000; (c) Parte del citoplasma de una célula con linfocistis de tres días de infección. Las flechas muestran una figura parecida al virus. x 16 000; (d) Parte del núcleo de una célula con linfocistis de tres días de infección. Observe que el núcleo contiene Intercromatina y que el multendoplasma aparece en el citoplasma. x 16 000.]

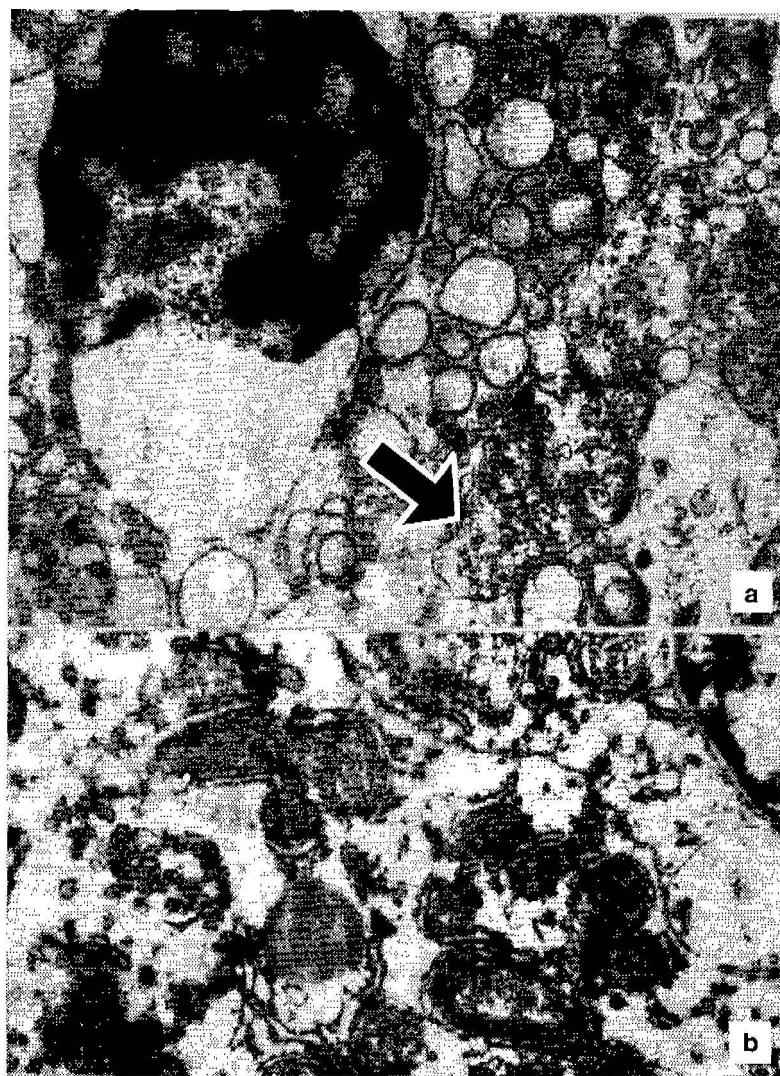


Fig. 4. (a) Plasma cell in the liver assumes a well-developed reticular system with vesicular cisternae fringed ribosomes. Arrow indicates a giant mitochondria in the cytoplasm of hepatocyte. x 10 000; (b) In the stage of late infection, the cytoplasm of hepatocyte shows an electron-lucent matrix with degenerated mitochondria and membranous residues. x 10 000. [(a) Plasma de una célula de hígado que supone un sistema reticular bien desarrollado con vesículas en el borde de la cavidad del ribosoma. Las flechas indican una mitocondria gigante en el citoplasma del hepatocito. x 10000; (b) En el estadio de infección tardía, el citoplasma del hepatocito muestra una matriz electro-luminada con residuos de mitocondria y membrana degeneradas.]



Fig. 5. (a) Kupffer cell with abundant vacuoles and peroxisomes in the liver. x 10 000. **(b)** Lymphocyte-macrophage association in the liver within two months of infection. Observe that the lymphocyte protrusion comes into contact with the protrusion of macrophage. At that point a complete cytoplasmic fusion occurs. x 16 000. [(a) Cuerpo de Kupffer con abundantes vacuolas y peroxisomas en el hígado; (b) Asociación linfocito-macrófago en hígado con dos meses de infección. Observe que la protuberancia del linfocito viene hacia un contacto con la protuberancia del macrófago. En este punto, ocurre una completa fusión citoplásica. x 16 000.]

cytoplasm was observed where material was being exchanged (Fig. 5b).

Spleen

In thin sections of the spleen, the following types of cells were distinguished: lymphocytes, blast type cells, reticulum cells, macrophages, granulocytes, and mature and immature erythrocytes. Macrophages were common both within ellipsoids and within the pulp. Some cells contained various kinds of inclusions, which usually could be identified as the debris of disintegrated erythrocytes at various stages of digestion. Some cells contained numerous indistinct mitochondria, minute vesicles and lysosomes. Where the lymphocyte came into contact with macrophages, it was observed to establish cytoplasmic contacts which took the form of an incomplete fusion at the point of contact of the protrusions of the membranes, obvious cell membrane boundaries still being present, however. Lymphocytes were one of the significant cell types associated with immunological processes in the spleen. They were readily seen there, with a characteristic electron-dense nucleus surrounded by a thin rim of cytoplasm containing few ribosomes and mitochondria. Other cell types related to immunological processes were macrophages, both sessile and free. The sessile macrophages within the spleen connected with adjoining cells by their cytoplasmic extensions, and free macrophages were usually observed to establish a cytoplasmic contact with lymphocytes (Fig. 6a). Few granulocytes were identified in the spleen.

Kidney

The kidney was, to various degrees, hyperplastic and necrotic; moreover, the severity of the condition increased progressively from posterior to anterior. The

posterior kidneys were prominently altered, and showed necrosis of tubular tissue. The tubular lumens had collapsed. The microvilli on the apical cytoplasm of the epithelial cells were in disorder or had separated. The cytoplasm contained numerous vacuoles and membrane-bound electron-lucent lysosomes, free ribosomes, mitochondria with indistinct cristae and endoplasmic reticulum. Some of the mitochondria were very large and contained vacuole-like inclusions (Fig. 6b). Glomeruli were slightly edematous. The main cellular component of the haematopoietic tissue in the kidney was lymphocyte-like cells. These cells constituted many zones of very active lymphocyte production. Various stages of development of lymphocytes were noted, characterized by a large nucleus and a small cytoplasmic volume. Nuclear chromatin was dense, and indentations of the nucleus were generally seen. The cytoplasm contained numerous ribosomes and small vesicles and a few mitochondria. No cytoplasmic protrusion was found (Fig. 6c).

Intestine

The intestine showed sloughing of mucus into the lumen. Ultrastructurally, the mucus epithelial cells presented irregular profiles and short microvilli. Numerous membrane-bound vesicles with many myelinated figures and vacuoles filled the apical cytoplasm. The cells appeared as an electron-lucent matrix on the background (Fig. 6d).

Discussion

Lymphocystis disease has been noted to associate with lymphocystis virus infection of the host connective tissue cells, and its agent has been propagated under laboratory conditions (Wolf 1962; Chao 1984). The literature concerning the pathological changes in the vital organs of fish with

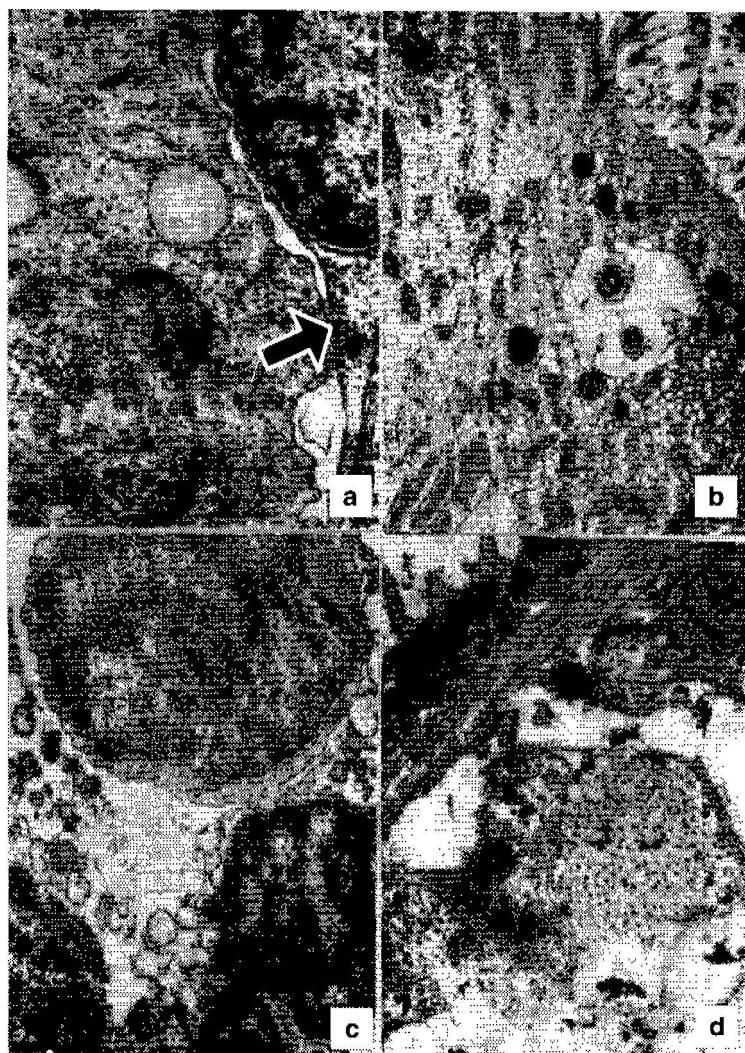


Fig. 6. (a) A lymphocystis-macrophage association in the spleen within two months of infection. Arrow shows a contact without cytoplasmic fusion between the membranes of the two cells. $\times 10\,000$. **(b)** Within two months of infection, epithelial cell of the tubule in kidney exhibits numerous vacuoles and membrane-bound electron-lucent lysosomes. $\times 4\,000$. **(c)** Various stages of developing lymphocytes in the kidney. $\times 10\,000$. **(d)** The mucus epithelial cell of the intestine shows numerous membrane-bound vesicles with many myelinated figures on an electron-lucent background. $\times 8\,000$. [**(a)\times 10\,000; **(b)** Célula epitelial del túbulo del riñón con dos meses de Infección mostrando numerosas vacuolas y membrana de lisosoma electro-luminadas. $\times 4\,000$; **(c)** Varlos estadios de desarrollo del linfocito en riñón. $\times 10\,000$; **(d)** Células de la mucosa epitelial del Intestino mostrando numerosas membranas de vesículas con muchas figuras mielinicas sobre un fondo electro-lumincente. $\times 8\,000$.]**

lymphocystis is sparse. Certain authors do not mention the cellular response to the FLDV. The present study has shown the transformation process of the lymphocystis cells. Ultrastructurally, the observations revealed a virus particle that attached to the membrane of fibroblast. The virus particle, which had decapsulated, merged into the membrane whose thickened plates may constitute the receptors for the FLDV. The genome of the FLDV would have existed in the host cell for a period of time, before the host cell exhibited a series of metamorphosis. The three types of fibroblasts in the present study are considered to be the transitional stages from a fibroblast to a lymphocystis cell. The following changes take place during this process: heterochromatin concentration, nucleolus metamorphosis, nucleus enlargement, target-like texture appearance, cytoplasmic layer-separation, tonofibrils' abnormal distribution, plasma membrane disappearance, and cellular enlargement. These changes are considered to be neoplastic features in cells (King et al. 1983). The virus infection alone would not destroy the susceptible cells, at least not during early infection. With the insertion of the FLDV DNA fragments into the genomes of the host cell, the DNA/RNA metabolism of the host cell lost its regulation, which resulted in a series of metamorphosis occurring in the host cell. After a period of time of at least one week, virus particles appeared in the cytoplasm of the susceptible cell and cellular organelles were progressively damaged. The membrane of the host cell was separated into inner and outer layers in the transformation process, the former probably a metamorphosis of the plasma membrane and the latter formed by surrounding connective tissue. It is difficult to escape the conclusion that the texture of these two layers prevented other virus particles from gaining access to the host cell again, and hence the new virus particles in the cell are duplicated by a single virus source.

After the mature lymphocystis cells collapse, the virus particles are released into the surrounding tissue or water environment. In the surrounding tissue, they can affect other fibroblasts and in water, they can initiate horizontal transmission among the cohabiting groupers. A similar opinion has been expressed concerning snake-skin gourami (Paperna et al. 1987) and seabass (Chao 1984).

It has been reported that affected fish develop small, pearl-like tumefactions either singly or in groups, on the skin of body, fins and tail and, less commonly, gill filament, pharynx, intestinal wall, mesenteries, liver, spleen and ovary (Roberts 1978). Paperna et al. (1987) have mentioned that pathological changes took place in the spleen and kidney. We have previously reported severe damage on the liver, kidney and heart with light microscopic observation (Yongjia 1992). The above-mentioned suggested that the lymphocystis virus may affect the cells in these organs although no virus particle has been found in these organs so far. The ultrastructural observations on the liver, spleen, heart, intestine of the infected kelp bass described in the present study agree with our previous descriptions. Although virus-like granules have been found in hepatocytes, virus particles, however, have not been confirmed in these organs, either in natural or in experimentally lymphocystis-infected fish. Cellular lesions on these organs suggested that potential susceptible cells may be affected by FLDV. A further possible hypothesis is that the mechanism of the damage may well be a neoplastic process. After having entered into potential susceptible cells, the virus is not duplicated (nonproductive infection), and causes only cell damage. The evidence presented strongly suggests that this virus may disturb the normal DNA/RNA metabolism in the infected cells, followed by a series of pathological changes; for example, giant mitochondria in hepatocytes and in epithelial cells of the kidney,

endoplasmic reticulum hyperplasia and an abnormal texture, abnormal nuclear chromatin concentration, and appearance of interchromatin granules and enlarged perinuclear spaces. Cellular synthetic and oxidative processes are bound to be reflected in the morphology of the endoplasmic reticulum and mitochondria associated with pathological changes of the nuclei. Other examples are the epithelial lesions in the intestine; in this case where the virus must pass through the intestine wall in order to infect dermal connective tissue cells (Yongjia et al. in press). The lesions resemble those described in the present study, i.e., within the apical cytoplasm, there were no more than a few inclusions containing myelinated figures of multivesicular bodies, with an empty background. This phenomenon can be explained by the fact that virus disturbed the stability of the lysosomal membrane, which resulted in intercellular lysis. The FLDV genome must exist or be transmitted either in the form of merging with the chromosomes or in a non-merging form in the host cells, because no virion could be observed within the cytoplasm of the host cells (King et al. 1983).

In the present study, there were abundant lymphocytes within the liver, spleen and dermal connective tissue in natural and experimental late infections of kelp bass, which caused immunological activity. Their cytoplasmic protrusions came into contact with those of the macrophages. Plasma cells also occurred in the tissue of the liver and spleen; they are one of the principal cell types in the immunological processes. The frequency of above-mentioned cells varies with the immunological activities of the fish. The significance of the macrophage-lymphocyte association in the liver and in the spleen is that some kind of immunological interchange may be taking place, since a complete fusion of the cytoplasm of the cells was noted. Rosenthal et al. (1975) suggested from *in vitro* studies that such

an association could serve to facilitate the presentation of antigen by macrophages to immune T lymphocytes. Although B and T lymphocytes were not morphologically identified in kelp bass, it is possible to speculate that the function of these associations is the macrophage presenting processed antigen to lymphocyte. The present study has shown that plasma cells in the liver and in the spleen during late infection carry out an active synthetic process. Therefore, we may conclude that it is possible to find a suitable vaccine for prevention of FLD. Experimental protection against FLD of groupers for at least six months has been conferred by injecting inactivated nodule homogenate (Yongjia et al. in press). This experiment provides proof of the cellular response and does not agree with the work of Wolf (1962), in which he established second infection of bluegill. Further work on antibody detection and immunological response is needed.

Acknowledgements

I thank Dr. Supranee Chinabut of the Aquatic Animal Health Research Institute of Thailand for comments on the draft of this contribution.

References

- Chao, T.M. 1984. Studies on the transmissibility of lymphocystis disease occurring in seabass (*Lates calcarifer*, Bloch). Singapore J. Prim. Ind. 12(1):11-16.
- Chong, Y.C. and T.M. Chao. 1984. Common diseases of marine foodfish. Prim. Prod. Dept., Rep. of Singapore, Fisheries Handbook No.2, 34 p.
- Flugel, R.M. 1985. Lymphocystis disease virus. Curr. Topics Microbiol. Immunol. 116:133-150.
- King, D.W., C.M. Fenoglio and J.H. Lefkowitch. 1983. General pathology: principles and dynamics. Lee & Febiger, Philadelphia.

- Paperna, I., T.M. Ventura and A.P. de Matos. 1987. Lymphocystis infection in snake-skin gourami, *Trichogaster pectoralis* (Regan), (Anabantidae). *J. Fish Dis.* 10:11-19.
- Roberts, R.J. 1978. *Fish pathology*. Bailliere Tindall, London.
- Rosenthal, A.S., P.E. Lipsky and E.M. Shevach. 1975. Macrophage-lymphocyte interaction morphologic and functional correlates, p. 813-825. In R. Van Furth (ed.) *Mononuclear phagocytes in immunity, infection and pathology*. 2nd edn. Blackwell Scientific Publications.
- Wolf, K. 1962. Experimental propagation of lymphocystis disease of fishes. *Virology* 16:249-256.
- Yongjia, Z. 1992. Light and electron microscopic studies on cagecultured kelp bass (*Epinephelus moara* Temmick et Schlegel). *Acta Oceanol. Sin.* 14(6):97-102.
- Yongjia, Z. and W. Zeyang. 1993. Preliminary studies on lymphocystis disease of marine fish. *Fish Dis. Res.* 14:8-9.

ENTERED IN NAGA

APR 14 1998

Development from Egg to Juvenile of the Red Grouper (*Epinephelus morio*) (Pisces: Serranidae) in the Laboratory

P.L. COLIN

*Coral Reef Research Foundation
P.O. Box 1765 Koror, Palau 96940*

C.C. KOENIG

*Department of Biological Sciences
Florida State University, Tallahassee, Florida 32306-2043, USA*

W.A. LAROCHE

*Stonefish Environmental Consulting
P.O. Box 216, Enosburg Falls, Vermont 05450, USA*

COLIN, P.L., C.C. KOENIG and W.A. LAROCHE. 1996. Development from egg to juvenile of the red grouper (*Epinephelus morio*) (Pisces: Serranidae) in the laboratory [Desarrollo de huevo a juvenil del mero americano (*Epinephelus morio*) (Pisces: Serranidae) en laboratorio], p. 399-414. In F. Arreguin-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly (eds.) Biology, fisheries and culture of tropical groupers and snappers. ICLARM Conf. Proc. 48, 449 p.

Abstract

Red groupers were reared from artificially spawned eggs, which hatched in 30 hours at 24°C. Eggs required salinities of at least 32 ppt to float. Yolk absorption was completed by about 30 hours, eye pigmentation and first feeding observed at 72 hours post-hatch. Dorsal and pelvic spine development was first noted at nine days post-hatch with rapid length increase over the next seven days. Flexion occurred starting at 16 days post-hatch at a stage with well developed dorsal and pelvic spines. Behavior of larvae was closely examined and at all stages larvae were active predators on small zooplankton. Metamorphosis occurred at a minimum of 35 days post-hatch at 20 mm SL. Juveniles grew at a rate between 0.26 and 0.61 mm·day⁻¹ reaching a mean of about 55 mm SL at 130 days post-hatch and were aggressive and territorial. Reared juveniles tagged and released on an artificial reef off the Florida Panhandle survived and continue to be monitored.

Resumen

El mero americano fué criado de huevos desovados artificialmente. Los huevos requirieron salinidades de al menos 32 ppt para flotar y fueron incubados durante 30 horas a 24°C. La absorción del saco vitelino se completó a las 30 horas, la pigmentación y primera alimentación se observó a las 72 horas después de la incubación. El desarrollo de las espinas dorsal y pérvica fué observado primero a los 9 días después de la incubación con un rápido incremento en longitud durante los 7 días siguientes. La flexión ocurrió al inicio, 16 días después de la incubación con las espinas dorsal y pérvica bien desarrollada. El comportamiento de las larvas fué examinado estrechamente y durante todos los estados larvarios fueron predadores activos sobre pequeño zooplancton. La metamorfosis ocurrió a un mínimo de 35 días después de la incubación a 20 mm de longitud estandar (SL). Los juveniles crecieron a una tasa entre

0.26-0.61 mm por día, alcanzando un promedio de 55 mm SL a 130 días después de la incubación; y fueron agresivos y territoriales. Los juveniles criados fueron marcados y liberados en un arrecife artificial en aguas fuera de Florida donde los supervivientes continúan siendo monitoreados.

Introduction

The red grouper (*Epinephelus morio*) is the most common grouper captured in both commercial and recreational fisheries in US and Mexican waters of the Gulf of Mexico (Goodyear and Schirripa 1991). In the Exclusive Economic Zone of the US Gulf of Mexico, it accounts for two-thirds of the total commercial grouper catch, some 3 400 t in 1989 (Goodyear and Schirripa 1991). Despite its commercial and recreational importance, relatively little has been published on its biology since the study of Moe (1969) (see Brûlé and Déniel, this vol.).

Although the larvae of epinepheline serranids have been recognized for more than a century (Kendall 1984), largely due to their elongate dorsal and pelvic fin spines, few identifiable to a particular species have been described in detail. Virtually nothing is known of the specific larval development of *E. morio* (Moe 1969) and the wild-caught larvae could not be separated from *E. guttatus* and *E. drummondhayi* based on ray counts (Johnson and Keener 1984).

As part of a study to delineate life histories of Gulf of Mexico groupers, we were able to rear red groupers in the laboratory from artificially fertilized eggs through the juvenile stage. These laboratory-reared juveniles were released in the field successfully and have survived.

Materials and Methods

Live adult *E. morio* females were obtained by fishing from commercial hook-and-line fishing boats during the spawning season in the northern Gulf of Mexico.

Fish captured at depths between 20 and 40 m had their swim bladders deflated immediately upon surfacing and were placed in flowing seawater tanks. Survival rates were high unless the fish had been gill-hooked or otherwise injured. Individual fish were returned to the Florida State University Marine Laboratory and maintained in 2 000-l tanks in a closed-circuit seawater system.

Freshly caught ripe *E. morio* males were obtained from commercial fishers at the dock. Testes were removed from the body cavity within a few hours of capture and stored in plastic bags on ice (not frozen). Sperm remained capable of fertilizing eggs for a number of days afterwards.

In the aquarium facility at Florida State University Marine Laboratory (FSU), live fish were catheterized to determine sex and stage of gonad development. Females were injected with 1 000 units human chorionic gonadotropin (HCG) per kg body weight, followed, if necessary, by a second injection of 500 units HCG 18-24 hours later.

Adult fish were maintained in recirculating seawater of approximately 25 ppt (the salinities of inshore areas of North Florida during spring) until eggs were fully hydrated. Once hydrated, eggs were stripped from females, into plastic containers, with gentle pressure on the body cavity. A sperm and water mixture was added immediately. Sperm were obtained either by stripping live male fish or macerating a piece of fresh or chilled testes. An additional few milliliters of sea water (36 ppt) were added to the sperm and egg mixture, which caused the eggs to become buoyant.

Initiation of development was confirmed microscopically by the onset of first cleavage and occurred within an hour of addition of sperm. Eggs were then transferred

to 20-l aerated buckets of 36 ppt seawater at 22°C, and then moved to the rearing aquariums (36 ppt seawater) within 3-4 hours.

The absolute density of eggs and newly hatched larvae was determined by pipetting eggs and larvae into small beakers with seawater of different salinities (between 27 and 35 ppt); eggs and larvae were either negatively buoyant, positively buoyant or neutrally buoyant.

Larvae were reared largely using the methods of Houde and Taniguchi (1977). Floating fertile eggs were transferred to 80-l aerated rearing aquariums with twin 20-W fluorescent lights. Larvae were fed zooplankton collected offshore of the FSU Marine Laboratory starting approximately 72 hours after hatching (depending on water temperature). Zooplankton was maintained on various species of cultured microalgae, which also served to absorb toxins generated in the rearing tanks. Initially, plankton 53-88 μ in size were offered, followed a few days later by plankton in the 53-125 μ size fraction.

Larvae were preserved every few days in order to obtain a representative size series for describing developmental stages. Preservation was initially in 5% formalin and later in 70% ethanol. The specimens selected for preservation at any one time were generally among the larger, more advanced individuals in the rearing tanks. Specimens were measured either with dial calipers or by ocular micrometer in a dissecting microscope. Preflexion larvae were measured from the tip of the snout to the end of the notochord (NL) whereas post-flexion larvae and juveniles were measured to standard length (SL). All development times given in this paper (e.g., 24 hours, 5 days) are times post-hatching.

Several hours of excellent video recordings of live larvae were obtained using a dissecting scope with attached color video camera. Larvae were chilled to make them quiescent. Additional recordings were made of larvae remaining in rearing tanks by

using additional closeup diopters and extreme telephoto settings on the video camera lens. Drawings of larvae were made by one of us (WAL) using a camera lucida attachment on a stereo microscope. Color illustrations were prepared from fresh specimens.

The series of larval specimens are deposited in the US National Museum as lot number USNM 326839.

Results

Eggs were almost spherical, approximately 0.95 mm in diameter. They contained a single oil globule and were unpigmented. The germinal disk of the eggs was visible 25 minutes after addition of sperm; first cleavage occurred 54-59 minutes post-fertilization. Hatching occurred 30-38 hours post-fertilization, although the exact time of hatching was not observed.

Fertilized eggs and newly hatched red grouper larvae were positively buoyant in full-strength seawater (36 ppt); fertilized eggs were negatively buoyant in 25 ppt seawater. Eggs at 4 hours post-fertilization were neutrally buoyant in seawater between 28 and 30 ppt. Eggs at over 20 hours post-fertilization were slightly more dense; they were neutrally buoyant in 32 ppt. Newly hatched larvae were more positively buoyant at 27 ppt, with some floating and some sinking. Eggs in 25 ppt seawater underwent limited embryonic development while on the bottom of the container. Very few of these eggs hatched. None of the larvae that hatched at this salinity was reared.

Larval and pelagic juvenile development

Meristics and morphometrics. Meristic and morphometric data on larvae and juveniles were based on a series of 44 specimens (Tables 1 and 2). The larval and early

juvenile stages are illustrated in Figs. 1 to 10. Members of the genus *Epinephelus* have a single dorsal fin; thus, all subsequent references to the second dorsal fin spine refer to the second spine of the dorsal fin, not to a second of two dorsal fins.

Development of yolk sac larvae. Yolk sac larvae up to about 48 hours (Fig. 1) hatch at 1.6 to 1.7 mm NL. At this stage they hang head down in the water column. The yolk and oil globules were absorbed by 3 days (Fig. 2, lower). Eye

pigmentation is first evident at about 60 hours; eyes are darkly pigmented by about 72 hours. At this stage the larvae drift in the water column, not orienting to gravity or light and react to pressure waves by an undirected burst of swimming for a few seconds.

Shortly after 3 days, the larvae begin maintaining orientation in the water column. The mouth has been formed and the gut is functional. First feeding is initiated a few hours post-mouth formation and is evidenced by feeding strikes at plankters.

Table 1. Meristics of larval and juvenile *Epinephelus morio*, based on unstained specimens. Counts of pelvic fin elements (1,5) and superior and inferior principal caudal fin rays (8,7) were constant throughout the series following development. [Relaciones merísticas de larvas y juveniles de *Epinephelus morio* basado en especímenes no teñidos. El conteo de los elementos de la aleta pérvica (1, 5) y los rayos de la aleta caudal principal superior e inferior (8,7) fueron constantes a lo largo de las series siguiendo el desarrollo.]

Age	Stage	Standard length	Dorsal fin spines and rays	Anal fin spines and rays	Pectoral fin rays
3	Preflexion	2.5	-	-	-
4	Preflexion	2.5	-	-	-
4	Preflexion	2.6	-	-	-
4	Preflexion	2.6	-	-	-
6	Preflexion	2.6	-	-	-
8	Preflexion	2.8	-	-	-
8	Preflexion	2.8	-	-	-
9	Preflexion	2.9	I	I	-
9	Preflexion	3.3	I	-	-
9	Preflexion	3.5	I	-	-
11	Preflexion	3.7	II	-	-
11	Preflexion	3.7	II	-	-
11	Preflexion	3.8	II	-	-
12	Flexion	4.1	III	-	-
15	Flexion	5.5	III	-	-
18	Flexion	5.7	III	-	-
16	Flexion	6.2	IV, forming	forming	-
20	Flexion	6.6	IV, forming	forming	forming
17	Flexion	7.0	V, 6	I, 8	forming
18	Flexion	7.4	IV, forming	forming	forming
20	Flexion	7.4	XI, 16	II+1, 9	forming
21	Postflexion	8.8	X+1, 16	II+1, 9	17
21	Postflexion	9.3	X+1, 16	II+1, 9	17
21	Postflexion	9.5	X+1, 15	II+1, 9	16
21	Postflexion	9.6	X+1, 15	II+1, 9	16
27	Transforming	12.2	X+1, 15	II+1, 9	16
27	Transforming	15.1	X+1, 14	II+1, 9	16
25	Transforming	20.2	XI, 15	III, 9	17
25	Transforming	26.2	XI, 16	III, 9	17

Table 2. Body proportion of larvae and juveniles of *Epinephelus morlo*. Values given are percent of standard length (SL) and head length (HL) including mean, standard deviation and range in parentheses. Number of specimens measured indicated in parentheses, listed by stage. [Proporción corporal de larvas y juveniles de *Epinephelus morlo*. Los valores dados son porcentajes de la longitud estandar (SL) y longitud de la cabeza (HL) incluyendo media, desviación estándar e intervalo entre paréntesis. El número de especímenes medidos es indicado entre paréntesis, listado por estado.]

	Body depth at cleithrum (SL)	Body depth at anus (SL)	Caudal peduncle depth (SL)
Yolk sac (15)	30.5±9.3 (18.4-45.3)	8.8±1.7 (6.6-12.7)	- -
Preflexion (13)	19.9±1.8 (17.5-24.2)	8.6±1.5 (6.7-11.6)	- -
Flexion (8)	28.2±3.1 (22.9-31.8)	17.2±3.8 (9.8-22.6)	8.8±0.5 (8.4-9.6)
Postflexion (4)	32.4±0.9 (31.2-33.6)	24.5±0.3 (24.1-24.9)	11.4±0.3 (11.1-11.9)
Transforming (2)	31.8±1.4 (30.4-33.2)	24.8±0.8 (24.0-25.7)	11.7±0.5 (11.3-12.2)
Juvenile (2)	34.6±1.5 (33.1-36.1)	27.5±0.8 (26.7-28.2)	11.5±0.0 (11.4-11.5)
	Head length/ SL	Eye diameter/ Head length	Upper jaw length/ Head length
Yolk sac (15)	19.9±3.2 (16.0-27.0)	50.8±10.5 (40.0-77.8)	- -
Preflexion (13)	24.8±3.3 (18.8-30.0)	42.3±5.1 (37.1-53.3)	38.7±7.0 (26.3-50.0)
Flexion (8)	34.6±2.5 (30.3-37.7)	31.9±2.1 (28.6-35.0)	41.0±4.0 (34.1-46.4)
Postflexion (4)	37.6±0.8 (29.7-32.1)	30.6±1.0 (29.7-32.1)	42.9±4.2 (38.1-49.5)
Transforming(2)	37.7±2.0 (35.7-39.6)	28.2±0.6 (27.6-28.8)	47.9±0.2 (47.7-48.1)
Juvenile (2)	41.3±1.0 (23.8-25.7)	24.8±1.0 (23.8-25.7)	41.1±2.0 (41.1-45.0)
	Snout length/ Head length	Longest anal spine length/SL	Pectoral fin length/SL
Yolk sac (15)	- -	- -	- -
Preflexion (13)	24.1±0.8 (22.9-25.0)	-	8.5±2.3 (4.8-11.6)
Flexion (8)	28.6±4.3 (19.6-33.3)	7.6±2.2 (5.2-10.9)	9.6±0.9 (8.9-11.4)
Postflexion (4)	31.1±2.2 (28.8-34.6)	11.7±0.2 (11.7-12.1)	13.1±1.0 (12.0-14.7)
Transforming(2)	25.1±0.8 (24.4-25.9)	12.6±1.3 (11.3-14.0)	17.0±0.3 (16.6-17.3)
Juvenile (2)	25.1±1.7 (23.4-26.8)	17.8±0.6 (17.2-18.4)	26.6±0.7 (25.6-27.7)

Fin formation. The sequence of fin development is pectoral, spinous dorsal and spinous pelvic simultaneously, caudal, soft dorsal and soft anal simultaneously, and finally the spinous anal. Elements of the caudal, the soft dorsal and anal, and spinous anal develop from the center of each fin outwards in both directions. Development begins anteriorly and progresses posteriorly in the spinous-dorsal-fin elements; it progresses from dorsal to ventral in the pectoral fin.

Pectoral fin development begins in larvae 2.6 mm NL. Pectoral fin length increases from 5.4 to 25.6% of NL or SL

between preflexion and transformation stages. Fin elements begin to develop at 6.6 mm, attaining the full adult complement of fin rays by 9.5 mm.

Dorsal and pelvic fin spines begin to develop simultaneously at 7 days (Fig. 2, center). The anlagen of the second dorsal spine first appears at 2.8 mm, initially visible only as nubs, protruding from the myomeres into the finfold, but subsequently protrude beyond the fin fold at 8-9 days (Fig. 2, upper). The second dorsal spine and pelvic spine are the longest elements in their respective fins throughout the larval development.

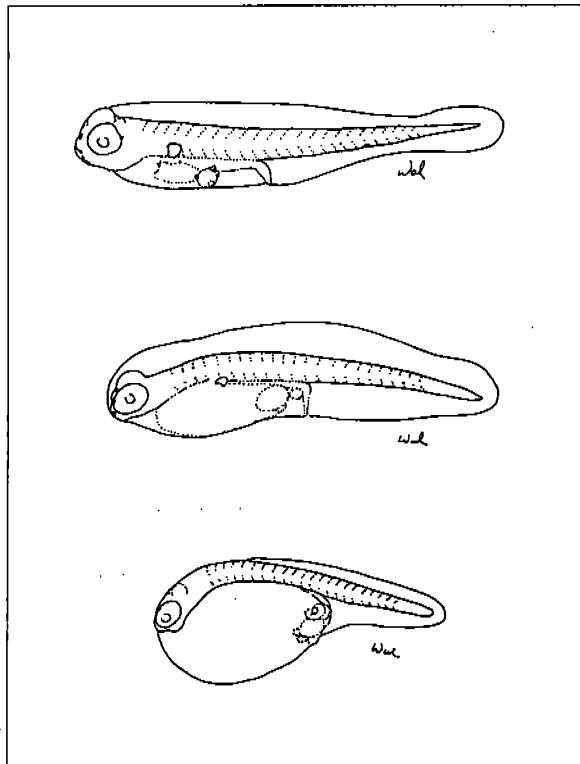
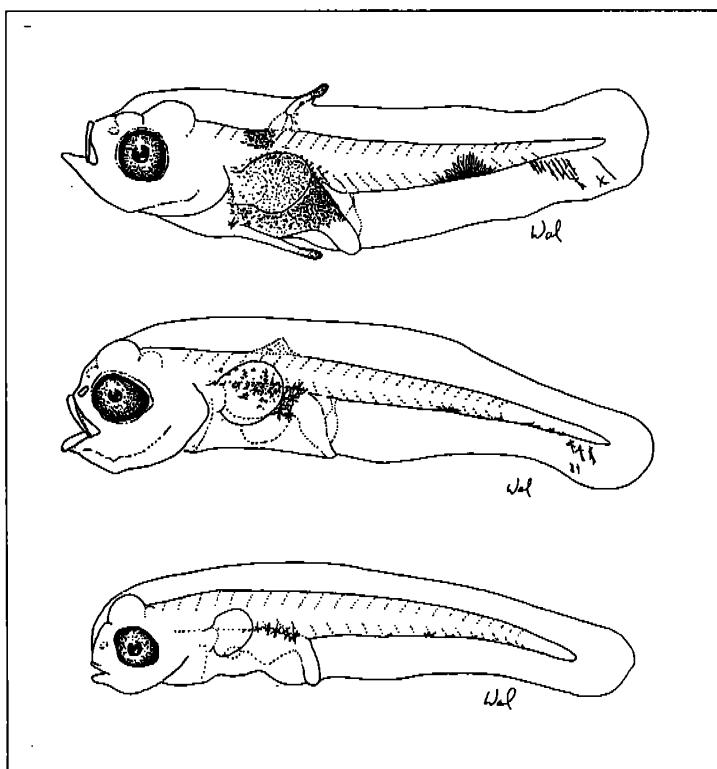


Fig. 1. Yolk sac larvae of *Epinephelus morio*, laboratory-reared. Upper: At hatch, 1.7 mm NL; Middle: 24 hours, 2.3 mm NL; Lower: 48 hours, 2.4 mm NL. [Larva de *Epinephelus morio* con saco vitellino, criado en laboratorio. Arriba: Al incubarse 1.7 mm NL; en el medio, a las 24 horas, 2.3 mm NL; Abajo: a las 48 horas con 2.4 mm NL.]

Fig. 2. Early stage laboratory-reared larvae of *Epinephelus morio*. Lower: 3 days, 2.7 mm NL, at time of first feeding; Middle: 8 days, 3.0 mm NL, with dorsal fin spine bud visible; Upper: 9 days, 3.5 mm NL, developing second dorsal fin and pelvic fin spines; the ventral melanophore spot is well-developed. [Estadio temprano de larva de *Epinephelus morio* criadas en laboratorio. Abajo: 3 días con 2.7 mm. NL, al tiempo de primera alimentación; En el medio, 8 días con 3.0 mm NL, con el brote de la espina de la aleta dorsal visible. Arriba: 9 días con 3.5 mm NL, con las espinas de la segunda aleta dorsal en desarrollo, el melanóforo ventral está bien desarrollado.]



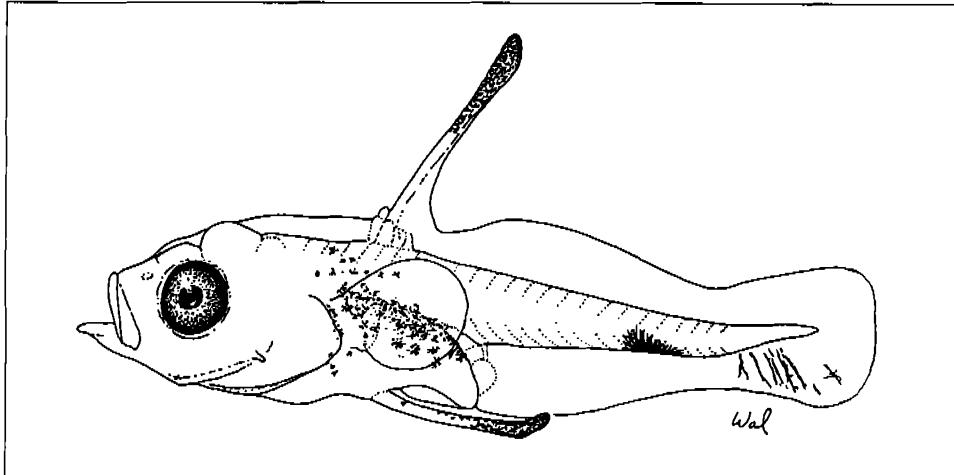


Fig. 3. Twelve-day larvae of *Epinephelus morio*, 4.1 mm NL. Initial ossification of the caudal fin supporting elements can be seen. Dark ends of the dorsal and pelvic fin spines are evident. [Larvas de 12 días de *Epinephelus morio*, 4.1 mm NL. Puede observarse una osificación inicial de la aleta caudal soportando los elementos. Los extremos opacos de las espinas de las aletas dorsal y pélvicas son evidentes.]

Development of the second dorsal and pelvic fin spine is extremely rapid over the next 7-10 days (Figs. 3 and 4). For larvae 4-10 mm SL pelvic fin spine length was 72-88% of second dorsal fin spine length. The spines reach their longest length relative to SL when larvae are 5.5-7.5 mm SL (15-20 days post-hatch) (Figs. 4-6). Some of the largest specimens (>15 mm SL) had the pelvic fin spine somewhat longer than the second dorsal fin spine.

Development of the first dorsal spine is next, in larvae at about 3.7 to 3.8 mm SL (11 days) (Fig. 3). It develops a few small spinelets. It is followed by development of the third dorsal spine, forming at about 4.1 mm SL (12 days) (Fig 4).

Soft dorsal, soft anal, and caudal fin rays begin development at 5.5 mm. The adult complement of eight superior and seven inferior principal rays develops by

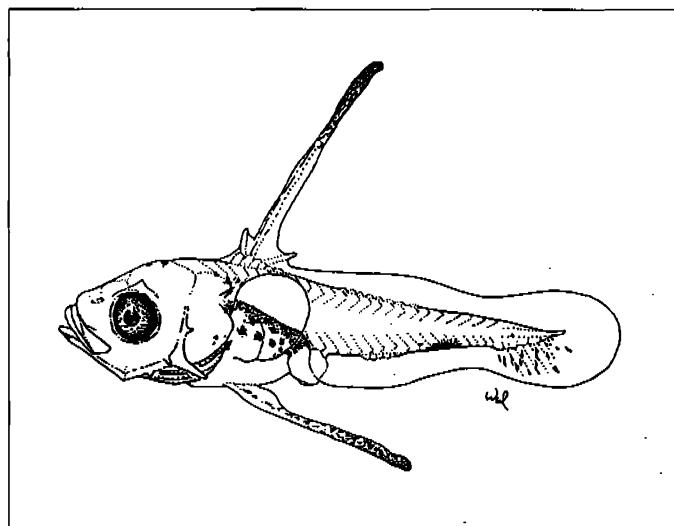


Fig. 4. Thirteen-day larvae of *Epinephelus morio*, 5.8 mm NL, showing further development of spination, including elongation of the second dorsal and pelvic fin spines, appearance of the first and third dorsal fin spines and appearance of the preopercular spines. This stage is at the greatest relative development of the elongate spines. Flexion is just beginning to occur. [Larva de 13 días de *Epinephelus morio* de 5.8 mm NL mostrando el futuro desarrollo de las espinas, incluyendo el alargamiento de las espinas de la segunda aleta dorsal y de la aleta pélvica, aparición de las espinas de la primera y tercera aleta dorsal, y aparición de las espinas preoperculares. En este estado se observa el más grande desarrollo relativo del alargamiento de las espinas. La flexión está a punto de ocurrir.]

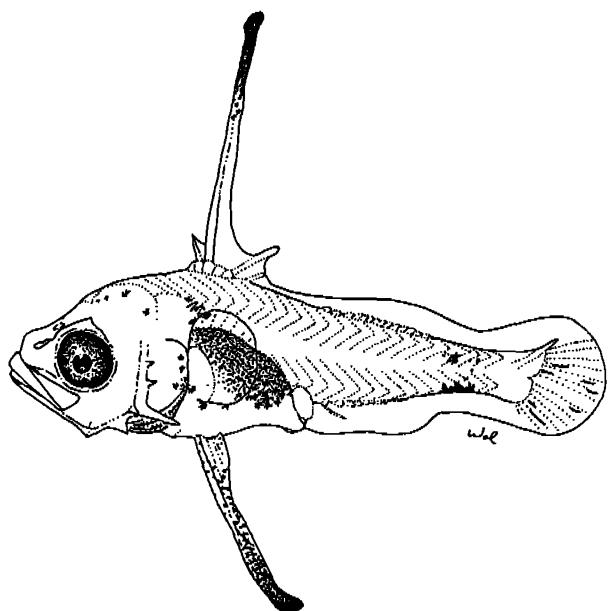


Fig. 5. Sixteen-day flexion larvae of *Epinephelus morio*, 6.5 mm NL. [Larva flexionada de 16 días de *Epinephelus morio*, de 6.5 mm NL.]

7.4 mm. The adult complement of soft dorsal (15 or 16) and anal fin (9) rays develops by 9.3 mm. The spinous anal fin is the last fin to begin development at 7.4 mm. The third anal fin spine is the last fin element to ossify at 20 mm.

The dorsal and pelvic spines are sheathed with tissue and have heavily pigmented fleshy lobes at their tips from the time of their first appearance through the juvenile stage (Figs. 3 to 10). The mobility of the dorsal and pelvic spines are described in Colin and Koenig (in press).

Spination of the head.
Spines on the head begin to develop at 4 mm. The

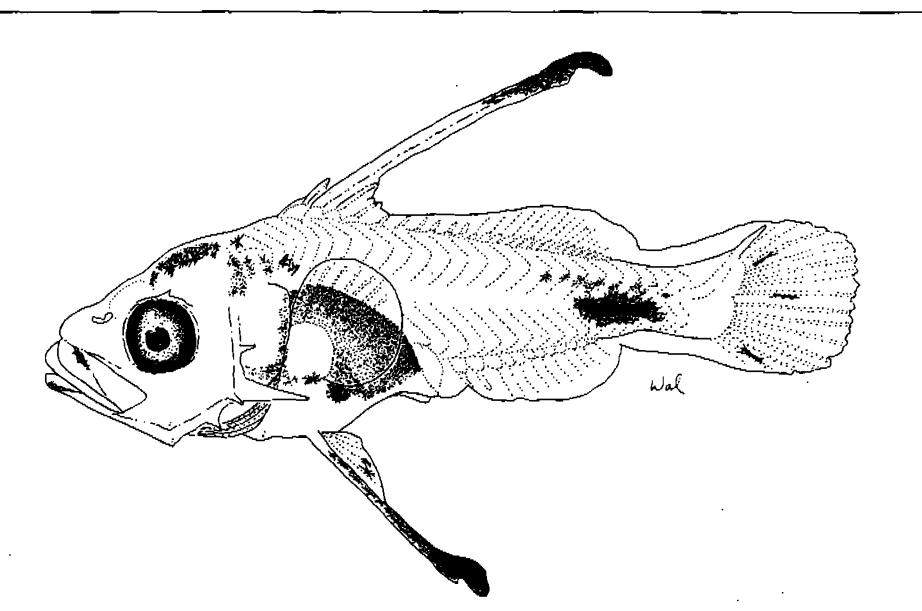


Fig. 6. Eighteen-day post-flexion larvae of *Epinephelus morio*, 7.4 mm SL. [Larva de 18 días en etapa de post-flexión de *Epinephelus morio*, de 7.4 mm SL.]

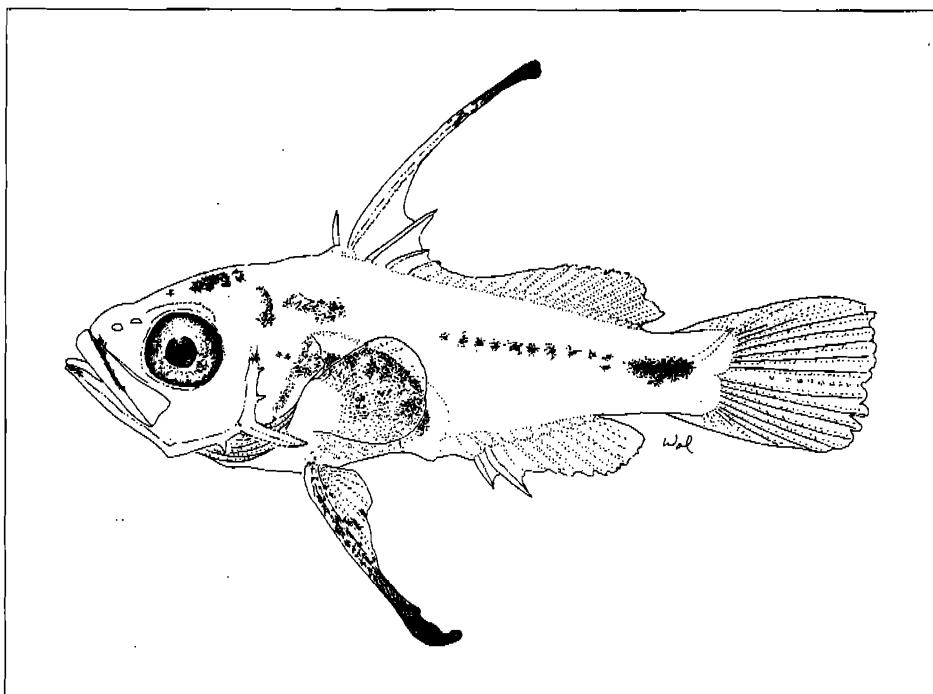


Fig. 7. Twenty-one-day post-flexion larvae of *Epinephelus morio*, 9.8 mm SL.
[Larva de 21 días en etapa de post-flexión de *Epinephelus morio*, de 9.8 mm SL.]

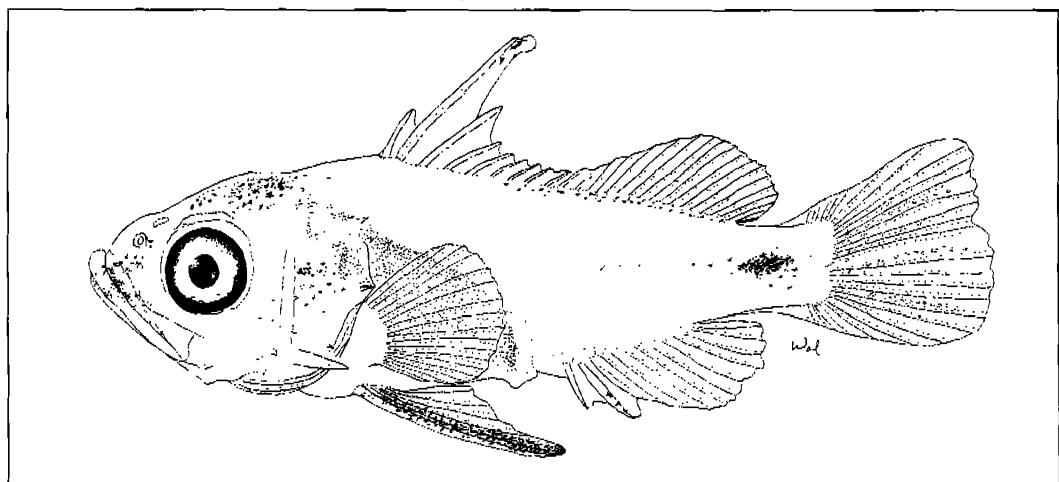


Fig. 8. Twenty-seven-day pelagic juvenile of *Epinephelus morio*, 12.6 mm SL. [Juvenil pelágico de *Epinephelus morio* de 27 días, de 12.6 mm SL.]

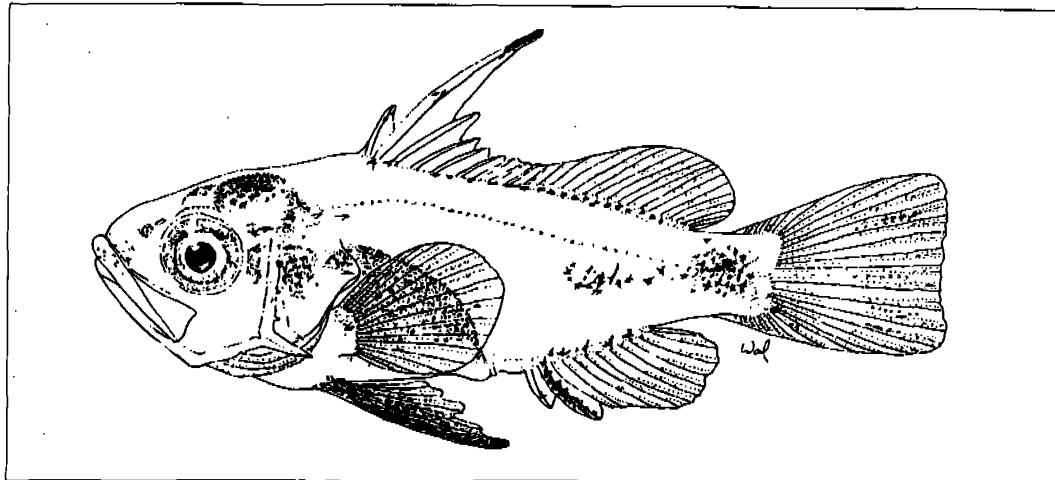


Fig. 9. Twenty-seven-day pelagic juvenile of *Epinephelus morio*, 13.9 mm SL. [Juvenil pelágico de *Epinephelus morio* de 27 días, de 13.9 mm SL.]

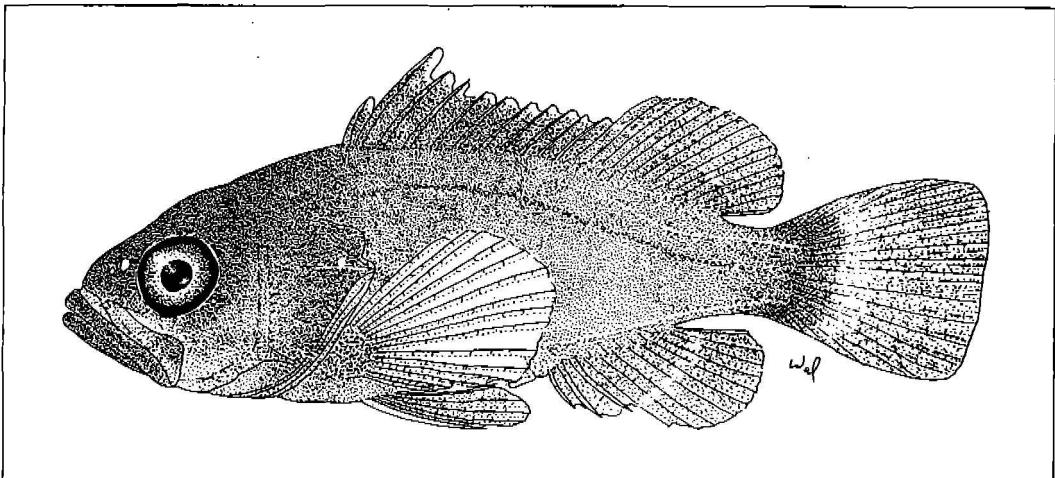


Fig. 10. Sixty-day laboratory-reared benthic juvenile *Epinephelus morio*. [Juvenil bentónico de *Epinephelus morio* criado en laboratorio de 60 días.]

angle spine of the posterior preopercular series forms first. Subsequent preopercular spines form from dorsal to ventral along the posterior margin away from the angle spine. Single spines develop on each side of the angle spine, at the angle of the anterior margin of the preopercle, on the frontal bone over the eye (supraocular spine), and on the supracleithral bone by 5.3 mm. Two or three preopercular spines appear dorsal

to the angle spine and one spine remains ventral to the angle spine from post-flexion (6.8 mm) through transformation (20 mm). A second supracleithral spine develops by 7.4 mm. The single supraocular spine is reduced in size and becomes part of a serrated supraocular ridge on the frontal bone by 9.6 mm. A subopercular and an interopercular spine begin to develop by 9.6 mm. During the transformation stage

several spines become overgrown with tissue and/or bone: the spine ventral to the angle spine, the angle spine of the anterior peropercular margin, and the supracleithral spines. Posterior preopercular spines on the dorsal margin rapidly increase in number, with 12 small spines giving a serrated appearance in small juveniles.

Lateral line and scale formation. Lateral line organs (indicated by a row of light colored spots on the flesh and caudal fin membrane) are visible on transforming specimens (15.1 mm). Scale development also appears to begin on the dorsal surface of the body and proceed from anterior to posterior (15.1 mm). The body is fully-scaled by the beginning of the juvenile period (20 mm).

Pigmentation: general. Larvae lack pigmentation at hatching. Pigmentation is first observed on 2.4 mm larvae as two small melanophores on the tip of the snout, two small melanophores over the forebrain and three small melanophores at the anterior to the yolk sac. The eyes become pigmented by day 3, with a scattering of melanophores over the gut and along the ventral area of the tail.

As the larvae grows, the caudal pigment spot moves slightly to the posterior onto the caudal peduncle and dorsally to the level of the centra. When the elongate dorsal and pelvic spines are folded back their dark tips are located very close to the caudal spot. In live larvae, the caudal end of the body is nearly transparent and it is sometimes difficult to distinguish the caudal spot from the dark tips of the spines.

From the earliest stages of dorsal and pelvic fin spine formation, the spines have fleshy tips with dense melanophores. As these spines lengthen greatly, the dark markings on their tips become more prominent, covering the outer one-third to one-half, making the spines readily apparent

(Colin and Koenig, in press). The tips of other spines of the dorsal fin and the anal fin are not pigmented in larvae. Late stage larvae acquire melanophores on the upper surface of the head and a line along the base of the dorsal fin.

Pigmentation: head region. Head pigmentation is lacking on most preflexion larvae (2.5-3.8 mm). Two preflexion larvae were observed with a melanophore located on each side of the ventral midline near the tip of the lower jaw while one specimen had only one of the two melanophores. This pair of melanophores near the tip of the lower jaw is present on all flexion larvae (5.5-7.4 mm). Flexion larvae >5 mm have a melanophore on the upper jaw on the anterior margin of the maxillary. Melanophores generally increase in number over the dorsal surface of the midbrain and forebrain during the flexion stage. By 7.4 mm, a cap of melanistic pigmentation covers the dorsal surface of the midbrain. In larvae >5 mm, internal melanophores appear over the hind brain and extend anteriorly from the anterior end of the notochord onto the perineural sheath in the nape region. Melanophores first appear on the opercle and color first appears on the head during post-flexion (9 mm).

Yellow (xanthophoric) pigmentation is present on the dorsal surface of the head and extends ventrolaterally to the eye which appears silvery for the first time. Silvery color (guanine crystals) appears on the preoperculum and operculum posterior to the eye during transformation (13 mm) with lavender pigmentation on the eye and a few orange chromatophores around the opercular spines. During the transformation stage, melanophores rapidly increase in number and spread over all surfaces of the head until the entire head is covered with melanophores obscuring color pigmentation by the beginning of the juvenile stage (20 mm).

Pigmentation: preanal region. Three to five melanophores appear over the dorsal surface of the gut at the beginning of the preflexion stage (2.5 mm). Melanophores over the gut increase in number and fuse to form an internal melanistic shield by 3 mm in preflexion larvae. This shield extends anteroventrally and ventrolaterally with development and is clearly visible until external melanistic pigmentation obscures it early in the juvenile stage. Internal melanophores appear dorsal and ventral to the notochord above the anterior of the gut at 2.6 mm and appear to extend anteriorly to the perineural sheath and hind brain by 5.0 mm. Internal pigmentation may extend from the notochord nearly to the dorsal margin of the body in 3.6 mm preflexion larvae and flexion larvae. Increasing body musculature and external pigmentation during transformation obscures this pigmentation in later stages. Melanophores appear along the dorsal margin of the body early in the transformation stage. Melanistic pigmentation rapidly increases over the surface of the body during transformation and completely covers the body of small juvenile specimens.

Color first appears on late preflexion larvae (7.4 mm). Yellow pigmentation and silvery color appear along the ventral margin of the melanistic shield lining the peritoneum. Xanthophoric pigmentation spreads anteriodorsally and appears as a wash of color covering the gut region and nape; silvery color covers the ventrolateral region of the peritoneal shield in post-flexion and transformation fish. Color pigmentation in the preanal region becomes obscured by melanistic pigmentation on transformation to the juvenile stage.

Pigmentation: post-anal region. In the post-anal region, melanophores first appear along the ventral midline of the body about one-third post-anal length anterior from the notochord tip at 2.4 mm and increase in number to seven to nine by 2.6 mm.

One of the anteriormost melanophores in this series usually appears notably larger than the others. This melanophore appears to be expanded in larvae of 2.8 mm and appears to form what Powell and Tucker (1992) have described as an inverted saddle on the ventrolateral surface of the body in the vicinity of myomeres 17-20. Three to five internal melanophores appear along the dorsal surface of the notochord in the region dorsal to the inverted saddle at 6 mm. Late in the flexion stage (7.4 mm), internal and external pigmentation associated with this saddle begins to move dorsally towards the notochord and lateral midline of the body. By the end of the flexion at 9.6 mm, internal melanophores extend along the dorsal surface of the notochord from the caudal peduncle to midbody and a patch of external pigmentation has moved to the lateral midline of the body on the caudal peduncle.

Color first appears in 9 mm larvae in the post-anal region. A wash of yellow pigmentation surrounds the melanistic pigment patch on the caudal peduncle and a few orange chromatophores appear along the lateral midline near the caudal peduncle patch. This yellow wash of pigmentation persists through the larval and transformation stages. Orange chromatophores increase in number and by the beginning of transformation (12 mm) extend anteriorly along the lateral midline from the caudal peduncle patch to a position under the origin of the soft dorsal fin. Internal pigmentation, color pigmentation and the caudal peduncle patch are obscured by musculature and external pigmentation by the beginning of the juvenile period at 20 mm.

Pigmentation: fins. Fin pigmentation first appears in the caudal fin membrane, ventral to the notochord tip at 2.6 mm. Two to twelve melanophores generally appear as a line of pigment extending away from the ventral tip of the notochord prior to flexion. As the caudal fin develops, these

melanophores become fewer in number through post-flexion and appear on the fin membrane between the developing caudal rays. During transformation, a few orange chromatophores and a "crescent" area in the anterior third of the fin becomes covered with leucocytes. Towards the end of transformation stage small melanophores appear, except for a crescent-shaped area in the anterior third of the fin, which remains lightly pigmented and appears white due to presence of leucocytes. Melanophores appear flag-like on the fin membrane at the distal tips of the second dorsal and the pelvic fin spines immediately after they begin to develop at 2.9 mm. Melanistic pigmentation over the second dorsal fin spine extends proximally and covers the distal one-third of the spines and is the only melanistic pigmentation present on the spinous and soft dorsal fin until melanistic pigmentation rapidly develops and obscures larval pigmentation during transformation.

Orange pigmentation appears around the flag only during the transformation stage at 12 mm. The spinous dorsal fin membrane of juveniles is densely covered by small melanophores except for the distal fringes between the spines, which lack melanophores and appear as white "flags". Melanistic pigmentation extends proximally over the pelvic fin spine to the pelvic fin base by 5 mm. Melanophores appear on the pelvic fin membrane coinciding with initiation of pelvic fin development (6.5 mm), and persist through larval development. The pelvic fin spine is covered by an orange wash of chromatophores during the post-flexion stage (9.5 mm). Orange chromatophores extend posteriorly onto the pelvic fin membrane and cover the entire pelvic membrane during the transformation stage. Rapid development of melanistic pigmentation on the pelvic fin late in transformation obscures all larval pigmentation in juveniles.

Orange chromatophores appear over the distal tip of the second anal fin spine early

in the transformation stage (12.5 mm). By 14 mm, a row of orange chromatophores appear at the insertion of the anal rays and a crescent-shaped band of leucocytes extends across the middle of the anal fin. Larval pigmentation is obscured by melanistic pigmentation by the beginning of the juvenile stage (20 mm), except for the crescent-shaped band of white pigmentation.

Juveniles in rearing aquariums did not quickly acquire the dark juvenile color pattern, which is similar to the adult. Rather, the barred pattern found on large juvenile and adults was first faintly acquired.

Swim bladder. Swim bladder inflation was first noted at day 12 when the silvery-sheen of the swim bladder was noted inside the gut of the larger larvae in the rearing tank.

Larval growth rate. Data for growth rate (Fig. 11) were taken from preserved specimens which show shrinkage averaging 7% after preservation and are indicative of the growth rate of the more advanced larvae in the rearing tanks.

Juvenile growth. Six red grouper juveniles were individually maintained in 80-l aquaria and fed to satiation with juvenile pinfish (*Lagodon rhomboides*). From days 66 to 134, these juveniles grew at rates from 0.26 to $0.61 \text{ mm} \cdot \text{day}^{-1}$ (mean = $0.41 \text{ mm} \cdot \text{day}^{-1}$) (Fig. 12). From 134 to 557 days, growth rates were 0.20 to $0.29 \text{ mm} \cdot \text{day}^{-1}$ (mean = 0.27). All six juveniles were released in October 1992 on an artificial reef offshore of Cedar Key, Florida, in water 15 m deep. They were freeze-branded (Colin and Koenig, in press) and dart-tagged and their survival is being monitored.

Discussion

The eggs of red grouper would be indistinguishable, in the field, from the eggs of most other species of *Epinephelus*. The

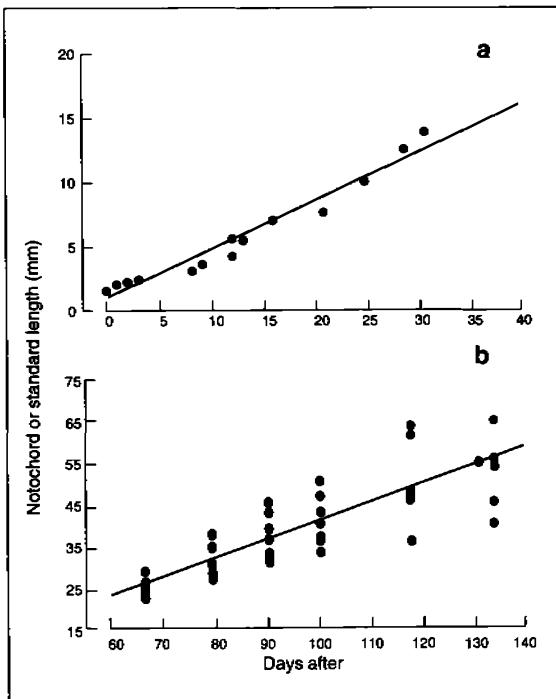


Fig 11. a) Growth of larval and pelagic juvenile *Epinephelus morio* in the laboratory. [Crecimiento de larvas y juveniles pelágicos de *Epinephelus morio* en el laboratorio.] b) Growth of benthic juvenile *Epinephelus morio* in the laboratory. [Crecimiento de juveniles bentónicos de *Epinephelus morio*.]

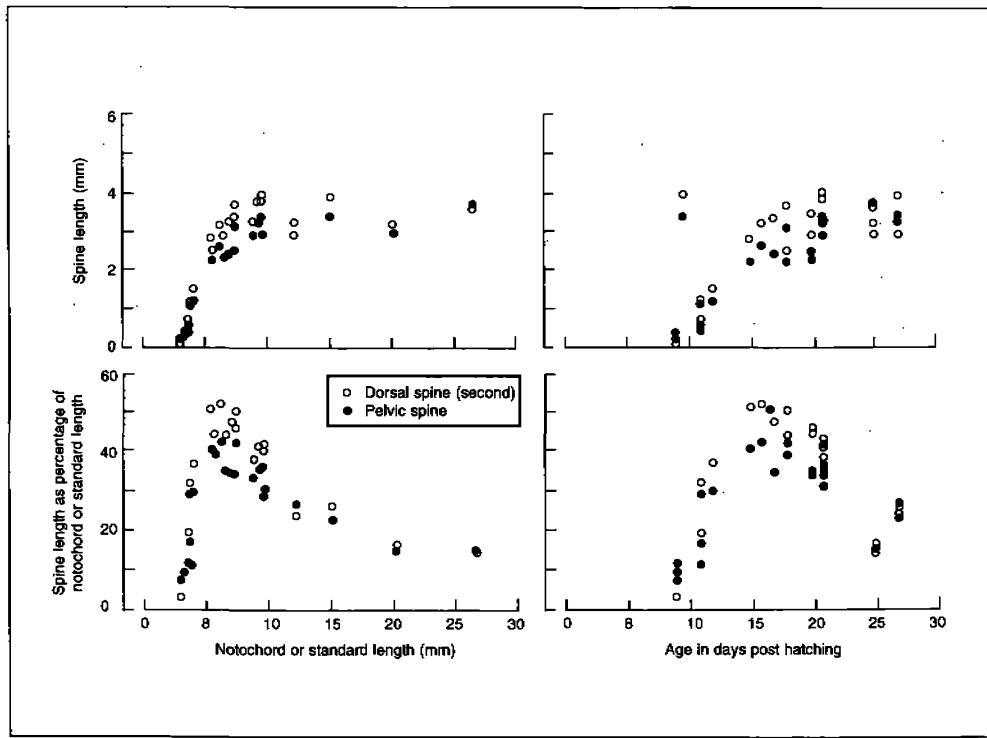


Fig 12. The relationship of the absolute and relative lengths of the second dorsal and pelvic fin spines of larval *Epinephelus morio* with the length (notochord length in preflexion larvae and standard length in postflexion larvae) and post-hatch age in days. [Relación entre las longitudes absoluta y relativa de la segunda espina de la aleta dorsal y la espina de la aleta pélvica de larvas de *Epinephelus morio* con la longitud y edad post-crianza, en días (longitud del notocordio en larvas en estado de preflexión, y longitud estándar en larvas en estado de postflexión).]

density of eggs indicates that they must be spawned initially in water of 28 ppt or greater to be positively buoyant and late stage eggs require about 32 ppt for neutral buoyancy. Almost certainly, eggs which are not floating have little chance of successful development, although embryonic development can proceed. Such eggs would come into contact with the bottom fairly soon after spawning and the conditions would not favor survival of the egg or early larvae.

As salinities lower than the 32 ppt which are necessary for positive buoyancy are common in inshore areas of the coast of Florida of the Gulf of Mexico, this is one factor which would limit the areas where *E. morio* could spawn. There are also often haloclines occurring in this area, and it is probable that eggs would rise to the upper limit of high salinity water and remain there, probably developing successfully.

Spine development

Relative to standard length, the second dorsal fin spine reached its maximum of about 50% and the pelvic spine its peak of 40% of SL at 5.5-7.4 mm SL (Fig. 12). The longest absolute spine lengths were obtained at these same stages. Powell and Tucker (1992) reported slightly smaller relative spine lengths (maxima of 48% and 32%) for laboratory-reared *E. striatus*. For larvae smaller than 6.0 mm SL, they did not report any relative dorsal spine lengths over about 36% and pelvic spine lengths over 27%. For *E. morio*, larvae as small as 4.0 mm SL exceeded these relative values for spine length.

Colin and Koenig (in press) argued that the major function of the elongate dorsal and pelvic spines of planktonic epinephelins was antipredator. The early and rapid development of spines, plus their orientation, resulted in a larvae representing a considerably larger and more difficult prey item

to a potential predator. The melanophore-rich fleshy tabs at the tips of the spines were very apparent in live larvae and are thought to mark clearly to potential predators the tips of the spines and the effective size of the larvae. When seen in living larvae the location of the caudal pigment spot tends to enhance the pattern produced by the three outward projecting spines with their dark tips. It is seen as a fourth dark spot centered within the triangle produced by the spine tips.

Larval growth rate

We feel that the growth rates of larvae and pelagic juveniles, shown in Figs. 11 and 12 are relatively similar to those which would occur in nature. Given the rates shown and the timing observed in our rearing aquaria where transformation from pelagic juvenile to benthic juveniles occurred at about 20 mm SL and 35-50 days post-hatch, this agrees reasonably well with ages determined for recruiting grouper juveniles in the field. Unfortunately there are no such data available for *E. morio*, but pretransition ages determined from otolith increments were found to be 37-45 days (mean 41.6) for *E. striatus* and 34-42 days (mean 38.6) for *E. fulvus* in the Bahamas (Colin et al., in press). For other Western Atlantic groupers, *Mycteroperca microlepis* had mean pretransition ages of approximately 42 days and SL of 15 mm and *M. bonaci* of 41 days (Keener et al. 1988). The data presented by Powell and Tucker (1992) for laboratory reared *E. striatus* indicate a slower growth rate for that species. For example, their 17-20 days post-hatch larvae were 5.5-6.5 mm SL, while the present *E. morio* were 5.7-7.4 mm SL; and at 26-30 days lengths were 8.5-9.4 mm SL vs. 12.1-15.1 mm SL, respectively. Their largest larvae at 13.2 mm SL was of an age (40 days) at which transition of *E. striatus* to benthic existence would be expected, normally at 20 mm

SL or more (Colin et al., in press). Whether their slower larval growth rate was due to rearing conditions needs to be determined.

Keener et al. (1988) also collected a small number of recruiting *E. morio* in nets anchored in a channel leading to an estuarine area off Charleston, South Carolina. Compared to the gag, *Mycteroperca microlepis* and other grouper pelagic juveniles, these comprised less than 1% of the epinepheline catch, but were generally collected during mid-April to mid-May, at a time consistent with the known spawning season of *E. morio* and the time believed required for development to the benthic juvenile stage.

Juvenile growth

The growth rates of the juveniles in aquaria indicate considerable individual variation. However, the mean rate observed, $0.41 \text{ mm} \cdot \text{day}^{-1}$ is similar to that reported by Colin et al. (in press) for *Epinephelus striatus* in the Bahamas.

The release of the laboratory-reared juveniles on a Florida artificial reef represents, we believe, the first release of cultured groupers into the wild.

Acknowledgements

Numerous individuals assisted with field and laboratory work. Local commercial fishers, particularly Clay Bailey, provided adult fish for spawning work. Mike Chasar was involved in all aspects of the field and laboratory work. Lori J. Bell and Felicia Coleman assisted in many ways.

This work was supported by the MARFIN program of the National Marine Fisheries Service and the Florida State Department of Natural Resources fishing license revenue research program.

References

- Colin, P.L., W.A. Laroche and E.D. Brothers. Timing of ingress and settlement in the Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae), with relationship to spawning occurrence. Bull. Mar. Sci. (In press).
- Colin, P.L. and C.C. Koenig. Spines in larval red grouper, *Epinephelus morio*: development and function. Proc. Gulf Caribb. Fish. Inst. (In press).
- Goodey, C.P. and M.J. Schirripa. 1991. The red grouper fishery of the Gulf of Mexico. Miami Lab. Contrib. No. MIA-90/91-86, Southeast Fisheries Center, U.S. Natl. Mar. Fish. Serv. 80 p.
- Johnson, G.D. and P. Keener. 1984. Aid to identification of American grouper larvae. Bull. Mar. Sci. 34: 106-134.
- Houde, E.D. and A.K. Taniguchi. 1977. Procedures used to culture larvae of marine fishes at the Rosenstiel School of Marine and Atmospheric Science. Report to Environmental Prot. Agency. 17 p.
- Keener, P., G.D. Johnson, B.W. Stender and E.B. Brothers. 1988. Ingress of postlarval gag, *Mycteroperca microlepis* (Pisces: Serranidae) through a South Carolina barrier island inlet. Bull. Mar. Sci. 42(3):376-396.
- Kendall, A.W., Jr. 1984. Serranidae: development and relationships, p. 499-510. In H.G. Moser, W.J. Richards, D.M. Cohen, M.P. Fahay, A.W. Kendall, Jr. and S.L. Richardson (eds.) Ontogeny and systematics of fishes. Amer. Soc. Icht. Herp. Spec. Publ. No. 1.
- Moe, M.A. 1969. Biology of the red grouper, *Epinephelus morio* (Valenciennes) from the eastern Gulf of Mexico. Florida Dept. Nat. Res., Mar. Res. Lab. Prof. Pap. Ser. 10:1-95.
- Powell, A.B. and J.W. Tucker, Jr. 1992. Egg and larval development of laboratory-reared Nassau grouper, *Epinephelus striatus* (Pisces: Serranidae). Bull. Mar. Sci. 50(1):171-185.

APPENDIX 1

List of Participants

Arreguín-Sánchez, Francisco

Centro Interdisciplinario de Ciencias
Marinas, Instituto Politécnico Nacional
A.P. 592, 23000 La Paz
Baja California Sur, México
Fax 52(112) 25322
Phone 52(112) 25344/25366
E-mail farregui@vmredipn.ipn.mx

Auil, Stephanie

Fisheries Department
Princes Margaret Drive P.O. Box 148
Belize City, Belize
Fax (501) 2 32983

Ault, Jerald

Marine Biology and Fisheries Division
University of Miami
RSMAS Campus
4600 Rickenbacker Causeway
Miami, Florida, 33149-1098
Fax (305) 361 4600

Bush, Phillip G.

Natural Resources Unit
Department of the Environment
Grand Cayman, Cayman Islands, BWI
Fax (809) 9497544
E-mail godytlas@candw.kg

Campos, José Luis

Department of Natural and
Environmental Resources
P.O. Box 9066600
Puerta de Tierra Station
San Juan, Puerto Rico 00906-6600
Fax (787) 724 7335
Phone (787) 722 4204
E-mail CARIBEFISH@UPR1.UPR.CLU.EDU

Caverivière, Alain

Institut Francais de Recherche Scientifique
Pour le Développement en
Coopération (ORSTOM)
B.P. 1386, Dakar, Sénégal
Fax (221) 32 43 07
Phone (221) 34 75 95
E-mail caverivi@isra.isra.sn

Chapman, Robert W.

Marine Resources Research Institute
South Carolina Wildlife & Marine
Resources Department
Charleston, South Carolina 29412, USA
Fax (803) 762 5110
Phone (803) 762 5402
E-mail chapmanr@mrd.dnr.state.sc.us

Chávez, Ernesto A.

Centro Interdisciplinario de Ciencias
Marinas, Instituto Politecnico Nacional
A.P. 592, 23000 La Paz
Baja California Sur, Mexico
Fax (112) 25366
Phone (112) 25322/25344

Collins, L. Alan

National Oceanic and Atmospheric
Administration
National Marine Fisheries Service
Southeast Fisheries Science Center
Panama City Laboratory
3500 Delwood Beach Road
Panama City, Florida 32408, USA
Fax (904) 235 3559
E-mail acollins@nmfspc.ssp.nmfs.gov

Collins, Mark R.

Marine Resources Research Institute
 South Carolina Wildlife & Marine
 Resources Department
 P.O. Box 12559 Charleston
 South Carolina 29422-2559 USA
 Fax (803) 762 5110
 Phone (803) 762 5008
 E-mail collinsm@cofc.edu

Cotte, Ricardo

Caribbean Fishery Management Council
 268 Avenue Muñoz Rivera, Suite 1108
 San Juan, Puerto Rico 00918-2577
 Fax (787) 766 6239
 Phone (787) 766 5926/766 5927/
 766 5928
 E-mail CARIBEFISH@UPR1.UPR.CLU.EDU

Domeier, Michael L.

California Department of Fish and Game
 Marine Resources Division
 330 Golden Shore, Suite 50
 Long Beach, California 92648, USA
 Fax (310) 590 5193
 E-mail 103727.3530@compuserve.com

Ehrhardt, Nelson M.

Division of Marine Biology and Fisheries
 Rosentiel School of Marine and
 Atmospheric Science
 University of Miami
 4600 Rickenbacker Causeway
 Miami, Florida 33149-1098, USA
 Fax (305) 361 4902
 Phone (305) 361 4741
 E-mail nehrhardt@rsmas.miami.edu

Estrada Garcia, Jaime

Centro Regional de Investigación
 Pesquera Veracruz
 Av. Manuel Avila Camacho #195
 Col. Centro, Veracruz, Veracruz, México
 Phone (52-28) 15 61 18

Flores-Hernández, Domingo

Programa de Ecología, Pesquerías y
 Oceanografía del Golfo de México
 (EPOMEX)
 U.A.C. Apartado Postal 520
 Campeche 24030, Campeche, México
 Fax (981) 65 954

García Moliner, Graciela

Caribbean Fishery Management Council
 268 Avenue Muñoz Rivera, Suite 1108
 San Juan, Puerto Rico 00918-2577
 Fax (787) 766 6239
 Phone (787) 766 5926/766 5927/
 766 5928
 E-mail CARIBEFISH@UPR1.UPR.CLU.EDU

Gómez, Gabriel J.

FONAIAP
 Centro Invest. Agrop. Pesq. Sucre
 P.O. Box 236, Cumaná 6101, Venezuela
 Fax 58 (93) 318 454
 E-mail ciapes@sucre.udo.edu.ve

González Cano, Jaime

Instituto Nacional de la Pesca
 Chilpancingo
 # 70 Colonia Hipódromo Condesa
 06100 México, D.F.
 Fax (5) 286-1149

Jacobs, Noel

Fisheries Department
 Princes Margaret Drive P.O. Box 148
 Belize City, Belize
 Fax (501) 2 32983

Koenig, Christopher C.

Department of Biological Sciences
 Florida State University
 Tallahassee, Florida 32306-2043, USA
 Fax (904) 6449829
 E-mail koenig@bio.fsu.edu

Lara-Domínguez, Ana L.

Programa de Ecología, Pesquerías y
Oceanografía del Golfo de México
(EPOMEX)
U.A.C. Apartado Postal 520
Campeche 24030, Campeche, México

Legault, Christopher M.

Rosentiel School of Marine and
Atmospheric Science
University of Miami
4600 Rickenbacker Causeway
Miami, FL 33149-1098 USA

Leonce-Valencia, Claudia O.

Centro de Investigación y de Estudios
Avanzados del IPN
Apartado Postal 73
Cordemex C.P. 97310
Mérida, Yucatán, México
Fax (99) 812917

Luckhurst, Brian E.

Division of Fisheries
P.O. Box CR 52, Crawl CRBX, Bermuda
Fax (809) 2932716
E-mail blucky@ibl.bm

Manickchand-Heileman, Sherry

Instituto de Ciencias del Mar y
Limnología, Lab. Ecología del Benthos
Universidad Nacional Autónoma de
México, Apartado Postal 70-305, México
04510 D.F. México
E-mail sherry@mar.icm.unam.mx

Medina, Miguel

Secretaría de Medio Ambiente Recursos
Naturales y Desarrollo (SEMARNYD)
Gobierno del Estado de Campeche
Calle 10 #338, Barrio San Roman
C.P. 24040, Campeche, Campeche
Méjico
Phone (52-981) 1 29 20

Mees, Christopher C.

Marine Resources Assessment Group
47 Prince's Gate, London
SW7 2QA, UK
Fax (+44) 171 823 7916
Phone (+44) 171 594 9888
E-mail c.mees@ic.ac.uk

Mendoza, Jeremy J.

Dpto. de Biología Pesquera
Instituto Oceanográfico
Universidad de Oriente
Apartado Postal 245, Cumaná, Venezuela
Fax (58-93) 653 606
E-mail jmendoza@cumana.sucre.udo.edu.ve

Monroy-García, M. del Carmen

Centro Regional de Investigaciones
Pesqueras de Yucalpetén
Apartado Postal 73, Progreso 97320
Yucatán, México
Fax (993) 54028

Munro, John L.

ICLARM
MCPO Box 2631
0718 Makati, Metro Manila, Philippines
Fax (63-2) 816 3183
Phone (1-809) 973 2241
E-mail j.munro-t@cgnet.com

**Laboratoire de Biologie Marine et
Malacologie**

EPHE, Université de Perpignan
Perpignan 66860 Cedex, France
Fax (33) 68 50 36 86
Phone (33) 68 66 20 55

**Caribbean Marine Protected Areas
Project**

Discovery Bay Marine Laboratory
P.O. Box 35, Discovery Bay, Jamaica
Fax (1-809) 073 3091
Phone (1-809) 073 2241

Pauly, Daniel
 ICLARM
 MCPO Box 2631
 0718 Makati City, Metro Manila,
 Philippines
 Fax (63-2)816 3183
 and
 Fisheries Centre, 2204 Main Mall
 University of British Columbia
 Vancouver, B.C.
 Canada V6T 1Z4.
 E-mail pauly@fisheries.com

Pérez Mellado, Joaquín
 Instituto Tecnológico del Mar de
 Guaymas
 Secretaría de Educación Pública
 Apartado Postal 742, Guaymas, Sonora
 85400, México

Pitcher, Tony
 Fisheries Centre
 University of British Columbia
 2204 Main Mall, Vancouver, B.C.
 Canada V6T 1Z4
 Fax (604) 822 8934
 E-mail tpitcher@fisheries.com

Posada, Juan M.
 Department of Marine Sciences
 University of Puerto Rico
 Mayagüez 00681-5000, Puerto Rico
 Fax (787) 899 5500
 Phone (787) 899 2048

Ramm, David C.
 Commission for the Conservation of
 Antarctic Marine Living Resources
 23 Old Wharf, Hobart Tasmania 7000
 Australia
 Fax (61-3) 62349965
 Phone (61-3) 62319556
 E-mail David@CCAMLR.org

Ramos-Miranda, Julia
 Programa de Ecología, Pesquerías
 y Oceanografía del Golfo de México
 U.A.C. Apartado Postal 520
 Campeche 24030, Campeche, México

Render, Jeffrey H.
 Coastal Fisheries Institute, Center for
 Coastal Energy and Environmental
 Resources
 Louisiana State University
 Baton Rouge, Louisiana 70803-7503, USA
 Fax (504) 3886513

Rivera-Arriaga, Evelia
 Programa de Ecología, Pesquerías
 y Oceanografía del Golfo de México
 U.A.C. Apartado Postal 520
 Campeche 24030, Campeche, México

Rodrigues Cunha, Luis Paulo
 Universidade do Rio Grande
 Depto. de Oceanografia
 Cp 474, 96201-900 Rio Grande (RS), Brazil

Rolón, Miguel Angel
 Caribbean Fishery Management Council
 268 Av. Muñoz Rivera
 Suite 1108 San Juan, Puerto Rico, 00918
 Fax (809) 766 6239

Sadovy, Yvonne
 Department of Zoology
 University of Hong Kong
 Pokfulam Road, Hong Kong
 Fax (852) 5599114

Sánchez Chávez, Julio A.
 Universidad Autónoma de Campeche
 Dirección General de Estudios de
 Posgrado e Investigación
 Torre de Rectoría, Ciudad Universitaria,
 Av. Universidad y Agustín Melgar s/n
 Campeche 24030 Campeche, México
 Fax/Phone (52) (981) 1 29 67
 Phone (52) (981) 6 26 18 ext. 113
 E-mail dgpi@becan.uacam.mx

Sánchez-Gil, Patricia
 Program of Ecology, Fisheries and
 Oceanography of the Gulf of Mexico
 (EPOMEX)
 University of Campeche
 Apartado Postal 520
 Campeche 24030, Campeche, México

Salas, Silvia

Fisheries Centre, 2204 Main Mall
 University of British Columbia
 Vancouver, B.C.
 Canada V6T 1Z4.

Scott-Denton, Elizabeth

National Marine Fisheries Service
 Southeast Fisheries Science Center
 Galveston Laboratory
 4700 Avenue U, Galveston
 Texas 77551, USA
 Fax (409) 766 3508
 Phone (409) 766 3500

Shapiro, Douglas

Department of Biology
 Eastern Michigan University
 Ypsilanti, Michigan, 48197, USA
 Fax (313) 487 9235

Skov, Patricia

Caribbean Fishery Management Council
 268 Avenue Muñoz Rivera, Suite 1108
 San Juan, Puerto Rico 00918-2577
 Fax (787) 766 6239
 Phone (787) 766 5926/766 5927/
 766 5928
 E-mail CARIBEFISH@UPR1.UPR.CLU.EDU

Sluka, Robert

University of Miami
 Department of Biology
 Coral Gables, Florida 33124 USA
 Fax (305) 284 3013
 E-mail jvl2lc5m@umiami.ir.miami.edu

Sullivan, K.M.

University of Miami
 Department of Biology
 Coral Gables, Florida 33124 USA
 Fax (305) 284 3039

The Nature Conservancy, Florida and
 Caribbean Marine Conservation
 Science Center
 P.O. Box 249118, Coral Gables, Florida
 33124, USA
 Fax (305) 284 3002

Szedlmayer, Stephen T.

Auburn University Marine Extension and
 Research Centre
 Department of Fisheries and Allied
 Aquacultures
 4170 Commanders Drive, Mobile
 AL 36615-1413 USA
 Fax (205) 438 5670

Thompson, Bruce A.

Coastal Fisheries Institute, Center for
 Coastal Energy and Environmental
 Resources
 Louisiana State University
 Baton Rouge, Louisiana 70803-7503 USA
 Fax (504) 3886513

Tucker, John W., Jr.

Harbor Branch Oceanographic Institution
 5600 North U.S. Highway 1, Fort Pierce
 Florida 34946, USA
 Fax (407) 465 2446

Woodley, Cheryl M.

National Marine Fisheries Service
 Charleston Laboratory
 217 Johnson Road
 Charleston, South Carolina, USA

Xiao, Yongshun

Fisheries Division
 Department of Primary Industry and
 Fisheries
 GPO Box 990, Darwin NT 0801, Australia

Yáñez-Arancibia, Alejandro

Programa de Ecología, Pesquerías
 y Oceanografía del Golfo de México
 U.A.C. Apartado Postal 520
 Campeche 24030, Campeche, México

Zetina-Moguel, Carlos

Centro Regional de Investigaciones
 Pesqueras de Yucalpetén
 Apartado Postal 73, Progreso, 97320
 Yucatán, México
 Fax (993) 54028

APPENDIX 2

Author Index

- Abad, N. 3, 10
Abdel-Aziz, S.H. 241
Abella, A. 164, 172
Ablan, M.C. 10
Acero, A. 46, 48
Acosta, A. 12, 15, 17, 164, 171, 240
Adisukresno, S. 302
Aguirre-León, A. 4, 12, 18, 43, 44, 46, 48, 49, 278, 325
Agustin, L. 6, 8
Akamine, T. 164, 171
Al-Shoushani, M. 164, 172
Alagaraja, K. 115, 116, 117, 141, 146, 148
Alagarswami, K. 115, 117
Al-Baz, A.F. 241
Alcalá, A.C. 6, 10
Aleev, Y.G. 251, 253
Alegria, J. 237
Alexander, L.M. 91, 240
Alexander, R.McN. 245, 251, 253
Alió, J. 58, 336
Allan, G.L. 377
Allen, D.M. 75, 82
Allen, G.R. 3, 8, 86, 90, 92, 95, 116, 118, 129, 130, 131, 132, 133, 134, 135, 136, 220, 234
Allendorf, F.W. 86, 91
Alvarez-Guillén, H. 46, 48
Alvarez-Lajonchere, L. 239
Alverson, D.L. 360, 362
Alves, M.I.M. 139, 146, 148
Ambak, M.A. 238
Ameer Hamsa, K.M.S. 111, 115, 116
Amezcua Linares, F. 12, 14, 17
Amon Kothias, J.B. 236
Anderson, B. 302
Anderson, C. 187
Anderson, J. 187
Anderson, W.D., Jr. 65-67, 72, 118, 162
Andreoli, M.G. 164, 172
Anon. 20, 26, 111, 114, 115, 267, 275, 276, 332, 336
Ansley, H.L.H. 160, 162
Ansuini, F.J. 117
Appeldoorn, R.S. 12, 15, 17, 163-165, 171, 205, 240, 243
Arceo, P. 203, 211, 214, 215
Archer, B. 187
Arnold, C.R. 190, 199, 200
Arnold, G.P. 49
Arocha, F. 58
Arreguín-Sánchez, F. 1-4, 8, 10, 11, 15, 17, 19, 20, 21, 23, 25-30, 40, 43, 51, 59, 74-76, 85, 92, 96, 106, 137, 150, 158, 163, 164, 174, 189, 202-216, 218, 242-244, 254, 266, 277, 289, 307, 324, 331, 337, 350, 355, 358, 359, 360, 363, 378, 385, 399
Artiles, M. 241
Avadh, G.K. 107, 109, 118
Back, W. 29, 40
Bacon, P.R. 139, 149
Badrudin, M. 242, 302
Baez, C. 336
Baez Hidalgo, M. 239
Bagenal, T.B. 157
Bailey, C. 321, 414
Baisre, J. 242
Baisre, J.A. 240
Bakhader, A. 237
Bal, D.V. 116
Balgos, M.C. 1, 4, 9, 11, 19, 28, 43, 51, 59, 74, 85, 92, 106, 137, 150, 158, 163, 174, 189, 202, 218, 242-244, 254, 266, 277, 289, 307, 324, 331, 337, 350, 355, 360, 363, 378, 385, 399
Ballantine, W.J. 6, 10
Bambino, C. 3, 9, 220, 236
Bannerot, S.P. 5, 8, 44, 48, 75, 76, 82, 278, 288, 308, 321, 322
Bapat, S.V. 107, 111, 117
Baranov, F.I. 219, 234
Barans, C.A. 60, 61, 71, 72, 73, 162, 190, 200

- Barber, R.C. 86, 90
 Bardach, J.E. 173, 278, 288
 Barnes, J.A. 165, 172, 364, 377
 Baron, M. 302
 Barr, E.E. 241
 Basheeruddin, S. 117
 Basson, M. 206, 215
 Basu, S.P. 107, 110, 118
 Basurto-Origel, M. 44, 48
 Bauchot, M.L. 42
 Baxter, J.H.S. 154, 157
 Beamish, R.J. 2, 8, 151, 152, 154, 157,
 159, 162, 231, 234
 Beatty, H.R. 317, 322, 413, 414
 Beaumariage, D.S. 76, 82
 Beaumont, A. 91
 Beddington, J.R. 206, 215, 216, 265
 Beets, J. 4, 8, 9, 75, 82, 83, 165, 171
 Bell, J.D. 77, 83
 Bell, L.J. 414
 Bellwood, D.R. 7, 10
 Benco, R. 264, 265
 Benitez, L.V. 383
 Bennett, J. 175, 187
 Bensam, P. 115, 117
 Bentzen, P. 87, 91
 Berrios, J. 46, 48, 49
 Berry, F.H. 61, 73
 Bertin, L. 103, 105
 Betancourt, M. 57, 58, 242
 Beverton, R.J.H. 141, 148, 164, 172, 219,
 220, 228, 235, 342, 349
 Bhar, P.K. 107, 110, 119
 Bhargava, P.K. 107, 110, 118
 Bhattacharya, C.G. 164, 171
 Bianchi, G. 95, 116, 117
 Binohlan, C. 3, 6, 8, 218, 220, 235
 Birdsong, R.S. 165, 172
 Birkeland, C.E. 238
 Blaber, S. 302
 Blaber, S.J.M. 302
 Blache, J. 92, 95
 Boa, A.G. 241
 Boerema, L.K. 340, 349
 Bogdanov, A.S. 200, 239
 Böhlke, J.E. 63, 65, 72, 204, 215
 Bohnsack 75
 Bohnsack, J.A. 75, 82, 83, 165, 171, 320-
 322, 364, 377
 Bolden, S. 165, 171
 Bortone, S.A. 4, 44, 61, 85, 86, 90, 190,
 200, 237, 241
 Bouain, A. 240
 Bouhlel, M. 237
 Brahmi, B. 240
 Branford, R. 302
 Bravington, M. 265
 Brewer, D. 302
 Briggs, J.C. 165, 172, 175, 187
 Briggs, P.T. 241
 Brock, V.E. 39, 41
 Brothers, E.B. 192, 200, 317, 322, 413,
 414
 Brouard, F. 171, 172, 236
 Brown, A., Jr. 75, 83
 Bruger, G.E. 240
 Brulé, T. 20, 28, 35, 38-41, 75, 76, 204,
 400
 Brusher, H.A. 44, 49, 175, 180, 187
 Bruslé, J. 105
 Buchanan, C.C. 160, 162
 Buckworth, R.C. 300, 302
 Buddemeyer, R.W. 238
 Buesa-Mas, R.J. 333, 336
 Buesa, R.J. 242
 Bullis, H.R., Jr. 27, 82, 240
 Bullock, L.H. 76, 82, 83, 165, 172, 187,
 240, 308, 310, 321, 322
 Burgos, R. 2, 3, 20, 26, 27, 29, 76, 164,
 202-205, 206, 215, 242, 355, 358
 Burgos Rosas, R. 245, 350, 360
 Burmer, G.C. 90, 91
 Burnett-Herkes, J. 165, 172, 239, 364, 377
 Burrell, V.G., Jr. 60, 61, 73
 Burton, M. 190, 200
 Bush, P.G. 2, 39, 42, 150, 151, 157, 159,
 364, 366, 368, 373, 377
 Butler, J.N. 165, 172, 364, 377
 Buxton, C.D. 6, 10

 Cabral, C. 197-199
 Cabrera, M.A. 20, 27, 30, 40, 205-208,
 211, 214, 215
 Cabrera-Vasquez, M.A. 12, 18
 Caddy, J.E. 355, 359
 Cadenat, J. 92, 95, 237

- Campbell, R. 302
 Camper, J.D. 86, 90
 Camus, A. 251
 Cansado, E. 359
 Cantarell, E. 243
 Carlot, A. 264, 265
 Carr 317
 Carranza, J. 30, 41
 Carrara, G. 237, 241
 Carrillo de Albornoz, C. 242
 Carter, H.J. 60, 72
 Carter, J. 364, 377
 Casal, C. 6, 8
 Cassie, R.M. 164, 172
 Caverivi  re, A. 92, 94, 95, 96, 100, 105
 Celaya, J. 138, 148, 267, 276
 Cervig  n, F. 52, 57, 58, 169, 172, 336, 357, 359
 Chacko, P.I. 117, 118
 Chac  n, R. 52, 57, 58, 336
 Chao, T.M. 383, 386, 394, 396, 397
 Chaplin, C.C.G. 63, 65, 204, 215
 Chapman, F. 176, 187
 Chapman, R.W. 4, 44, 61, 85, 87, 91
 Chasar, M.P. 321
 Chasar, M. 414
 Chauvet, C. 240
 Ch  vez, E. 12, 15, 17, 243
 Ch  vez, E.A. 20, 26, 207, 215, 216, 324
 Ch  vez, J. 49
 Chen 115, 117
 Chen, C.H. 290, 302
 Chen, C.Y. 238, 240
 Chen, S.C. 290, 302
 Chen, T.T. 86, 91
 Cheong, L. 379, 383, 384
 Chi, T.H. 290, 302
 Chiappone, M. 82
 Chidambaram, K. 110, 117
 Childress, J.J. 251, 253
 Chilton, D.E. 151, 152, 154, 157
 Chinnery, L.E. 241
 Chong, Y.C. 386, 397
 Christensen, J.M. 237
 Christensen, V. 4, 8, 10, 21-23, 27
 Christiansen, H.E. 57, 58
 Chua, T.E. 115, 117, 119
 Cillauren, E. 264, 265
 Clarke, M.E. 190, 197, 200
 Claro, R. 12, 17, 147, 148, 205, 215, 239, 242, 243
 Claro, R.M. 197, 198, 201
 Clavijo, I.E. 166, 172
 CMFRI (Central Marine Fisheries Research Institute) 110, 117
 Cochran, W. 52, 53, 58
 Cohen, D.M. 414
 Coleman 317
 Coleman, F. 4, 189, 414
 Coleman, F.C. 307
 Coleman, R.M. 31, 41
 Coleman, S.E. 30, 42
 Colin, P.L. 6, 7, 10, 29, 39, 41, 166, 172, 198-201, 204, 307, 317, 319, 321, 322, 323, 377, 399, 406, 409, 411, 413, 414
 Collins et al. 1977-1982 off SC 51 17
 4 1.3 253 82 314
 Collins, L.A. 138, 174, 175, 180, 187, 190, 307
 Collins, M.R. 2, 4, 12, 44, 52, 59, 61, 62, 68, 72, 86, 151, 158-160, 162, 245, 267, 278, 308, 309, 317, 322, 323, 335
 Contreras, M. 2, 3, 20, 26, 27, 29, 76, 164, 202, 205-207, 211, 214, 215, 242, 355, 358
 Cooper, S.G.C. 149
 Corpuz, A. 237
 Cousseau, M.B. 57, 58
 Craik, G.J.S 77, 83
 Crispin, D.A. 90, 91
 Crocker, R.A. 197, 200, 237
 Crowder, C. 187
 Crowder, L.B. 6, 10
 Crowther, J.R. 162
 Cruz-Romero, M. 324, 325, 330
 Csirke, J. 164, 172, 355, 359
 Csirke, S. 57, 58
 CSIRO (Commonwealth Scientific and Industrial Research Organisation) 299
 Cuellar, N. 4, 12, 44, 52, 59, 61, 72, 86, 245, 267, 278, 335
 Cupka, D.M. 200
 Curio, E. 252, 253
 Cury, P. 238

- Cushing, D.H. 326, 330
- Davis, C.D. 162
- Day, J.W., Jr. 18
- Dahl, J. 187
- Dall, W. 377
- Dalzell, P. 240, 264, 265, 300, 302
- Dalzell, P.J. 238
- David, N. 164, 173
- Davies, C.R. 6, 8
- Davis, C.D. 162
- Davis, D.H.S. 257, 265
- Davis, T.L.O. 199, 200, 240
- Davis, W.P. 165, 172
- Day, J.W., Jr. 12, 18
- Dayton, P. 6, 10
- de León , M.E. 356, 359
- DeMaria, D. 197, 199, 317, 322
- de Matos, A.P. 396, 398
- De Menezes, M.F. 237
- De Moraes, N.U.A. 139, 147, 148
- de Sousa, M.J.B. 139, 148
- De Silva, D.P. 12, 17
- Déniel, C. 20, 28, 75, 76, 204, 400
- Dennis, G.D. 44, 49, 172
- Denton, E.J. 251, 253
- Deshmukh, V.M. 107, 111, 117
- Devanesan, D.W. 110, 117
- deVlaming, V.L. 176, 187
- Dhokia, H.K. 119
- Dias, J.K. 159, 162
- Dias, R.K. 162
- Díaz, I. 46, 48, 49
- Díaz-Ruiz, S. 4, 12, 43, 44, 46, 48, 49, 278, 325
- Dickey, B. 321
- Dixon, R.L. 63, 65-67, 72
- Dizon, L.B. 9, 236
- Djabali, F. 240
- Dodson, J.J. 49
- Doherty, P.J. 3, 4, 7, 9, 10
- Doi, M. 383, 384
- Doi, T. 20, 27, 206, 207, 215, 242, 325, 330
- Domeier, M.L. 4, 189, 190, 197-201, 319, 323
- Dominguez Rivas, F. 29, 41
- Dos Santos, E.P. 139, 147, 148
- Douglas, J. 197, 201
- Drennon, C.L. 240
- Druzhinin, A.D. 238
- Duray, M. 115, 118
- Dustan, P. 76, 83
- Ebanks, G.C. 2, 39, 42, 150, 159, 364, 366, 368, 377
- Ebenezer, I.P. 118
- Ebersole, J.P. 44, 50
- Ecklund, A.M. 319, 322
- Edwards, A. 118
- Edwards, R.R.C. 154, 157, 237, 240, 290-292, 299-303
- Edwards, S.V. 87, 91
- Ehrhardt, N.M. 5, 337, 340, 342, 349, 360
- Eklund, A.M. 308, 322
- El-Musa, M.M. 164, 172
- Eldridge, P.J. 200
- Eleby, B. 91
- Elizarov, A.A. 355, 359
- Emata, A.C. 378
- Erdman, D.S. 197, 198, 200
- Erdmann, M.V. 8, 9
- Erhardt, H. 197, 198, 200
- Erhardt, N.M. 245, 351
- Erzini, K. 164, 172, 241
- Espino, E. 324, 325, 330
- Espinosa, L. 57, 58, 240-242
- Eullaran, B. 383
- Evermann, W. 190, 197, 200
- Ezzat, A.A. 241
- Fable, Jr., W.A. 240
- Fahay, M.P. 414
- Fan, K.C. 290, 302
- Fange, R. 252, 253
- FAO (Food and Agriculture Organization) 379, 384
- Fenner, D.P. 44, 49
- Fenoglio, C.M. 397
- Ferreira, B.P. 2, 6, 9, 10, 241
- Ferreira de, M. 237
- Figueroa, M. 6, 10, 74, 83
- Filatova, N.A. 238
- Findley, L.T. 165, 173
- Fine, J.C. 39, 41, 364, 377
- Finlayson, D.M. 154, 157

- Finucane, J.H. 175, 180, 187
 Fischer, W. 52, 57, 58, 61, 65, 66 72, 95,
 116, 117, 138, 148
 Fitzhugh, G.R. 176, 187
 Flugel, R.M. 386, 397
 Fonteles-Filho, A.A. 137, 139, 145, 147-
 149, 237, 243
 Foreman, T. 159, 162
 Formación, S.P. 12, 17
 Fournier, D. 164, 173
 Fowler, A.J. 3, 7, 9, 10
 Fowler, H.W. 165, 172
 Fox, W.W., Jr. 5, 8, 44, 48, 75, 76, 82,
 278, 288, 308, 322
 Freeberg, M.H. 362
 Friedlander, A. 75, 82, 83
 Froese, R. 3, 8, 9, 234, 235
 Fuentes Castellanos, D. 20, 40, 243
 Fuentes, D. 20, 26, 27, 203, 206, 211, 214,
 215
 Futch, R.B. 240

 Gabe, M. 41
 Gabrie, C. 172
 Gade, H. 139, 141, 148
 Gaertner, D. 53, 58
 Gapasin, R.S.J. 379, 384
 García, A. 324, 325, 330
 García, C. 356, 357, 359
 García, E. 44, 49
 García, F. 211, 215
 Garcia, L.M.B. 379, 384
 Garcia, S. 255, 265
 García-Abad, M.C. 46, 48
 Garcia-Arteaga, J.P. 241, 242, 243
 Garcia-Cagide, A. 242
 Garcia-Moliner, G. 7, 10, 319, 323
 Garduño-Andrade, M. 245, 350, 360
 Garnet 148
 Garrity, B. 321
 Garzon, J. 48
 Gaut, V.C. 147, 149, 197, 198, 200
 Gavaris, S. 342, 349
 Gayanilo, F.C., Jr. 2, 9, 12, 17, 141, 148,
 166, 172, 220, 228, 229, 231, 234,
 235
 Gesteira, T.C.V. 139, 140, 145-149, 237,
 238
 Gil, C. 336
 Gill, H.S. 219, 236
 Gilmore, R. G. 314, 317, 319, 320, 322
 Ginés, H. 52, 58, 332, 336, 359
 Giron, E. 327, 330
 Gladfelter, E.H. 44, 48, 49
 GMFMC (Gulf of Mexico Fisheries
 Management Council) 86, 91, 175,
 187, 340, 349, 343
 Godcharles, M.F. 82, 83, 240
 Goeden, G.B. 238
 Gold, B.D. 91, 240
 Gold, J.R. 86, 90
 Gomez, E. 238
 Gómez, G.J. 44, 51, 52, 57, 58, 138, 331
 Gonzalez, A. 327, 330
 González-Cano, J. 8, 26, 27
 Gonzalez, J.K. 46, 48, 49
 González, L. 267, 276
 Gonzalez, L.W. 138, 147-149
 González, M.E. 20, 27, 205, 216, 243
 González, P.D. 29, 30, 34, 36, 39, 41, 42,
 206, 216, 242
 González y De la Rosa, M.E. 245, 250
 Goodyear, C.P. 175, 187, 321, 322, 340,
 342, 349, 400, 414
 Gopal, C. 119
 Gopalan, V.K. 154, 157
 Gopinath, K. 107, 114, 117
 Gotshall, D.W. 245, 253
 Grandperrin, R. 171, 172, 236
 Grassé, P.P. 105
 Grigg, R. 239
 Grimes, C.B. 63, 65-67, 72, 146-148, 175,
 184, 187, 198, 200, 236, 352, 353,
 354, 383, 384
 Grimes, P.W. 251, 253
 Grosslein, M.D. 61, 72
 Grossman, G. 176, 187
 Grundy, M. 157
 Guardiola, M. 57, 58, 242
 Guderian, M. 157
 Guerrero, R.D. 9
 Guitart Manday, D. 366, 377
 Gulland, J.A. 206, 217, 255, 265, 303, 325,
 330, 340, 342, 349
 Gundermann, N. 237
 Guzmán, E. 206, 207, 216, 242

- Guzmán, R. 331
 Guzmán, R.A. 51
- Haimovici, M. 159, 160, 162, 239
 Halas, J.C. 76, 83
 Hall, N. 302
 Halver, J.E. 374, 377
 Handy, S. 321
 Han-lin, L. 238
 Hanshaw, B.B. 29, 40
 Hanson, A.J. 139, 149
 Haridas, C. 118
 Harper, D. 75, 83
 Harris, D.A. 7, 9
 Harris, S. 200
 Hashem, M.T. 241
 Hastings, P.A. 241
 Hatcher, A.I. 48, 50
 Hawke, J.P. 190, 200, 383, 384
 Heck, K.L. 48, 49
 Heemstra, P.C. 3, 9, 111, 117, 118, 120-127, 220, 235
 Heller, E. 165, 173
 Henderson, R.J. 374, 377
 Heng, H.H. 384
 Hernández, D.F. 238
 Hettler, W.F. 159, 162
 Hilge, V. 12, 17
 Higuchi, M. 115, 119
 Hilborn, R.Y. 255, 257, 264, 265, 291, 292, 300-303, 351, 353, 354
 Hildebrand, S.F. 165, 169, 172
 Hinde, P. 60, 73
 Hioki, S. 199, 201
 Hixon, M.A. 4, 8, 9
 Hoar, W.S. 253
 Hobson, E.S. 40, 41
 Hochachka, P.W. 91
 Hoenig, J.M. 164, 172
 Hoesse, H.D. 165, 169, 172
 Holden, M.J. 52, 58
 Holling, C.S. 325, 330
 Holt, S.J. 141, 148, 164, 172, 219, 220, 228, 235, 342, 349
 Hood, P.B. 309, 314, 315, 321, 322
 Horn, M.H. 251, 253
 Horn, M.W. 251, 253
 Hornell, J. 112, 117
- Hosillos, L.V. 9, 236
 Hostetter, E.B. 241
 Houde, E.D. 401, 414
 Houston, W. 300, 302
 Howard, N. 264, 265
 Howe, G.E. 162
 Hsi-Chiang, L. 238
 Hudson, J.H. 76, 83
 Huguenin, J.E. 117
 Hulley, R.B. 76, 83
 Hunter, J.R. 175, 176, 180, 187
 Huntsman, G.R. 63, 65-67, 72, 160, 162, 200, 239, 241, 308, 322
 Hureau, J.C. 42, 165, 173
 Hussain, N. 115, 117
 Hyslop, E.J. 12, 17, 32, 41
- Ingham, J.P. 288
 Ingles, J. 237, 238
 Isaac, V.J. 2, 9
 Iverson, E.S. 76, 82, 83
 Ivo, C.T.C. 138, 139, 140, 146-149, 238
- Jaap, W.C. 76, 77, 83
 James, P.S.B.R. 106, 115, 117
 Jayasankar, P. 112, 117
 Jernakoff, P. 290, 300, 302
 Job, T.J. 117
 Joel, J.J. 118
 Johannes, R.E. 8, 9, 238
 John, C.C. 114, 118
 John, M.E. 109, 115, 118, 119
 John, V. 118
 Johnson, A.G. 138, 174, 176, 187, 190, 239
 Johnson, G. 302
 Johnson, G.D. 317, 322, 400, 413, 414
 Jones, A.C. 27, 82, 240
 Jones, J.A. 77, 83
 Jones, R.J. 314, 317, 319, 320, 322
 Jones, S. 114, 118
 Jordán, D.E. 44, 49
 Jordan, D.S. 190, 197, 200
 Jory, D.E. 76, 82, 83
 Joseph, A. 118
 Joseph, K.M. 107, 109, 110, 115, 118
 Joseph, P.J. 107, 109, 118
 Ju, D.R. 238

- Juárez, L. 214
 Juarez Fernandez, M. 366, 377
 Juario, J.V. 115, 118, 383
- Kagwade, P.V. 107, 111, 117
 Kailola, P.S. 300, 303
 Kangrong, C. 368, 385
 Karrer, C. 165, 173
 Kasim, H.M. 117
 Kawaguchi, K. 267, 275, 276
 Kedidi, S.M. 237
 Keener, P. 317, 322, 400, 413, 414
 Keim, C.P. 138, 174, 190
 Kendall, A.W., Jr. 400, 414
 Kenny, J.S. 139, 149
 Kerr, S.R. 255, 265
 Kerstitch, A.N. 165, 173
 Kiefert, A. 321
 Kimbrell, C.A. 175, 187
 Kimmel, J.J. 165, 172
 Kindinger, J.L. 76, 83
 King, D.W. 396, 397
 Kitalong, A.H. 240
 Kleinow, K.M. 84
 Klima, E.F. 20, 27, 29, 41
 Knott, D.M. 60, 61, 73
 Kobayashi, D. 264, 265
 Kocher, T.D. 87, 91
 Koenig, C.C. 4, 6, 29, 189, 204, 307, 308,
 317, 321, 322, 399, 106, 409, 411,
 413, 414
 Kohno, H. 115, 118
 Kostlan, E. 238
 Koudil, M. 240
 Krishnamoorthi, B. 107, 111, 117
 Krishnapillai, S. 107, 111, 117
 Krulisch, L. 84
 Kumaran, M. 114, 118
 Kurisaka, S. 139, 148
- Labisky, R.F. 82, 83, 238
 Lablache, G. 237, 241
 Lai, H.L. 238, 290, 302
 Lai, H.C. 115, 119
 Lal Mohan, R.S. 114, 118
 Laloe, F. 53, 58
 Landless, P.J. 118
 Lane, E.D. 2, 150, 159, 364
- Lanjumin, L. 6, 9, 115, 118
 Laplace, J.A. 39, 41, 239, 317, 322
 Lara-Domínguez, A.L. 11, 12, 18, 26, 44,
 190, 215
 Lárez, A. 61, 266
 Laroche, W.A. 6, 29, 190, 200, 204,
 399, 413, 414
 Lasker, R. 187
 Latu, T. 264, 265
 Lazard, J. 236
 Le Bail, J. 29, 41
 Lee, E.S. 115, 118
 Lee, H.B. 384
 Lee, J.U. 241
 Lee, R.F. 251, 253
 Lefkowitz, J.H. 397
 Legault, C.M. 5, 245, 337, 340, 342, 349,
 351, 360
 Legendre, M. 236
 Leis, J.M. 46, 48, 49
 Leonce-Valencia, C.O. 243
 Leong, R.J.H. 175, 180, 187
 Leslie, P.H. 257, 265
 Levi, D. 164, 172
 Levy, J. 82
 Lewis, S.M. 44, 49
 Leyland, G.G. 300, 303
 Lidz, B.H. 76, 83
 Lim, L.C. 383, 384
 Lima, F.R. 139, 145, 147, 149, 239
 Linares, G. 359
 Lincoln 148
 Link, G.W., Jr. 192, 200, 310, 322
 Lipsky, P.E. 397, 398
 Liu, D.C. 290, 302
 Liu, H.C. 238, 240, 290, 302
 Lo, N.C.H. 175, 180, 187
 Lokani, P. 264, 265
 Longhurst, A.R. 2, 9, 220, 236
 López, G. 171
 Lou, D.C. 6, 10
 Loubens, G. 238
 Lovell, T. 374, 377
 Low, R.A. 61, 72
 Luckhurst, B.E. 8, 48, 49, 277, 278, 279,
 280, 283, 288
 Lutz, R.A. 157
 Lyons, W.G. 76, 83

- MacDonald, P.D.M. 164, 172, 206, 216
 McErlan, A. 237
 Macewicz, B.J. 175, 176, 187
 Machado, I. 355, 359
 Machowski, D.J. 4, 12, 44, 52, 59, 72, 86,
 245, 267, 278, 335
 Maclean, J.L. 9, 236
 McPherson, G.R. 237, 240
 Macuitl, C. 4, 12, 43, 49, 278, 325
 Madan, M. 114, 118
 Madrid, J. 327, 330
 Maldonado Montiel, T. 35, 41
 Maling, D.H. 78, 83
 Manickchand-Dass, S. 2, 9, 15, 17, 147,
 149, 240
 Manickchand-Heileman, S.C. 1, 8, 137-
 139, 147, 149, 159, 190, 243
 Manooch, C.S., III 15, 17, 29, 41, 63, 65-
 67, 72, 82, 83, 147, 149, 151, 157,
 159, 160, 162, 164, 165, 167-169,
 171, 172, 173, 206, 216, 238-240,
 241, 243, 342, 349
 Maravilla, A. 379
 Marcano, L.A. 44, 51, 138, 331
 Marcano, R. 336
 Marciewicz, D. 321
 Margalef, R. 57, 58, 359
 Marking, L.L. 159, 162
 Márquez, M. 336
 Marsh, Jr., J.A. 238
 Marshall, R.H. 30, 42
 Mason, D.L. 15, 17, 65, 72, 82, 83, 149,
 165, 167-169, 171, 173, 239, 243
 Masuma, S. 6, 9
 Matheson, R.H., III 65, 66, 72, 239, 241
 Mathew, G. 114, 118
 Mathew, K.J. 107, 111, 117
 Mathews, C.P. 206, 217, 238, 240
 Mathews, C.V. 154, 157
 Mathis, P. 321
 Matos, D. 165, 171
 May, R.M. 265
 McClain, J. 187
 McClanahan 251, 253
 McCleave, J.D. 49
 McErlean, A.J. 75, 83, 319, 322
 McFarland, W.N. 44, 50, 192, 200
 McFarlane, G.A. 2, 8, 152, 157, 159, 162,
 231, 234
 McGovern, J.C. 60, 61, 72
 McLoughlin, K. 302
 McManus, J.W. 10
 Meek, S.F. 165, 169, 172
 Mees, C.C. 241, 254, 255, 264, 265
 Mehailia, A. 240
 Melo, A.M. 239
 Mendizabal, D. 20, 27, 206, 207, 215, 242
 Mendoza, F. 203, 216
 Mendoza Rodríguez, I. 29, 41
 Mendoza, J.J. 61, 266
 Menezes, M.F. de 139, 145, 147, 149
 Menon, M.D. 107, 109, 116, 118
 Menzel, D.W. 173, 278, 288
 Merino, M. 204, 214, 216
 Mesdouze, J.P. 190, 197, 198, 199, 201
 Metzelaar, J. 169, 172
 Mexicano-Cíntora, G. 12, 15, 17, 18, 30,
 35, 40, 41, 204-206, 208, 215, 216,
 243
 Meyer, A. 87, 90, 91
 Meyer, J.L. 44, 49
 Meyers, S. 165, 171
 Mikail, M.Y. 241
 Miller, G.C. 60, 72
 Miller, S.L. 44, 50
 Milon, W. 6, 10
 Minton, R.V. 190, 200, 383, 384
 Miranda, J.R. 238
 Mitchell, M.E. 82, 83, 240
 Mito, S. 115, 119
 Miyamoto, G.T. 240
 Moe, M.A., Jr. 29, 36, 40, 41, 76, 82, 83,
 191, 192, 115, 118, 200, 204-206,
 216, 239, 310, 321, 322, 400, 414
 Mohamed Kasim, H. 111, 115, 116
 Mohamed, M.I.H. 238
 Mohr, E. 219, 236
 Mohsin, A.K.M. 238
 Mommsen, T.P. 91
 Monroy, C. 243
 Monroy-Garcia, M.D.C. 245, 350, 360
 Moore, C.M. 82, 83, 238
 Moore, E.A. 241
 Moore, R.H. 165, 169, 172
 Morales-Nin, B. 241

- Moran, D. 86, 91
 Moreau, J. 3, 9, 10, 220, 228, 231, 236
 Moreno, S. 355
 Moreno, V. 2, 3, 20, 26, 27, 29, 76, 164,
 202, 205-207, 211, 214, 215, 216,
 242, 355, 358
 Morgan, G.R. 10, 17, 164, 172, 173, 206,
 216, 217, 231, 236, 237, 330
 Moser, H.G. 414
 Moussac, G. de 241
 Muchsin, I. 302
 Muhlia, A. 20, 27, 207, 207, 213, 216, 242
 Mukundan, C. 107, 111, 115, 117
 Muller, R. 245, 253
 Mullin, K. 349
 Munro, J.L. 1, 3, 4, 9, 10, 11, 13, 15, 17,
 19, 28, 43, 44, 48, 49, 51, 57-59, 74,
 76, 80, 84, 85, 92, 96, 106, 137, 140,
 147, 149, 150, 158, 163, 164, 167,
 172, 173, 174, 189, 197, 198, 200,
 201, 202, 206, 216, 218, 236-239,
 242-244, 254, 266, 276, 277, 289,
 307, 319, 322, 324, 331-333, 336,
 337, 350, 355, 360, 363, 378, 385,
 399
 Munroe, T.A. 241
 Murawski, S.A. 362
 Murphy, M.D. 82, 83, 240
 Murray, P.A. 241
 Murray, S. 187
 Murty, V.S. 114, 118
 Muthiah, C. 107, 111, 117
 Muthu, M.S. 115, 117
 Naamin, N. 302
 Nagelkerken, W.P. 76, 80, 83, 238
 Nair, K.N.V. 118
 Nammalwar, P. 106
 Nance, J. 5, 340, 360
 Narayana Rao, K.V. 115, 117
 Nath, G. 264, 265
 Nayar, K.N. 117
 Nazario, A. 171
 Neill, J.R. 104, 105
 Neill, W.H. 49
 Nelson, R.S. 147, 149, 165, 167-169, 171,
 173, 175, 176, 187, 239, 243, 342,
 349
 Newman, S.J. 2, 6, 9
 Newton, G. 302
 Nichols, S. 340, 342, 344, 346-349
 Nieland, D.L. 245, 253
 Nielsen, J. 42
 Nikolsky, G. 57, 58
 Ninan, T.V. 107, 110, 118
 Ninnis, C. 199
 NMFS (National Marine Fisheries Service)
 317
 Núñez, E. 49
 Nygaard, M.H. 251, 253
 Obregón, M.H. 356, 359
 O'Connor, M. 235
 Ogburn, N.J. 379
 Ogden, J.C. 44, 48-50
 O'Hop 190
 Oleachea, A. 204, 216, 242, 356, 359
 Olsen, D.A. 39, 41, 242, 317, 322
 Ommanney, F. 237
 Oomen, V.P. 107, 109, 111, 116, 118
 Opic, P. 92, 95
 Orbach, M.K. 6, 10
 Ordaz, D. 205, 216
 Ostrowski 383
 Outerbridge, L. 288
 Owens, S. 321
 Paabo, S. 87, 91
 Padrón, G. 34, 36, 39, 40, 42, 206, 207,
 217, 243
 Paez, J. 240
 Palazon, J.L. 147, 149
 Palko, B.J. 44, 49
 Pannella, G. 151, 154, 157
 Paperna, I. 396, 398
 Paprocki, C. 187
 Parker, J.D. 90, 91
 Parker, R.O., Jr. 160, 162
 Parks, W. 317
 Parrish, J.D. 40, 41, 48, 49, 61, 72, 165,
 173, 252, 253
 Parsons, G. 157
 Parsons, J.E. 39, 42, 364, 366, 368, 377
 Patton, J.C. 91
 Pauly, D. 1-4, 6, 8-13, 15, 17-19, 21-23,
 27, 28, 43, 51, 59, 74, 85, 92, 96,

- 106, 137, 140, 141, 148-150, 158, 163, 164, 166, 167, 171-173, 174, 189, 202, 206-208, 216, 217, 218, 220, 228, 229, 231, 235, 236-238, 242-244, 254, 266, 277, 289, 300, 302, 307, 324-326, 330, 331, 337, 342, 349, 350, 355, 360, 363, 378, 385, 399
- Pech de Quezada, A.M. 40
- Pedrosa Tabio, B. 239
- Pellegrín, G.J., Jr. 340, 342, 344, 346-349
- Pender, P.J. 300, 302
- Peraza Menendez, J. 29, 41
- Perez, A. 242
- Pérez, O. 4, 12, 43, 278, 325
- Person-Le Ruyet, J. 103, 105
- Pet-Soede, L. 8, 9
- Petersen, C.G.J. 219, 236
- Pfund, R. 239
- Phares, P. 175, 187
- Philip, K.P. 107, 109, 118
- Phillip, D.A.T. 2, 137, 138, 149, 159, 190, 243
- Phleger, C.F. 251, 253
- Piedra, G. 197, 198, 200, 239, 242
- Pietsch, T.W. 90, 91
- Pili, H. 264, 265
- Pinckney, J.L. 68, 72
- Pinto, L. 171, 173, 240
- Pisté, J.C. 203, 216
- Pitcher, T.J. 8, 164, 172, 206, 216
- Plan Development Team 80
- Plaut, P. 336
- Pol, J. 355
- Pollard, D.A. 83
- Polovina, J.J. 4, 8, 10, 41, 44, 48, 49, 72, 82, 90, 148, 149, 157, 164, 169, 171-173, 187, 200, 216, 217, 229, 236, 240, 253, 255, 264, 265, 288, 292, 302, 322, 323, 354, 384
- Pope, J.G. 342, 349, 362
- Popper, D. 237
- Posada, J.M. 163, 164, 171, 205, 243
- Post, A. 173
- Potts, G.W. 42
- Potts, T. 82
- Powell, A.B. 369, 377, 410, 413, 414
- Powers, D.A. 5, 86, 87, 91
- Powers, J.E. 5, 8, 44, 48, 75, 76, 82, 278, 288, 308, 322
- Powles, H. 60, 61, 72
- Powles, H.W. 200
- Pozo, E. 57, 58, 243
- Prager, M.H. 2, 10, 140, 149
- Premalatha, P. 111, 118
- Premchand, B. 107, 109, 118
- Prince, E.D. 235
- Puerto, R. 211, 214, 215
- Pullin, R.S.V. 6, 8, 236
- Pulos, L.M. 235
- Quero, J.C. 165, 173
- Quevedo, R. 242
- Quinn, N. 365, 373, 377
- Quinn, T.P. 48, 49
- Quintana, M. 242
- Rafail, S.Z. 237
- Raffield, Mark 184
- Raffield, Mike 184, 187
- Ragonese, S. 164, 172
- Rahim, B. 115, 118
- Raitt, D.F.S. 52, 58
- Rajagopalan, M. 111, 119
- Rajagopalan, M.S. 115, 117
- Ralston, S. 8, 41, 44, 48, 49, 72, 82, 90, 148, 149, 157, 164, 167, 169, 171-173, 187, 200, 216, 217, 229, 231, 236, 238-240, 253, 264, 265, 288, 302, 322, 323, 354, 384
- Ramamirtham, C.P. 107, 111, 117
- Ramirez, E.M. 215
- Ramírez Rodríguez, M. 40
- Ramírez, Solís, M. 42
- Ramírez, T. 58
- Ramiro, M.E. 242
- Ramis, H.E. 29, 30, 41; 206, 216, 242
- Ramm, D.C. 289-291, 300, 302
- Ramos, J.R. 49
- Ramos-Miranda, J. 11, 44, 190
- Rand, A.S. 32, 42
- Randall, D.J. 253
- Randall, J.E. 9, 29, 39-41, 117, 118, 173, 165, 169, 235, 237
- Rangarajan, K. 111, 118, 119
- Rao, K.S. 119

- Rao, K.V. 116, 119
 Rasheed, M. 241
 Raoul 148
 Ray, G.C. 60, 65-67, 72, 197, 201
 Recksiek, C.W. 2, 10, 140, 149
 Reece, R. 187
 Reeson, P.H. 147, 149, 197, 198, 200
 Reigle, M. 171
 Remy, M. 187
 Render, J.H. 180, 188, 244, 245, 253, 351, 366
 Render, J. 187
 Reshetnikov, Y.S. 12, 15, 17, 147, 148, 197, 198, 201, 239
 Restrepo, V. 342
 Rhoads, D.C. 157
 Richards, A.H. 238
 Richards, W.J. 60, 72, 190, 192, 201, 414
 Richardson, L.R. 86, 90
 Richardson, S.L. 414
 Ricker, W.E. 10, 140, 149, 208, 216, 325, 326, 330
 Riepen, M. 8, 9
 Rihani Vales, C. 29, 41
 Rios, V. 27
 Rivas, L.R. 36, 41
 Rivera-Arriaga, E. 11, 16, 17, 44, 190
 Robert 148
 Roberts, C. 6, 10
 Roberts, C.M. 365, 373, 377
 Roberts, D.E., Jr. 319, 323
 Roberts, R.J. 396, 398
 Robertson, D.R. 276
 Robins, C.R. 60, 65-67, 72, 197, 201
 Rodrigo, J.X. 115, 117
 Rodríguez, H. 205, 206, 216, 243
 Rodriguez, W.T. 241
 Rodríguez Canché, L.G. 35, 38-41
 Rodriguez Castro, J. 243
 Rodriguez-Pino, Z. 15, 17, 197, 198, 201, 237
 Roff, D.A. 87, 91
 Rohlf, F. 52, 58
 Rohlf, F.J. 176, 188
 Roman, A. 6, 10
 Romero, M.C. 241
 Rongo, J.M. 17
 Rosado, M. 171
 Rosario, A. 6, 10, 165, 171
 Rosenberg, A.A. 206, 215, 216
 Rosenthal, A.S. 397, 398
 Rossouw, J. 265
 Roumillat, W.A. 159, 160, 162, 241, 309, 322
 Rubio, R. 57, 58, 242
 Ruiz, A. 327, 330
 Ruiz, F. 204, 214, 216
 Russ, G. 8
 Russ, G.R. 2, 6, 9, 10, 241, 278, 288
 Russel, B.C. 83, 300, 302
 Ryder, R.A. 255, 265
 Sadovy, Y. 6, 7, 10, 30, 41, 75, 83, 152, 165, 171, 193, 198, 199, 201, 279, 288, 307, 317, 319, 323, 364, 377
 Saeger, J. 237
 Saenz, M. 203, 216
 SAFMC (South Atlantic Fishery Management Council)/NMFS 86, 91
 Said, M.Z.M. 238
 Saif, M. 115, 117
 Saila, S.B. 2, 10, 140, 149
 Sainsbury, K.J. 290, 291, 292, 299, 300-303
 Sainsbury, L. 3, 10, 300
 Saksena, V.P. 190, 192, 201
 Salahange, P. 57, 58, 242
 Salas Márquez, S. 12, 15-18
 Salazar, A.R. 206, 207, 217, 243
 Saldanha, L. 173
 Sale, P.F. 45, 48, 49, 173, 276, 288
 Saloman, C.H. 240
 Salvat, B. 172
 Sambilay, V. 237
 Sambilay, V.C. 17
 Samoilys, M.A. 7, 9, 10
 Samuel, M. 238, 240
 Sánchez, J.A. 20, 27, 205, 207, 211, 214, 215
 Sánchez-Gil, P. 11-14, 17, 18, 44, 190, 238
 Sanders, M.J. 164, 172, 237, 241
 Sano, M. 44, 49
 Sargent, J. 374, 377
 SAS 176, 177, 188
 Schaefer, M.B. 217

- Schaeffer, D.O. 84
 Schirripa, M.J. 322, 414
 Schlieder, R.A. 309, 314, 315, 319, 322, 323
 Schnute, J. 164, 173
 Schoener, T.W. 32, 41
 Scholander, P.F 154, 157
 Schroeder, R.E. 65, 72, 197, 201
 Schubert, P. 302
 Scott, W.B. 95
 Scott-Denton, E. 5, 340, 360
 Secretaria de Pesca 17
 Sedberry, G. 317, 323
 Sedberry, G.R. 2, 4, 12, 44, 52, 59, 60-62, 67, 68, 72, 73, 86, 151, 158, 160, 162, 245, 267, 278, 308, 317, 323, 335
 Seijo, J.C. 20, 26, 27, 208, 211, 215, 217
 Seijo Gutiérrez, J.C. 20, 30, 40
 Selman, K. 176, 188
 Selvaraj, G.S.D. 111, 119
 Séret, B. 92, 95
 Sesewa, A. 264, 265
 Sevilla, M.L 29, 41
 Shah, A. 340, 342, 349
 Shaher, S. 237, 240
 Shanmugam, S. 119
 Shapiro, D.Y. 7, 10, 34, 36, 39, 40-42, 164, 173, 193, 201, 204, 214, 217, 308, 317, 319, 322, 323, 377
 Shapiro, D. 8
 Shareef, H. 241
 Sharp, B.I. 45, 48, 49
 Sharp, G.D. 355, 359
 Shedlock, A.M. 90, 91
 Shedlock et al. 1992 90
 Shepherd, J.G. 2, 10, 12, 17, 206, 217, 342, 349
 Sherman, K. 240
 Sherriff, A.T. 118
 Shevach, E.M. 397, 398
 Shinn, E.A. 76, 83
 Shomura, R.S. 264, 265
 Shroeder, R.E. 201
 Shroud, R.H. 90
 Shulman, M.J. 44, 48, 50
 Shultz, E.T. 44, 49
 Sierra, L.M. 242
 Silas, E.G. 107, 109, 111, 114, 116, 119
 Silva, J. 276
 Simmons, N. 288
 Singhagraiwan, T. 383, 384
 Sivaprakasam, T.E. 107, 110, 119
 Slack-Smith, R. 302
 Slaybaugh, S. 157
 Slaybaugh, S.T. 151, 157, 364, 377
 Sluka, R. 20, 74, 278, 364
 Smeby, Sigurd 184
 Smeby, Steve 321
 Smith, C.L. 29, 39, 42, 75, 80, 83, 165, 169, 173, 204, 217, 278, 288, 319, 322
 Smith, G.B. 44, 50, 165, 172, 308, 310, 322
 Smith, J.L.B. 117
 Smith, M.K. 238
 Smith, T.D. 219, 236
 Snedecor, G. 52, 53, 58
 Snider, T.G. III 176, 187
 Snodgrass, R.E. 165, 173
 Soesanto, V. 9
 Sokal, R.R. 52, 58, 176, 188
 Soletchnik, P. 190, 197, 198, 199, 201
 Solís-Ramírez, M.J. 20, 26, 30, 40, 203, 206, 215
 Solokov, V. 326, 330
 Somavanshi, V.S. 107, 110, 118, 119
 Somerton, D.A. 53, 58
 Soriano, M. 148, 141, 172
 Soundararajan, R. 115, 117
 Sparre, P. 2, 9, 12, 17, 149, 166, 229, 235, 241
 Spataro, L. 321
 Sport Fishing Institute 245, 253
 Springer, V.G. 75, 83, 190, 201
 Squire, L. 240
 Squire, L.C. 7, 10
 Sriramachandra Murty, V. 106
 Staples, D. 302
 Starck, W.A. 190, 192, 198, 201
 Starck, W.A. II 75, 83, 197, 201
 Starck, W.B. III 65, 72
 Stauch, A. 92, 95
 Steel, W.J. 48, 49
 Steen, J.B. 252, 253
 Stender, B.W. 61, 73, 317, 322, 413, 414
 Stevens, J. 302

- Stevenson, D.K. 20, 27, 30, 42
 Stewart, S. 321
 Stewart, V.N. 76, 83
 Stobutzki, I.C. 7, 10
 Stone, R.B. 160, 162
 Struhsaker, P. 60, 72
 Stubbs, D.L. 159, 160, 162, 309, 322
 Sua, T. 264, 265
 Sullivan, K.M. 20, 74, 82, 83, 278, 364
 Sulochanan, P. 107, 109, 118, 119
 Supranee C. 397
 Suquet, M. 190, 197, 198, 199, 201
 Suzuki, K. 199, 201

 Tagami, D.T. 240
 Talbot, F.H. 238
 Tan, K.S. 119
 Tan, S.M. 119
 Taniguchi, A.K. 401, 414
 Tanomkiat, T. 115, 119
 Tanoue, K.Y. 240
 Tapia, M. 46, 48
 Tashiro, J.E. 30, 42, 75, 82
 Tatum, W.M. 190, 200, 383, 384
 Taylor, R. 187
 Teng, S. 115, 117, 119
 Teng, S.K. 115, 119
 Teruya, K. 6, 9
 Terver, D. 103, 105
 Tezuka, N. 6, 9
 Thomas, W.K. 87, 91
 Thompson, B. 187
 Thompson, B. (pers. comm.). 184
 Thompson, B.A. 176, 187
 Thompson, R. 57, 58, 76, 80, 84, 147, 149,
 197, 198, 200, 201, 236–243, 276
 Thomson, D.A. 165, 173
 Thouard, E. 190, 197, 198, 199, 201
 Thumber, B.P. 119
 Tiroba, G. 264, 265
 Tobias, W. 75, 83, 165, 171
 Tocher, D.R. 374, 377
 Tomeny, S. (pers. comm.) 245
 Tomlinson, D. 302
 Took, I. F. 169, 173
 Torres-Lara, R. 12, 15–17, 18, 29, 41, 243
 Tortonese, E. 29, 42

 Touré, D. 96, 100, 105
 Treece, G.D. 190, 199, 200
 Trexler, J. 6, 10
 Troadec, J.P. 103, 105
 Trott, N. 288
 Tsay, R.Y. 290, 302
 Tsuda, R.T. 238
 Tucker, J.W. 8, 39, 42, 151, 154, 157
 Tucker, J.W., Jr. 151, 363–366, 368, 369,
 371, 373, 377, 410, 413, 414
 Tulua, S. 264, 265

 Uchida, R.N. 240
 Uchiyama, J.H. 240
 Ukawa, M. 115, 117, 119
 Ulanowicz, R.E. 21, 22, 27
 UNEP/IUCN (United Nations Environment
 Programme/International Union for
 Conservation of Nature and Natural
 Resources) 265
 Urbaneja, A. 52, 57, 58, 336

 Valdés, E. 34, 36, 39, 40, 42, 206, 207,
 217, 243
 Valdés, R. 2, 3, 20, 26, 29, 76, 164, 202,
 242, 355, 358
 Valdés-Alonso, R. 243
 Valero, E. 4, 19, 21, 23, 25, 27, 29, 75,
 204, 215
 Van der Knapp, M. 241
 Van Dolah, R.F. 60–62, 72, 73
 Van Furth, R. 398
 Van Oosten, J. 143, 149
 Van Sant, S.B. 2, 61, 151, 158, 160, 162,
 307, 308, 317, 323
 Varghese, C.P. 107, 109, 116, 118
 Venema, S.C. 237, 241
 Venkataraman, G. 119
 Venkataraman, R. 118
 Ventura, T.M. 396, 398
 Venugopal, K.M. 114, 118
 Victor, B.C. 48, 50
 Villablanca, F.X. 87, 91
 Villalobos, G.J. 46, 48
 Vivekanandan, E. 119
 Vizcaino, G. 52, 57, 58, 336
 Vodyanitskii, V.A. 253

- von Bertalanffy, L. 204, 217, 220, 235
- Wadie, W.F. 241
- Waheed, Z. 241
- Wakeman, J.M. 190, 199, 200
- Wallace, R.A. 176, 188
- Wallace, R.K. 32, 42
- Walters, C.J. 4, 6, 10, 265, 291, 300-303, 255, 257, 264, 291, 292, 351, 353, 354
- Walters, G.G. 217
- Waltz, C.W. 159, 160, 162, 241, 309, 322
- Ward, J. 165, 172, 364, 377
- Ward, J.A. 278-280, 283, 288
- Ward, R. 187
- Ward, W.C. 30, 41, 42
- Waschkewitz, R. 317, 323
- Waters, J.R. 308, 322
- Weatherley, A.H. 219, 236
- Weidie, A.E. 30, 41, 42
- Weiler, D. 41, 39, 317, 322, 377
- Weinstein, M.P. 48, 49
- Wenner, C.A. 60-62, 71-73, 159, 160, 162, 241
- Wenner, E.L. 60, 61, 73
- Wessel, J. 302
- West, G. 176, 188
- West, G.J. 199, 200, 240
- Wetherall, J.A. 141, 149, 164, 169, 171, 173, 229, 236
- Wheeler, J. 237
- Whitehead, P.J.P. 42, 117
- Wicklund, R. 199, 201
- Williams, D.B. 386
- Williams, D.M. 4, 9, 48, 50
- Williams, D.McB. 2, 6, 9, 164, 165, 172, 173, 237
- Williams, J.L. 190, 200
- Williams, H.A. 238
- Williams, T.D. 190, 199, 200
- Williams, T.P. 2, 10
- Willing, R.S. 300, 302
- Wilson, A.C. 87, 91
- Wilson, C.A. 188, 244, 245, 253, 351, 366
- Wirtz, P. 317, 323
- Wolf, K. 394, 397, 398
- Wolf, N.G. 44, 50
- Wolstenholme, G.E.W. 235
- Wong, M. 326, 330
- Woodburn, K.D. 190, 201
- Woodley, C.M. 4, 44, 61, 85
- Woodward, P.N. 151, 363, 368, 377
- Wootton, R.J. 42
- Worms, J. 238
- Worthington, D.G. 3, 10
- Wright, A. 238
- Xiao, Y. 289
- Ximenes, M.O.C 139, 145, 147, 149, 243
- Yañez-Arancibia, A. 11-14, 17, 18, 26, 44, 46, 48, 190, 215, 330
- Yeates, C. 148
- Yeh, S.Y. 238, 240, 290, 302
- Yongjia, Z. 368, 385, 386, 396, 398
- Young, I. 157
- Young, P. 237
- Zaret, T.M. 32, 42
- Zerguera, P. 359
- Zetina, C. 27, 205, 207, 217
- Zeyang, W. 368, 385, 386, 398
- Zimmerman, R.J. 48, 49
- Zupanovic, S. 29, 30, 34, 36, 39, 41, 42, 206, 216, 242

APPENDIX 3

Geographic Index

- Abidjan (Côte d'Ivoire, West Africa) 92
Africa 93
 West 92
African Continental Shelf 92
Agolega Islands 256
Alabama (USA) 87, 89, 338, 362
Alacranes Reef (Campeche Bank, Yucatán, Mexico) 31, 350, 352
Aldabra Group (Seychelles) 255, 256
Aldabra Islands (Seychelles) 256
Alleppey (Kerala, India) 108, 109, 114
Alligator Reef (Ridge) (Florida, USA) 77, 79, 81
Amazon (South America) 139
 River delta (Brazil) 52
American Samoa (Pacific Ocean) 225
Amirante(s) (Seychelles) 255
 Group 255, 256
 Plateau 256
Andaman Islands (India) 108, 115, 124
Andhra Pradesh (India) 107, 108, 112, 113
Angola (Africa) 93
Anjengo (Kerala, India) 114
Antilles (West Indies) 52, 65, 66
 Lesser Antilles 67
Apalachicola (Northwest Florida, USA)
 South of 307, 309
 Southeast of 309, 311
Asia
 Southeast 8, 115, 386
Arabian Sea (Indian Ocean) 108
Arafura Sea 289, 290-295, 297, 299-304
Arenas Key (Campeche Bank, Yucatán, Mexico) 350, 352
Atlantic (*Atlántico*) 165, 268, 270-274, 308, 309, 314, 317
 Coast 361
 East 94, 95
 East of Trinidad and Orinoco delta 266, 267
 East tropical 94
 Sector 269, 275, 276
 Southeastern 360
 Southeastern US 361
 Subarea 266-269, 275
 US coast 361
 West(ern) Atlantic 60, 65, 75, 86, 95, 196-198, 363
 Western Atlantic, tropical 75, 190
 West tropical 94
 Atlantic Ocean 138
 West central 332
Australia 223-227, 291
 Australian Fishing Zone (AFZ) 290, 300
 Northern 290
 Northern continental shelf 290
 Northern trawl fishery 289, 291-295, 298-301, 303, 305
 Sector 290
 Waters 290
Aves Islands [Bird Islands] (Venezuela) 336
Bahamas [Bahama Islands/ The Commonwealth of the Bahamas] 39, 52, 65, 66, 365
Bahía Magdalena 325
Baja California (Mexico)
 West coast of 325
Banjul (Gambia, West Africa) 98
Bangladesh 108
Barbados (Lesser Antilles, West Indies) 66
Barcelona (Venezuela) 53
Belize 198
Bengal, Bay of 108
Bengal, West (India) 107, 108, 112, 113
 Coast 112
Bermuda(s) [Bermuda Islands] 52, 66, 67, 165, 204, 221, 277, 278, 280, 281, 287, 288, 364
 Narrow shelf edge 283
 Platform 279, 280, 283, 288
 Seamount [*Marina*] 277, 278
Berry Islands (Bahamas) 365
Blanquilla Island, La (Venezuela) 53, 331,

- 332, 334, 335
- Boca de Apiza 326
- Boca Grande [South Channel]
 - Bar 191
 - Channel 191
 - Keys 191
- Bombay (India) 108, 123, 125
- Brazil 30, 52, 65-67, 86, 145-147, 226, 228, 267, 364
 - Northeast(ern) 66, 138, 139
 - South(ern) 63, 66
 - Southeastern 63, 65, 66
- Brest (France) 30
- Broome (Australia) 291
- Bulldog Bank 258, 259
- Buttonwood Cay (Belize) 197
- Caicos [Islands], West 196
- Cameron (Louisiana, USA) 247
 - South of Cameron 246
 - Coast 30
- Cameroon (West Africa) 93
- Campeche (Mexico) 205
 - Shelf 29
- Campeche Bank [*Banco de Campeche*]
 - (Yucatán, Mexico) 11, 20, 28-31, 34, 37, 40, 63, 147, 202-204, 206-213, 350-353, 355-358
 - East 39
 - Eastern part 350, 352
 - North 352
 - Northeastern part 350
 - West 39
 - Western side 350, 351
- Campeche, Gulf of 65
- Campeche Sound [*Sonda de Campeche*]
 - 11-16
- Continental Shelf 12
- Canaveral, Cape [*Cañaveral, Cabo*] (Florida)
 - 59-61, 63-65
- Cancun Island 30
- Cannanore (India) 108, 109
- Cape Fear (North Carolina, USA) 61, 62, 64
- Cape Hatteras (North Carolina, USA) 30, 60
- Cape San Blas 312
- Caribbean 30, 40, 44, 57, 66, 86, 138, 147, 197, 276
- Caribbean Sea (Atlantic Ocean) 30, 45, 53, 138, 166, 332, 364
- Carolina(s) (USA) 46, 66
 - North 52, 59, 60-62, 64-67
 - South 61, 65, 67, 309, 364
 - Middle shelf off 66
 - Shelf edge off 66
- Carpentaria, Gulf of 290, 291, 302
- Casamance River [Kasamansa] (Sénégal, Africa) 97, 98
 - North 97
- Cay Bokel 197
- Cayman Islands [*Islas Caimán*] (Caribbean Sea) 39, 150, 151
- Celestún (Yucatán, Mexico) 31, 38, 351
- Central America
 - Shelves 138
- Channel Patch Reef 77, 80
- Charleston (South Carolina, USA) 159
- Chavara 114
- China 8, 225, 385, 386
- Coche Island (Venezuela) 53, 332
- Cochin (India) 108, 114, 123, 125
- Coetivy Island (Seychelles) 256
- Colima (West Central Mexico)
 - Coast 325
 - State of 325
- Colombia (South America) 66
- Colombia Lagoon (Cozumel, Quintana Roo, Mexico) 45
- Columbus Channel 138
- Comoros [Comoro Islands] (Mozambique Channel) 256
- Conch Reef (Ridge) (Florida, USA) 74, 77-79, 81
- Congo (Central Africa) 93
- Constant Bank (Mahé Plateau, Seychelles) 258, 259
 - Continental 198
 - Continental habitats 198
- Coral Sea (Pacific Ocean) 291
- Correira 264
- Correira Bank [*Banco Correira*] (Mahé Plateau, Seychelles) 259, 261-264
- Cosmoledo Group (Seychelles) 255, 256
- Costa Rica (South Central America)
 - East coast 197
- Côte d'Ivoire [Ivory Coast] (West Africa) 93, 103

- South of the coast of 94
- Cozumel (Quintana Roo, Mexico)** 45
 - Coral reef system 44-47
 - Reef(s) 43
 - System 44
- Cuba** 15, 29, 30, 57, 66, 203, 222-227, 338
 - Southern coast 138
- Cubagua Island (Venezuela)** 53, 332
- Cumaná (Venezuela)** 52, 53, 332
- Curaçao (Island) [Netherlands Antilles]** 76, 221
- Dakar (Sénégal)** 97, 98, 100, 101, 104
- Darwin (Australia)** 291
- Davis Reef (Ridge) (Florida, USA)** 77, 78
- Demerara (Guyana)** 268
- Dhanushkodi (Tamil Nadu, India)** 112
- Djibouti [Jibuti] (East Africa)** 226
- Dry Tortugas** 196, 197
- Dwarka (Gujarat, India)** 123
- Eastern Tropical Pacific [*Pacífico Occidental Tropical*]** 324
- Egypt** 221
- Elbow Reef (Florida, USA)** 77, 78
- El Carmen (Terminos Lagoon, Mexico)** 12, 13
- English Cay (off Belize)** 196
- Esequibo [Guyana]** 268
 - River 268
- Farquhar (Seychelles)** 259, 261-264
 - Atoll 259, 264
 - Group 255, 256, 260
- Florida (USA)** 15, 59-62, 64, 65, 69-71, 75, 76, 82, 87, 89, 190, 197, 198, 204, 307-310, 312, 338, 362, 367, 414
 - Coast 362, 413
 - Deep water off 66
 - Gulf coast of 310, 312, 314, 318
 - Inshore waters 194, 195
 - Middle shelf off 66
 - North 400
 - North coast 65
 - Northeastern coast 75
 - Northwest 174, 177, 184, 309
 - Offshore waters 194, 195
 - Panhandle 399
- South Atlantic coast of 317**
- South(ern)** 65, 66, 160, 190, 191, 197
- Southwest 75**
- Waters 204**
- West coast 29, 36, 310**
- Western 30, 82, 191**
- Florida Keys (USA)** 75, 76, 79, 80, 82, 190, 310
 - North 310
 - Upper 74
- Florida Middle Grounds** 165, 312
- Flower Banks (Gulf of Mexico)** 165, 169
- Fortune Bank (Mahé Plateau, Seychelles)** 256, 258, 260, 263
- Freeport (Texas, USA)** 87, 89
- French Guiana (South America)** 52, 267
- French Polynesia (South Pacific)** 223
- French Reef (Florida, USA)** 77
- Gabon (West Africa)** 93
- Galapagos Islands [Tortoise Islands]**
 - (Ecuador; Pacific Ocean) 223
- Gambia (West Africa)** 98
 - North 97, 99-102
 - River 98
- Georgia (USA)**
 - Middle shelf off 65
- Georgia/Florida**
 - Border 66
 - Inner shelf depths 66
 - Middle shelf depths 66
- Ghana (West Africa)** 93
- Goa (India)** 107, 113
- Grand Cayman (Cayman Islands)** 151, 365, 366
- Grande Côte (Sénégal)** 97, 98, 100
- Great Barrier Reef (Queensland, Australia)** 6
- Grenada** 267, 268
- Guangdong (China)** 385, 386
- Guanica (Puerto Rico)** 166
 - Southwest 166
- Guianas [Guyana]** 30
- Guianas Plateau** 267, 275
- Guimaras Island (Central Philippines)** 378, 379
- Southwestern coast 379**
- Guinea-Bissau, Republic of** 97

- Guinea Conakry, Republic of 97
 Guinea, Gulf coast of [*Costas de Nueva Guinea*] (Atlantic Ocean) 92
 Guinea, Gulf of (Atlantic Ocean) 93
 Guiria (Venezuela) 332
 Gujarat (India) 107, 112, 113
 Gulf 308, 309, 314, 317, 320
 Coast 63
 Stream 65
 Stream waters 59
 Guyana [British Guiana] (South America)
 65, 66, 138, 266, 267
 Waters 266
 Havana (Cuba) 203
 Hawaii [Hawaiian Islands] (USA) 223, 224, 228
 Hawk Channel 76
 Hens-and-Chickens (Florida, USA) 77, 78
 Honduras (Central America) 39
 Continental shelf off Honduras 66, 138
 Hongkong [Hong Kong] (China) 8, 115, 380
 Iles Glorieuses 256
 India 106-108, 111, 115, 120-136, 225
 East coast 110
 West coast 110
 Indian Coast [*Costas de la India*] 106-108, 112
 Northeast 107
 Northwest 107, 115, 116, 127, 136
 Southeast 107, 115-116, 127, 136
 Southwest 107, 110, 114-116, 127, 136
 Indian Ocean 108
 Western 255
 Indonesia 115, 225, 291
 Indo-Pacific 300
 Insular 198
 Jacksonville (Florida) 62
 Jamaica (West Indies) 221-224, 227, 228
 Japan 115
 Joal (Sénégal) 97-100, 102
 Karnataka (India) 107, 108, 112-114
 Karumba (Australia) 291
 Katama Bay (Massachusetts, USA) 204
 Kayar (Sénégal) 98
 Keelakari 112
 Kenya [Kenya] (East Africa) 224
 Kerala (Southwest India) 107, 108, 112, 113, 115, 123-125, 127
 Coast 111, 112, 114
 Key Largo (Florida, USA) 80
 Key West (Florida, USA) 63, 75, 189, 191, 197
 Shallow inshore waters 189
 Offshore reef sites 189
 West 191
 Kilakkari (India) 108
 Kovalam 124, 125, 127
 Kulak Karai 126
 Kutch, Gulf of [Cutch, Gulf of] (India) 123
 Kuwait 115, 221, 222
 Laccadives: *see* Lakshadweep Islands
 Lakshadweep Islands 108, 114, 122-127
 La Digue (Mahé Plateau, Seychelles) 255
 La Tortuga (Venezuela) 53, 332
 Long Key (Florida, USA) 82
 Lookout, Cape [*Lookout, Cabo*] (North Carolina) 59-61, 63, 65
 Los Frailes Island (Venezuela) 53, 332
 Los Hermanos Island [*Islas Los Hermanos*] (Eastern Venezuela) 51, 53-56, 331, 332, 335
 Southwest 52
 Southeast 52
 La Parguera (Puerto Rico) 166
 Los Roques Archipelago (Venezuela) 168, 336
 Los Testigos Island (Venezuela) 53, 332, 334, 335
 Louisiana (USA) 245-247, 338, 362
 Luanda [Loanda] (Angola, Africa) 94
 Madagascar [Malagasy Republic] 256
 Madras [Tamil Nadu] (India) 108, 124, 125, 127
 Maharashtra (India) 107, 108, 112-114
 Mahé 255
 Mahé Plateau (Seychelles) 255, 256, 259
 Banks south of 256, 259

- South 260
- Southeast edge 259
- Malabar (Kerala, India) 123
- Malaysia 115, 224-226, 383
- Mandapam (India) 108, 112, 115, 124, 126
- Mannar, Gulf of (Indian Ocean) 108, 110-112, 115, 116
- Manzanillo 326
- Margarita Island [*Isla Margarita*] (Venezuela) 51-53, 268, 332
 - East(ern) (including Northern Trinidad) 266
 - East(ern) 266-275
 - Northwest 331
 - West(ern) 266, 268-275
- Marianas [Mariana Islands] 255, 264
- Massachusetts (USA) 65, 66
- Mauritania (West Africa) 97
- Mbour (Sénégal) 98, 101, 104
 - Coastal station 101
- Mérida (Yucatán, Mexico) 29, 30, 31, 205
- Mexican Caribbean [*Caribe Mexicano*] (Yucatán, México) 43, 44
- Mexico (México) 19, 26, 29, 30, 43, 211, 212, 221, 222, 224-227, 338, 350, 355, 356
 - West 329
 - West Central 325
 - West Coast 327, 328
- Mexico, Gulf of [*Golfo de México*] 5, 19, 20, 28-30, 45, 63, 65, 66, 75, 82, 86, 87, 138, 147, 169, 175, 190, 202-204, 308, 312, 337, 338, 340, 355, 361, 364, 400, 413
 - Eastern 29, 34, 36, 307, 308, 314, 319
 - Northeast(ern) 174, 177
 - Northern 90, 245, 400
 - Northern Coast 362
 - Southern 11, 12, 20, 28, 36
 - Mexican waters 400
 - Portion 67
 - US Gulf of Mexico 337, 340, 341, 345, 348, 349, 360, 400
 - US waters 400
 - Western coast 75
- Miami (USA) 197
- Middle Grounds 317
- North and West of 309
- Southwest 309
- Minicoy and Kulta (India) 127
- Mississippi (USA) 338, 362
- Monroe County (Florida, USA) 310
- Morocco (Africa) 221
- Nassau 366, 367
- New Caledonia (South Pacific) 221-226
- New Orleans (Louisiana, USA) 247
- Nicobar Islands (Bay of Bengal, India) 120-122, 125
- Nigeria (West Africa) 93
- N. Marianas 223-225, 228
- North America
 - East Coast 147
- North Keys 350, 352
- Northwest Shelf (Australia) 289-295, 299, 300, 301, 303
- Obslow Bay (North Carolina, USA) 67
- Okha Pt. (Sakhalin Oblast, Siberia, Russian Federation) 123
- Orange Beach (Alabama, USA) 87, 89
- Orchila Island, La (Venezuela) 336
- Orinoco (Venezuela) 139, 268
 - Delta 266
- Orissa (India) 107, 108, 112, 113
- Pacific
 - Eastern 165
 - South 8
- Pakistan 108
- Palau (Pacific Ocean) 225
- Palk Bay (India) 108
- Palmas, Cape 94
- Panama 66
- Panama City, Florida 87, 89, 175
- Papua New Guinea 221-227
- Paria, Gulf of [*Paria, Golfo del*] (Atlantic Ocean) 53, 138, 332
 - Peninsula 138
- Pensacola (Florida, USA)
 - Southeast of 317
- Peru (South America) 325
- Petite Côte (Sénégal) 98, 100, 101
- Philippines [*Filipinas*] 115, 222, 225, 226, 378-382, 383

- Central 378, 379
- Pickles Reef (Florida, USA) 77, 78
- Pigeon Point 138
- Platte Island (Seychelles) 256
- Platte Plateau (Seychelles) 256
- Pondicherry (India) 107, 108, 113, 127
- Ponnani (India) 108, 109, 114
- Port Hedland (Western Australia) 291
- Praslin (Seychelles) 255
- Progreso (Yucatán, Mexico) 30, 31, 38
- Providence (Seychelles) 259
 - Group 255, 256, 260
 - Island 256
- Puerto Real (Terminos Lagoon, Mexico) 11, 13, 15
 - Inlet 13
- Puerto Rico (West Indies) 15, 39, 166, 223, 226, 227
 - Southwest coast 165
 - Southwestern 164, 166, 168
 - Shelf edge off 168, 170
- Punta Jorobada 166
- Quilon (Kerala, India) 108, 114, 125
 - Southwest of 109
- Quintana Roo (Yucatán, Mexico) 43
 - Coastal region 44
- Recife, Brazil 30
- Riley's Hump (Dry Tortugas, Florida) 196, 199
- Rio de Janeiro [Guanabara Bay] (Brazil) 204
- Rio Lagartos 31, 38
- Roxo, Cape 97
- Rufisque (Sénégal) 98-100
- Sable, Cape 312
- Saint Lucia (West Indies) 223
- Sangomar Peninsula 97
- Saya de Mahla Bank 256
- Sea Mount '20' (Mahé Plateau, Seychelles) 259
- Sea Mount '25' (Providence/Farquhar, Seychelles) 258, 259
- Sénégal (West Africa) 96, 98, 103, 104, 221
- Sénégalese 103
 - Continental shelf 96, 97
- Waters 103
- Seychelles 221, 223, 224, 226, 254-256, 263
 - Remote banks 255
 - Island groups 255
 - Waters 254, 255
- Sherbro Island (Sierra Leone, West Africa) 92
- Sierra Leone (West Africa) 93
- Singapore 115, 383
- Small Constant Bank (Mahé Plateau, Seychelles) 259, 261, 263
- Sola Island (Venezuela) 53, 332
- Southern America
 - Continental shelf 139
 - Shelves 138
- South Atlantic Bight (USA) 60
- Sri Lanka (Indian Ocean) 108
- Sta. Fe (Venezuela) 53, 332
- St. Ann, Cape 92
- St. Louis (Sénégal) 98, 100, 104
- St. Marks (Florida, USA) 309
- St. Petersburg (Florida, USA) 310
- St. Thomas (U.S. Virgin Islands) 373
- Surinam [Suriname] 52, 66, 267
- Taiwan [Formosa] 115, 226
- Tamil Nadu (India) 107, 108, 112, 113
 - Coast 112
- Tampa (Florida, USA)
 - West 307, 308, 311
- Telchac Puerto 31, 38
- Tennessee Reef (Florida, USA) 77, 79
- Términos Lagoon [*Laguna de Términos*]
 - (Southern Gulf of Mexico) 11-13, 16, 20, 30
 - Eastern inlet 12
 - Western inlet (El Carmen) 12
- Texas (USA) 87, 89, 90, 338, 362
 - Coast 30, 362
- Thailand (Southeast Asia) 115, 383
- Three Points, Cape (West Africa) 94
- Three Sisters (Florida, USA) 77
- Timor Sea (Atlantic Ocean) 289-296, 299-304
- Tobago 139, 268
 - Northwest
 - Coast 139

- Continental shelf and slope 139
- Travancore (Kerala, India) 123, 124
- Trinidad 53, 66, 138, 268, 332
 - East 138
 - Continental shelf 138
 - Shelf edge 138
 - North coast 138, 139
 - Northeast continental shelf and slope 139
 - Northeastern coast 138
 - Northern 266, 275
- Trinidad and Tobago (Atlantic Ocean) 15, 137-139, 145-147, 226, 267
- Trivandrum (Kerala, India) 124
- Tunisia (North Africa) 222, 224, 227
- Turks and Caicos 196
- Tuticorin (Tamil Nadu, India) 108, 112, 124, 125, 127
- United States (of America) 74, 75, 86, 175, 198, 221-228, 338, 351, 361
 - Atlantic coast of the US 175
 - Continental shelf 175
 - Eastern 30
 - East coast 361
 - Exclusive Economic Zone (EEZ) 338
 - Southeastern 59, 61, 66, 147, 175, 308, 361
 - Coastal areas 60
 - Continental shelf 60
 - Live bottom 60
 - Lower shelf 60
 - Open shelf 60
 - Shelf edge 60
 - Upper slope 60
 - Southern 86
 - Southern Atlantic coast 138, 159
- Uruguay (South America) 66
- Vanuatu (Pacific Ocean) 223-225, 228
- Venezuela (South America) 52-56, 66, 138, 147, 224, 268, 332
 - Central marine province 268
 - Eastern 51, 331, 332
 - Northeastern 266, 267, 275
- Venezuelan Caribbean 336
- Virgin Islands (US) 39, 221-224, 373
- Vishakhapatnam (Andhra Pradesh, India) 124, 126
- Vizhinjam (India) 124, 127
- Wadge Bank (India) 108-110, 112, 114-116
 - Northeast region 116
- West Central Atlantic Ocean 332
- West Indies 204
- Winyah Bay (South Carolina, USA) 67
- Wizard Reef (Providence/Farquhar) 259
- Yemen 221, 222, 226
- Yoff (Sénégal) 101
 - Coastal station 102
- Yucatán Peninsula (México) 15, 28-31, 45, 138, 353
 - Continental shelf 66, 203-205
 - Central-Eastern End 20
 - North coast 29
 - Northern 29
 - North(ern) continental shelf 19-21, 25
 - Northern shelf 21, 23
 - Shelf 12
 - Peninsula 338
 - Northeastern continental shelf 355
 - State 350
- Zhanjiang (China) 386
- Zhejiang Province (China) 292

APPENDIX 4

Species Index^a

- Acropora cervicornis* 44
Acanthurids 110
Acanthurus lineatus 238
Acanthus armatus 253
Acropora palmata 44, 76
Actaea acantha 37
Aethaloperca rogaa 114
Agaricia spp. 76
 Agaricia agaricites 44
Alazán 325
Alepes sp. 305
Algae 76, 80
Alpheus sp. 37
 Alpheus armatus 37
Ambassis 110
Amphibians 84
Anadara notabilis 37
Anchovy 187
Annelids 25
Anthias squamipinnis 319, 323
Anthiinae 319
Aphareus rutilans 223
Aphareus sp. 114
Apolectus niger 305
Apriom sp. 114
 Apriom virescens 110, 223
Apsilinae 223
Apsilus dentatus 223, 228
Argentina silus 253
Argopecten gibbus 37
Argyrops spinifer 306
Argyrosomus sp. 306
Ariidae 294-297, 299-301, 303-306
Ariomma indica 289, 305
Ariommataidae 305
Arius thalassinus 305
Arius felis 362
Artemia sp. 363, 365, 369, 371, 372,
 375
Atlantic croaker 361, 362

Balistes sp. 334
Balistids 60
- Biajaiba* 17, 58, 148, 201, 237, 239, 242,
 243 see *Lutjanus synagris*
Blue runner 246
Bluefish 246
Bluegill 397
Bonaci gato 242 see *Mycteroperca tigris*
Brachionus plicatilis 365
Brachyura 40
Brachyrans 33, 40
Brine shrimp 365 see *Artemia* sp.
Brevoortia patronus 362
Butterfish 294-297, 299-301, 303-305 see
 Trichiuridae
 Gulf 362

Caballerote 239, 242 see *Lutjanus griseus*
Cabrilla 241 see *Epinephelus labriformis*
Calamus sp. 20, 334 see Porgies
 Calamus nodosus 205, 206
Callidactylus sp. 37
Callinectes sp. 37
 Callinectes similis 362
Carangidae 290, 294-297, 299-301, 303-
 306
Carangooides chrysophrys 305
Carangooides gymnostethus 305
Carangooides humerosus 305
Carangooides malabaricus 305
Carangooides uii 305
Caranx sp. 334
 Caranx bucculentus 305
 Caranx cryos 246
Carassius auratus 365
Carcharinidae 306
Carcharhinus duossumieri 306
Carideans 11
Carpilius corallinus 37
Catfish, hardhead 362
Caulolatilus sp. 334
Centrolophidae 305
Centropristes 200, 322
 Centropristes striata 158-162, 241
Cephalopholis 29

^aExcludes the species in the list from p. 120-136.

- Cephalopholis argus* 114
Cephalopholis cruentata 221
Cephalopholis fulva 221, 227, 277
Cephalopholis hemistiktos 221
Cephalopods 111, 253
Cethorinus maximus 229
Chanos chanos 384
Cherna americana 242, 359 see
Epinephelus morio
Cherna criolla 242, 377 see *Epinephelus striatus*
Choerodon sp. 306
Choerodon cephalotes 306
Choerodon schoenleinii 306
Cichlidae 9, 231, 236
Cod 90
Rock 9, 117-119, 236 see
Epinephelus tauvina
Colpophyllia natans 76
Comber, painted 241
Coney 74, 76, 83, 280, 282, 284, 286 see
Cephalopholis fulva; Epinephelus fulvus
Copepods 363, 365, 372, 373 see
Tigriopus japonicus
Copperbellies 320, 321
Coral 80, 109
Soft 191
Crabs 25, 58, 107, 110, 111, 371, 373
Fiddler 365
Iridescent swimming 362
Lesser blue 362
Longspine swimming 362
True 33, 40 see Brachyurans
Crassostrea gigas 365
Creole fish 163, 165, 167, 243, 277, 280,
282, 285, 286 see *Paranthias furcifer*
Crustaceans 11, 16, 37, 38, 40, 61, 361
Decapod 33, 40
Natant 37
Reptant 33, 37
Ctenochaetus striatus 238
Cumaceans 111
Cutlass fish 362
Cuttlefish 294
Cynoscion arenarius 362
Cyprinidae 365
Cystivirus 386
Damselfish 10
Dasyatidae 306
Dendrogyra cylindrus 44
Diagramma pictum 305
Diplectum formosus 237
Diploria spp. 76
Diploria strigosa 44
Dolphin 365
Dover sole 187
Echinoids 37
Ehu 238 see *Etelis carbunculus*
Engraulis mordax 187
Ephippididae 306
Epialtus bituberculatus 37
Epinephelinæ 9, 117, 118, 164, 218, 220,
221, 236
Epinepheline 41
Groupers 75
Serranids 400
Epinephelus 29, 42, 107, 204, 277, 279,
306, 402, 411
Epinephelus adscensionis 221
Epinephelus aeneus 96, 97, 103-
105, 221, 238, 241
Epinephelus akaara 115, 119
Epinephelus alexandrinus 105,
241, 323
Epinephelus amblycephalus 115
Epinephelus areolatus 107, 109-
111, 114, 221
Epinephelus bleekeri 110, 114,
115
Epinephelus chlorostigma 109,
111, 112, 114, 221, 386
Epinephelus coioides 221, 306
Epinephelus costae 221
Epinephelus cruentatus 80, 82
Epinephelus cyanopodus 221
Epinephelus diacanthus 109-112,
114, 221
Epinephelus drummondhayi 221,
227, 400
Epinephelus epistictus 114
Epinephelus fasciatus 107, 221
Epinephelus flavolimbatus 276
Epinephelus fulvus 80, 413

- Epinephelus fuscoguttatus* 221
Epinephelus guaza 96, 103, 105
Epinephelus guttatus 10, 39, 41,
 80, 82, 221, 227, 322, 328,
 334, 377, 400
Epinephelus hexagonatus 115
Epinephelus itajara 82, 221, 229
Epinephelus labriformis 221, 241
Epinephelus lanceolatus 107, 110
Epinephelus latifasciatus 107, 221
Epinephelus longispinis 110
Epinephelus maculatus 221
Epinephelus malabaricus 107, 110,
 112, 115, 386
Epinephelus marginatus 222, 227
Epinephelus merra 39, 222
Epinephelus moara 386
Epinephelus morio 28, 34, 36, 39,
 40, 80, 82, 204, 206, 207,
 217, 222, 239, 242, 243, 334,
 359, 402-408, 412-414 see
 Red grouper
Epinephelus morrhua 109, 114
Epinephelus multinotatus 222
Epinephelus mystacinus 280, 281
Epinephelus nigrilatus 222
Epinephelus niveatus 222, 227
Epinephelus ongus 222
Epinephelus polylepis 222
Epinephelus rivulatus 222
Epinephelus salmoides 117, 119
Epinephelus sexfasciatus 115, 222
Epinephelus striatus 39, 41, 80,
 82, 151, 154, 156, 157, 199,
 200, 222, 227, 242, 281, 288,
 322, 323, 377, 413, 414 see
 Nassau grouper
Epinephelus suillus 115
Epinephelus tauvina 109-112,
 114-117, 119, 222
Epinephelus undulatus 112
Etelinae 223
Etelis 72
 Etelis carbunculus 223, 228, 231,
 232, 238 see Ehu
 Etelis coruscans 223, 228
 Etelis oculatus 59, 63, 64, 223,
 241
- Euthynnus alletteratus* 246
Formionidae 295-297, 301, 303-305
Frog 90
Gag 158-162, 237, 239, 307, 308, 310-
 319, 321-323, 365, 414 see
 Mycteroperca microlepis
Gastropods 44
Geryon maritae 58
Glaucosoma burgeri 306
Glaucosomatidae 306
Gnathanodon speciosus 305
Gobies 373
Goldfish 365
Gonodactylus bredini 37
Gourami, snakeskin 398
Graysby 74, 76, 78, 80, 82, 83, 239, 280
Groundfish 72, 290
Groupers 83, 84 see *Epinephelus*
 American 42, 173, 414 see
 Epinephelus
 Black 74, 75, 78, 80, 82, 83, 277,
 279, 283, 284, 308, 310, 356,
 357 see *Mycteroperca bonaci*
 74
 Brownspotted 241 see *Epinephelus chlorostigma*
 Comb 97 see *Mycteroperca rubra*
 Coral 9, 117, 236
 Coral, leopard 9
 Dusky 90, 97, 104 see
 Epinephelus guaza
 Estuary 117, 119 see *Epinephelus salmoides; Epinephelus tauvina*
 Nassau 41, 42, 74-76, 80, 82, 83,
 150-152, 157, 198, 200, 277,
 279, 280, 287, 288, 319, 322,
 363, 364, 367-377, 414 see
 Epinephelus striatus
 Red 20-23, 25-30, 32, 34, 36, 38-
 42, 74-76, 80, 82, 83, 200,
 202-216, 239, 242, 280, 308,
 321, 322, 353, 355-359, 399-
 401, 411, 414 see
 Epinephelus morio
 Snowy 67, 82, 83, 238 see

- Epinephelus niveatus*
Tiger 201, 279, 281, 288, 323 see
 Mycteroperca tigris
Warsaw 82, 83, 243 see
 Epinephelus nigritis
White 97 see *Epinephelus aeneus*
Yellowfin 74, 198, 281 see
 Mycteroperca venenosa; M. venosum
Yellowedge 266, 267, 269, 271,
 274-276 see *Epinephelus flavolimbatus*
Yellowmouth 279, 281 see
 Mycteroperca interstitialis
Grunts 20, 23, 25, 50, 138, 331, 356 see
 Haemulidae; Haemulon spp.
 French 200
Gulf menhaden 362
Gymnocranius elongatus 306
Gymnothorax spp. 334
- Haemulids 49, 60
Haemulidae 149, 200, 290, 295-297, 299-301, 303-306, 332, 335
Haemulon aurolineatum 60
Haemulon melanurum 149, 187, 334 see
 Haemulidae
Haemulon flavolineatum 200
Hamoor 238
Hamra 238
Hapalogrenys kishinouyei 306
Harengula humeralis 32
Hemigaleidae 306
Hemipristis elongatus 306
Herring 23, 25, 374
 Lake 149
Heteractea ceratopus 37
Himantura uarnak 306
Hinds 9, 84, 117, 236, 276 see Serranidae
 Red 10, 74, 76, 83, 238, 239, 279,
 281, 284, 286, 319, 323 see
 Epinephelus guttatus
Rock 280 see *Epinephelus adscensionis*
 Speckled 239
Holocentrus ascensionis 334
Hoplopagrus 325
Huachinango 330 see *Lutjanus*
- campechanus*
Hypoplectrus 29
- Ichthyofauna 72
Invertebrates 361
Isochrysis 365, 372
 Tahitian 365, 371
Isognomon alatus 37
- Jacks 23, 25
Jewfish 82, 83, 198, 240, 331 see
 Epinephelus itajara
- Kalava 109, 118 see Rock cod
Katsuwonus pelamis 94
Kelp bass 237, 385, 386, 397, 398
- Labridae 306
Laevicardium mortoni 37
Lagodon rhomboides 411
Lane snapper 9, 12, 17, 63, 65, 72, 149,
 190, 197, 200, 201, 239, 240, 277,
 280, 282, 286, 287, 288 see *Lutjanus synagris*
Lates calcalifer 386, 397
Leptoseris cucullata 44
Lethrinidae 290, 294-297, 299-301, 303-306
Lethrinids 110
 Lethrinus spp. 289
 Lethrinus choeronyxchus 305
 Lethrinus fraenatus 305
 Lethrinus lentjan 294, 305
 Lethrinus nebulosus 305
 Lethrinus nematacanthus 305
 Lethrinus rubrioperculatus 238
Leucichthys artedi 149
Lizardfish 362
Lobopilumnus agassizii 37
Lobsters 25, 44, 107
Loligo spp. 295-297, 299-301, 304, 305
Lutjanids 41, 44, 46, 60, 63, 94, 107, 110,
 112, 114-116, 138, 147, 196, 198, 199,
 218, 355, 357, 383
Lutjanidae 44, 48, 50, 52, 60, 68, 72, 90,
 94, 95, 106, 107, 116, 149, 187, 189,
 198, 201, 218, 220, 223, 224, 229,
 231, 232-234, 237-239, 276, 281, 290,

- 295-297, 300, 301, 303, 304, 332, 333, 335, 354, 379, 384
Goldband 295-297, 299-301, 303-305
Red 289, 295-297, 299, 301, 303-305
Small 296, 297, 305
Lutjanus 20, 52, 59, 68, 90, 189, 197, 238, 241, 324, 325 see *Ocyurus*; Snappers
Lutjanus adetii 9, 224
Lutjanus agennes 92-94
Lutjanus altifrontalis 238
Lutjanus analis 43, 46, 57, 59, 63, 64, 192, 198, 224, 231, 356
Lutjanus apodus 43, 46, 47, 192, 198-110, 112, 224, 381, 383, 386
Lutjanus argentimaculatus 107, 110, 112, 224, 305, 378-384, 386
Lutjanus argentiventris 324, 325, 327-329
Lutjanus aya 239
Lutjanus bohar 114, 224
Lutjanus buccanella 57, 58, 59, 63, 64, 224, 228, 334, 335
Lutjanus campechanus 20, 27, 61, 63, 64, 85, 86-91, 138, 149, 159, 174, 175, 187, 190, 199, 200, 205, 216, 224, 228, 231, 239, 243, 244, 245, 253, 337, 338, 351, 356, 362, 384
Lutjanus carponotatus 225
Lutjanus chrysurus 192, 197-199
Lutjanus cyanopterus 43, 46, 192, 198, 225
Lutjanus dentatus 94
Lutjanus erythropterus 225, 305
Lutjanus fulviflamma 225
Lutjanus fulvus 107
Lutjanus gibbus 109, 114, 225
Lutjanus griseus 43, 46, 47, 59, 63, 64, 194, 195, 199, 200, 225, 231, 239, 242
Lutjanus guttatus 324, 327-329
Lutjanus goreensis 94
Lutjanus jocu 43, 46, 47, 192, 198, 199, 225
Lutjanus johnii 107, 115, 225, 305
Lutjanus kasmira 111, 114, 115, 119, 199, 201, 225, 231, 238
Lutjanus lutjanus 110, 225
Lutjanus mahogani 43, 46
Lutjanus malabaricus 107, 110, 112, 225, 228, 231, 241, 289, 290, 294, 305 see Red
Lutjanidae
Lutjanus monostigma 226
Lutjanus nebulosus 265
Lutjanus peru 324, 325, 327-330 see Huachinango
Lutjanus purpureus 59, 63, 64, 86, 137, 138, 141-147, 226, 228, 231, 243, 266, 267, 270, 273, 276
Lutjanus quinquelineatus 9, 226, 229
Lutjanus rivulatus 110, 112, 226
Lutjanus russelli 114, 115, 305, 386
Lutjanus sanguineus 107, 226, 238
Lutjanus sebae 115, 226, 231, 238, 305
Lutjanus synagris 9, 11-13, 15-18, 57, 58, 63, 148, 171, 200, 201, 226, 231, 237, 239, 240, 242, 243
Lutjanus vitta 107, 110, 226, 231, 232
Lutjanus vittus 199, 200, 240, 294, 305 see Small Lutjanidae
Lutjanus vivanus 54, 55, 56, 57, 59, 63, 64, 227, 241, 282, 334, 335
Lycodontys sp. 334
Lymphocystis 385, 390, 397
Lyretail 9, 117, 236
Mackerel 217
King 20, 23, 25
Spanish 349, 365
Macroalgae 373
Macrofauna, benthic 45
Macrocoeloma sp. 37
Macrocoeloma campptocerum 37
Macrocoeloma eutheca 37

- Madracis decactis* 44
Mahogany snapper 198 see *Lutjanus mahogani*
Mantis shrimp 362
Megalaspis cordyla 305
Menhaden 374
Menippe mercenaria 37
Mero 26, 27, 40, 41, 214-217, 242, 243
 see *Epinephelus morio*
Mérou 240 see *Epinephelus guaza*
Microalgae 371
Microcrustaceans 25
Micropogonias undulatus 361, 362
Microstomus pacificus 187
Milkfish 384
Millepora alcicornis 44
Minnows 365
Misty grouper 280, 281
Mithrax acuticornis 37
Mithrax forceps 37
Mithrax hispidus 37
Mithrax pleuracanthus 37
Mojarras 23, 25, 205, 216
Molluscs 25, 37, 38
Monacanthus hispidus 60
Montastrea spp. 76
 Montastrea annularis 76
Mugiloididae 50
Mullidae 295-297, 299-301, 303-305
Mutton snapper 63, 65, 72, 149, 190, 196,
 198, 199, 200, 239 see *Lutjanus analis*
Mycteroperca spp. 29, 277, 279, 283
 Mycteroperca bonaci 80, 222,
 281, 284, 310, 413
 Mycteroperca cidi 334
 Mycteroperca microlepis 222, 322,
 323, 413, 414
 Mycteroperca olfax 223, 241
 Mycteroperca phenax 223, 241,
 308
 Mycteroperca rubra 96, 97
 Mycteroperca tigris 199, 223, 242
 Mycteroperca venenosa 80, 223,
 227
Mysis 111

Nannochloropsis 365, 372
 Nannochloropsis oculata 365, 371

Nassarius hinia 37
Natantia 38
Nemipteridae 290, 294-297, 299-301,
 303-305
 Nemipterus spp. 289
 Nemipterus celebicus 305
 Nemipterus furcosus 294, 306
 Nemipterus hexodon 306
 Nemipterus virgatus 306
Newaiby 238

Octocorals 76
Octopus sp. 37
Octopuses 25, 373
Ocyurus chrysurus 17, 20, 43, 46, 47, 59,
 63, 64, 66, 200, 227, 228, 231 see
 Yellowtail snapper
Ophidiid fish 253
Oyster 363
 Pacific 365

Pagrus pagrus 149, 187 see Sparidae
Pagrus sedecim 162
Palaemonidae 37
Panopeus americanus 37
Paradicichthyinae 227
Paralabrax clathrus 237
Paranthias furcifer 167-170, 223
Parasitic trematodes 368
Pargo 48, 58, 148, 149, 237, 238, 243,
 239 see *Lutjanus analis*; *Lutjanus purpureus*
 Aleta negra 58 see *Lutjanus buccanella*
 Canané 17, 243 see *Ocyurus chrysurus*
 Cebal 149 see *Lutjanus analis*
 Colorado 276 see *Lutjanus purpureus*
 Criollo 239 see *Lutjanus analis*
 Del alto 58 see *Lutjanus vivanus*
 Ojo amarillo 58 see *Lutjanus vivanus*
 Parthenope agonus 37
Parupeneus pleurospilus 305
Penaeid shrimps 11, 16, 365, 372
Penaeus sp. 37
 Penaeus duorarum 365

- Penaeus duorarum notialis* 37
Peprilus burti 362
 Perches 108, 110, 112, 114, 115, 118 see
Epinephelus diacanthus
 Giant 118
 Sand 237
 Percoid fishes 60
 Phytoplankton 25, 103, 369
 Pigface breams 109, 110
 Pilchards 32
Pilumnus spp. 37
 Pilumnus dasypodus 37
 Pilumnus sayi 37
 Pinfish 362, 411
 Pink shrimp 365
Platax batavianus 306
Plectropomus leopardus 6, 9, 10, 223, 228
Plectropomus maculatus 9, 223, 306
Poecilia reticulata 229
Pogonias cromis 187
 Polychaetes 110
Polydactylus octonemus 17
Polyprion americanus 280, 282
Pomacentrus moluccensis 10
Pomacentrus wardi 10
Pomatomus saltatrix 246
 Porgies 20, 23, 25, 356 see *Calamus* spp.
 Longspine 361, 362
 Red 72, 158, 159, 161, 162 see
 Pagrus pagrus; Sparidae
Porites porites 44
Portunus spp. 37
 Portunus floridanus 37
 Portunus gibbesii 362
 Portunus sayi 37
 Portunus spinicarpus 362
 Portunus spinimanus 37
 Prawns 107, 110
 Priacanthidae 295-297, 299, 301, 303, 304,
 306
Priacanthus hamrur 306
Priacanthus tayenus 306
Pristipomoides 72
Pristipomoides aquilonaris 59, 63, 64
Pristipomoides argyrogrammatus 118
Pristipomoides auricilla 223, 228
Pristipomoides filamentosus 224, 228, 231,
 241, 255, 259, 262-265
Pristipomoides flavipinnis 224, 228
Pristipomoides freemani 59, 63, 64, 66
Pristipomoides macrophthalmalus 283
Pristipomoides multidens 224, 294, 305
 see Goldband Lutjanidae
Pristipomoides sieboldii 224
Pristipomoides typus 109-114, 224, 305
Pristipomoides zonatus 224, 228
Protonotaria diacanthus 306
Psenopsis humerosa 289, 305
Psenopsis humerosa 294 see Butterfish
Pseudotolithus senegalensis 105
 Queen conch 365
 Queen triggerfish 240
 Rabirubia 239, 242 see *Ocyurus chrysurus*
 Rachycentridae 294-297, 299, 301, 303,
 304, 306
Rachycentron canadus 306
Rastrelliger kanagurta 306
 Rays 295-297, 299, 301, 303, 304, 306
 Red bass 238 see *Lutjanus bohar*
 Red drum 253
 Reptantia 38
 Reptiles 84
Rhizoprionodon acutus 306
Rhizoprionodon porosus 334
Rhizoprionodon taylori 306
Rhomboplites aurorubens 59, 63, 149, 187,
 227, 228, 334, 335
 Rhyncobatidae 306
Rhynchosciurus djiddensis 306
 Rockfish 245, 253
 Rotifers 363, 365, 372, 373, 375
Rubia 17, 18 see *Lutjanus synagris*
 Sablefish 157
Salmo trutta 10
 Sandfish, belted 241
 Sardine 52, 333
Sardinella aurita 333
Saurida spp. 289, 306
 Saurida micropectoralis 306
 Saurida undosquamis 294, 306 see
 Synodontidae
 Scallops 365
 Scamp 308, 319, 241

Scaridae 306
Scarus ghobban 306
Sciaenidae 105, 295-297, 299, 301, 303, 304, 306
Sciaenops ocellatus 253
Scolopsidea 110
Scolopsis monogramma 306
Scomberomorus cavalla 20
Scomberomorus maculatus 349
Scombridae 295-297, 299, 301, 303, 304, 306
Scyllaridae 37
Sea fans 109
Seabass 172, 322, 384, 386, 397
 Black 158-162, 241 see
Centropristes
Seagrass 44
Seaweeds 369
Sebastodes 245, 253
Selar boops 305
Selaroides leptolepis 305
Sepiidae 295, 296, 297, 299, 301, 303, 304, 306
Sepia spp. 306
Seriolina nigrofasciata 306
Serranid 60, 104, 112, 114, 115, 199, 204, 218, 306, 319, 355, 357, 368, 377
Serranidae 9, 29, 48, 50, 52, 83, 84, 97, 105, 106, 117, 198, 201, 220, 221, 227, 229, 235-237, 241, 243, 276, 281, 290, 295-297, 299, 301, 303, 304, 308, 322, 331-333, 335, 364, 385, 399, 414
 see **Hinds**
Serranus 29
Serranus sciba 241
Serranus subligarius 241
Sesi 240, 242 see *Lutjanus bucanella*
Sharks 23, 25, 295, 296, 297, 299, 301, 303, 304, 306
 Hammerhead 90
Shrimps 5, 25, 360, 373
 Seabob 362
 Sugar 362
Siderastrea siderea 76
Siganidae 306
Siganus canaliculatus 115
Siganus fuscescens 306
Siganus javus 115

Sillago sihama 115
Snapper(s) 58 see *Lutjanidae*
 Black 281
 Blackfin 63, 66 see *Lutjanus bucanella*
 Blood 237 see *Lutjanus sanguineus*
 Brazilian 143
 Caribbean red 63, 66, 138, 149
 see *Lutjanus purpureus*
 Cubera 197 see *Lutjanus cyanopterus*
 Dog 196 see *Lutjanus jocu*
 Emperor red 237, 254 see
Lutjanus sebae
 Flamenco 325 see *Lutjanus guttatus*
 Gray 63, 65, 72, 189-196, 198-201, 237, 239, 277, 280, 287
 see *Lutjanus griseus*
 Grey 282, 285 see *Lutjanus griseus*
 Hawaiian 240 see *Pristipomoides filamentosus*
 John's 384 see *Lutjanus johni*
 Lunarejo 325 see *Lutjanus guttatus*
 Lane 200
 Mutton 200
 Queen 63, 66, 67, 241, 282, 283
 see *Etelis oculatus*
 Red 5, 23, 25-27, 59, 61-68, 70-72, 85, 86, 88, 90, 92-95, 137, 138, 147-149, 173, 174, 187, 176-186, 190, 200, 205, 239, 240, 243-250, 252, 253, 266, 267, 269, 270, 273, 275, 282, 325, 337-342, 344, 346-353, 360, 362, 378-384 see
Lutjanus
 Red eye 53 see *Lutjanus vivanus*
 Silk 63, 66, 283 see *Lutjanus vivanus*
 Southern 138
 Vermilion 59, 61-63, 64, 67-70, 72, 240, 266, 267, 269, 272, 275, 283 see *Rhomboplites aurorubens*
 Wenchman 283
 Yellow eye 51, 52 see *Lutjanus vivanus*

- Yellowtail 49, 63, 66, 187, 190,
 197, 200, 201, 239, 240, 277,
 279, 280, 282, 285, 287, 356,
 358 see *Ocyurus chrysurus*;
 Lutjanus ocyurus
Solenolambrus tenellus 37
 Sparidae 290, 295-297, 299, 301, 303,
 304, 306
 Sparids 60, 357
Sphyraena barracuda 334
Sphyraena putnamiae 306
 Sphyraenid 297
 Sphyraenidae 295-297, 299-301, 303, 304,
 306
 Sponges 60, 80, 191, 290
 Spot 362 *Leiostomus xanthurus* 362
 Squid 150, 152, 153, 294
Squilla spp. 362
Stenacionops furcata 37
Stenotomus caprinus 361
Stenotomus chrysops 60
Stenorhynchus seticornis 37
 Stomatopods 37, 38, 111
Strombus gigas 365
 Swordfish 253
Syphorus nematophorus 227
Synalpheus sp. 37
 Synalpheus brevicarpus 37
 Synodontid 297
 Synodontidae 290, 294, 295, 296, 297,
 300, 301, 303, 304, 306
Synodus foetens 362

 Tautog *Tautoga onitis* 241
 Teleosts 188
 Teraponidae 306
Terapon 110
 Terapon jarbua 306
Tetraselmis 372
Tetraselmis suecica 365

Thalassia testudinum 43, 44
Thunnus albacares 94
 Tilapia 9, 231, 236
 Tilefish 67, 365
Trachypenaeus spp. 362
 Trichiuridae 295-297, 300, 301, 303, 304,
 306
Trichiurus lepturus 294, 306, 362 see
 Trichiuridae
Trichogaster pectoralis 398
 Trout 9, 10, 23, 25, 83, 238, 241, 362
 Brown 10
 Coral 9, 10, 83, 238, 241 see
 Plectropomus leopardus
 Sea 23, 25
 Sand 362
 Tuna 92, 365
 Skipjack 94
 Yellowfin 92, 94, 217
 Tunny 246
 Turridae 37

Uca sp. 365

Variola louti 223
Vibrio 369
 Virus 397

 Wenchman 63, 65, 282, 283 see
 Pristipomoides aquilonaris;
 Pristipomoides macrophthalmus
 Yelloweye 63 see *Pristipomoides*
 freemani
 Whiting, sand 115
 Wreckfish 280, 282

Xiphias gladius 253
Xiphopenaeus kroyeri 362

 Zooplankton 25, 103, 369

Biology, fisheries and culture of tropical groupers and snappers.
F. Arreguín-Sánchez, J.L. Munro, M.C. Balgos and D. Pauly, Editors.
1996. ICLARM Conf. Proc. 48, 449 p.

TITLES OF RELATED INTEREST

FishBase 96: concepts, design and data sources. R. Froese and D. Pauly, Editors. 1996. ICLARM. 179 p. Distributed with one CD-ROM disk for US\$95 (airmail). Available free of cost for all collaborators of the FishBase Project. Available only from the FishBase Project, ICLARM.

Caribbean coral reef fishery resources. J.L. Munro, Editor. 1983. ICLARM Stud. Rev. 7, 276 p.

Baseline studies of biodiversity: the fish resources of Western Indonesia. D. Pauly and P. Martosubroto, Editors. 1996. ICLARM Stud. Rev. 23, 321 p.

Quantitative models of trophic interactions in Caribbean coral reefs. S. Opitz. 1996. ICLARM Tech. Rep. 43, 350 p.

Note on observations of daily rings on otoliths of deepwater snappers. F. Brouard, R. Grandperrin, M. Kulbicki and J. Rivaton. 1984. ICLARM Transl. 3, 8 p.

HOW TO ORDER

For book prices and more publication information, contact:

The Editor
ICLARM
MCPO Box 2631, 0718 Makati City, Philippines
Tel. nos. (63-2) 812-8641, 818-0466 ext. 110
Fax no. (63-2) 816-3183
E-mail: ICLARM@cgnet.com

Payment should be in US dollars by bankdraft or check (payable to ICLARM) from a US-based bank. We also accept payment through the American Express card.

Visit our homepage: <http://www.cgiar.org/iclarm/>