



THE UNIVERSITY OF QUEENSLAND
A U S T R A L I A

Biology, Taxonomy and Distribution of south-east Pacific Cartilaginous Fishes

Carlos Mario Bustamante Diaz

Bachelor of Science (Hon)



*A thesis submitted for the degree of Doctor of Philosophy at
The University of Queensland in 2014
School of Biomedical Sciences*

Abstract

Cartilaginous fishes (formerly Class Chondrichthyes) belong to an ancient, highly conserved taxonomic group. Despite the evolutionary success of the group, of which there are over 1,000 extant species, many are now threatened with extinction, regionally or globally, primarily as a result of human activities. The main reason for the susceptibility of these species is the *K*-selected life-history traits that characterise many species of cartilaginous fishes such as, slow growth, relatively late maturity, low fecundity and a low rate of potential population increase.

Cartilaginous fishes are generally predators that occupy the upper levels of marine food webs. They are naturally rare compared with other fishes, but have a vital role in the maintenance of marine ecosystem balance. Their biological characters make them highly susceptible to population depletion as a result of anthropogenic activity, including targeted fisheries, bycatch and habitat loss or modification. The life history strategy of cartilaginous fish species suggests the need for conservative management measurements that ensure sustainability with compatible fishery activities.

Cartilaginous fishes constitute an important component of the marine ecosystem in the south-east Pacific Ocean. Over 93 species of sharks, skates, rays and chimaeras inhabit Chilean waters and at least half of them are subjected to intense fishing pressure in a diverse range of fisheries. Many of these species are vulnerable to population collapse. Even though they are not directly targeted in commercial fisheries, they are caught as bycatch by longline, gillnet and trawl net fisheries within Chile's Exclusive Economic Zone. Limited biological information is available to assess the potential impacts that anthropogenic disturbance may produce in populations of cartilaginous fishes, and this thesis aims to improve our knowledge of the taxonomy, life history and fisheries of cartilaginous fishes commonly caught in Chilean waters.

The cartilaginous ichthyofauna in Chile was assessed through extensive surveys conducted in coastal artisanal, small to medium scale fisheries and larger semi-industrial oceanic fisheries. Here we review the taxonomy and fishery biology from a relatively basic level (checklist of living species, morphological descriptions and biology) towards complex conservation issues (distribution, habitat use and fishery mortality). However, these results represent the first attempt to quantify the abundance and distribution ranges of sharks, skates and chimaeras commonly caught along the Chilean coast. New biological and ecological data have complemented actual knowledge of cartilaginous fish dynamics in relation to fishing activity in the south-east Pacific Ocean.

As part of this thesis, three new species have been added to the Chilean cartilaginous fauna (Chapter 2): the spinetail mobula *Mobula japonica*, the eastern Pacific black ghostshark *Hydrolagus*

melanophasma and the thickbody skate *Amblyraja frerichsi*. The inclusion of these species improves identification methods of landing and fishery records. Each of these species addresses a different issue within the national fisheries context and in spite of none of these species is considered a ‘commercial resource’, all were obtained as bycatch arising from the targeting of other fishes.

The occurrence of sharks, skates, rays and chimaeras in Chile is revised and information on the functional biodiversity provided (Chapter 3). A review of the primary literature on cartilaginous fishes, together with new information suggests that 106 species occur in Chilean waters; comprising 56 sharks, 30 skates, 13 rays and 5 chimaeras. Ninety-three species were confirmed to be present through validated sighting and/or catch records from national fisheries and from fisheries-related research cruises of which 30 species were encountered rarely. Also, the cartilaginous fish community in the continental shelf and slope off Chile was described, based on abundance and species richness from 20 species (9 sharks, 10 skates and 1 chimaera) caught in a 3,500 km² trawl fisheries operation area.

Additionally, the reproductive biology of the three main elasmobranchs that are target species were reported (Chapter 4): yellownose skate *Zearaja chilensis*, shortfin mako *Isurus oxyrinchus* and blue shark *Prionace glauca*. In the case of *Z. chilensis*, 5,477 specimens were analysed from three localities in South Chile and in a similar effort, 1,241 *Isurus oxyrinchus* and 1,153 *Prionace glauca* were analysed from a single locality in North Chile. Despite the fact that these species are caught in two fisheries that use different fishing gear and fish different zones, all three species experience one concerning similarity: over 80% of the total catch comprise immature specimens. This trend may compromise the stock integrity if intrinsic vulnerability and probable long-life spans of cartilaginous fishes are considered. Consequences for the species’ survival and possible signs of a fishery collapse must be reviewed in the short-term by management authorities to ensure the sustainability these fisheries. In the case of the shortfin mako, a pupping, and possibly a nursery area in the fishing zone was found which increase the urgency of management, such as the introduction of a minimum catch sizes, conservative fishing quotas and delimitation of fishing areas.

Overall, the current thesis has expanded our knowledge of regionally important populations of cartilaginous fishes, and provides a biological baseline to define priorities for management and conservation.

Declaration by author

This thesis is composed of my original work, and contains no material previously published or written by another person except where due reference has been made in the text. I have clearly stated the contribution by others to jointly-authored works that I have included in my thesis.

I have clearly stated the contribution of others to my thesis as a whole, including statistical assistance, survey design, data analysis, significant technical procedures, professional editorial advice, and any other original research work used or reported in my thesis. The content of my thesis is the result of work I have carried out since the commencement of my research higher degree candidature and does not include a substantial part of work that has been submitted to qualify for the award of any other degree or diploma in any university or other tertiary institution. I have clearly stated which parts of my thesis, if any, have been submitted to qualify for another award.

I acknowledge that an electronic copy of my thesis must be lodged with the University Library and, subject to the General Award Rules of The University of Queensland, immediately made available for research and study in accordance with the *Copyright Act 1968*.

I acknowledge that copyright of all material contained in my thesis resides with the copyright holder(s) of that material. Where appropriate I have obtained copyright permission from the copyright holder to reproduce material in this thesis.

Carlos Bustamante

Publications during candidature

Conference abstracts

Bustamante, C. & Bennett, M.B. (2014). Fishing the youth: Sustainability of a pelagic shark fishery in a nursery area. Shark International conference, held during 2-6th June at the Southern Sun Elangeni-Maharani Hotel, Durban, South Africa.

Bustamante, C., Kyne, P.M. & Bennett, M.B. (2013). Comparative morphology of the egg cases of *Asymbolus analis*, *Asymbolus rubiginosus* and *Figaro boardmani* (Carcharhiniformes: Scyliorhinidae) from southern Queensland, Australia. Conference of the Oceania Chondrichthyan Society held on 19th and 20th September 2013 at Royal on the Park, Brisbane, Queensland, Australia.

Bustamante, C. & Bennett, M.B. (2012). Reproductive and fishery insights of two commercially exploited sharks, *Isurus oxyrinchus* (Rafinesque, 1810) and *Prionace glauca* (Linnaeus, 1758), in the south-east Pacific Ocean. International Postgraduate Symposium in Biomedical Sciences, 24-26th September 2012, The University of Queensland, Australia.

Bustamante, C. & Bennett, M.B. (2012). Reproductive and fishery insights of two commercially exploited sharks, *Isurus oxyrinchus* (Rafinesque, 1810) and *Prionace glauca* (Linnaeus, 1758), in the south-east Pacific Ocean. Australian Society for Fish Biology and Oceania Chondrichthyan Society Joint Conference and Symposium, 15-18th July 2012, Sebel Playford Hotel, Adelaide, South Australia.

Bustamante, C., Vargas-Caro, C. & Bennett, M.B. (2011). Redescription of the thickbody skate *Amblyraja frerichi* (Krefft, 1968) (Rajiformes: Rajidae) from south-east Pacific Ocean. SBMS 2011 International Postgraduate Symposium, 26-27th September 2011, The University of Queensland, Australia.

Bustamante, C., Vargas-Caro, C. & Bennett, M.B. (2011). Redescription of the thickbody skate *Amblyraja frerichi* (Krefft, 1968) (Rajiformes: Rajidae) from south-east Pacific Ocean. Workshop and Conference of the Oceania Chondrichthyan Society, 13-15th September 2011, Sea World Resort and Water Park, Gold Coast, Queensland, Australia.

Bustamante, C., Vargas-Caro, C., Acuña, E. & Lamilla, J. (2011). Redescripción de la raya de hondura *Amblyraja frerichi* (Krefft, 1968) (Rajiformes: Rajidae) en el sudeste del océano Pacífico. XXXI Congreso de Ciencias del Mar, Viña del Mar, Chile.

Bustamante, C., Vargas-Caro, C., Flores, H., Lamilla, J. & Bennett, M.B. (2011). Reproductive biology of *Zearaja chilensis* (Guichenot 1848) (Chondrichthyes: Rajidae) in the southeast Pacific Ocean. Workshop and Conference of the Oceania Chondrichthyan Society, 13-15th September 2011, Sea World Resort and Water Park, Gold Coast, Queensland, Australia.

Bustamante, C., Vargas-Caro, C., Oddone, M.C., Concha, F., Bennett, M.B. & Lamilla, J. (2011). Biología reproductiva de la raya volantín *Zearaja chilensis* (Guichenot, 1848) (Chondrichthyes: Rajidae) en el sureste del océano Pacífico. XXXI Congreso de Ciencias del Mar, Viña del Mar, Chile.

Concha, F., Oddone, M.C., Bustamante, C. & Morales, N. (2011). Description of the egg capsules of the yellownose skate, *Zearaja chilensis* (Guichenot 1848) and of the Roughskin skate, *Dipturus trachyderma* (Krefft & Stehmann 1974) (Rajiformes, Rajidae) off Chilean coast. VIII Encontro da Sociedaade Brasileira do Elasmobranquios, 07 a 12 de agosto. Instituto de Oceanografia da Universidade Fereral do Rio Grande, Rio Grande, Brasil.

Listed journals with editorial committee

Bustamante, C. & Ovenden, J.R. (2014) The complete validated mitochondrial genome of the silver gemfish *Rexea solandri* (Cuvier, 1832) (Perciformes, Gempylidae). *Mitochondrial DNA* (early online) DOI:10.3109/19401736.2014.898279

Bustamante, C., Vargas-Caro, C. & Bennett, M.B. (2014). Not all fish are equal: Functional biodiversity of cartilaginous fishes (Elasmobranchii and Holocephali) in Chile. *Journal of Fish Biology* (early view).

Vargas-Caro, C., Bustamante, C., Bennett, M.B., & Ovenden, J. (2014). The complete validated mitochondrial genome of the yellownose skate *Zearaja chilensis* (Guichenot 1848) (Rajiformes, Rajidae). *Mitochondrial DNA* (early online) DOI:10.3109/19401736.2014.945530

Bustamante, C., Vargas-Caro, C. & Bennett, M.B. (2014). Biogeographic patterns in the cartilaginous fauna (Pisces: Elasmobranchii and Holocephali) in the southeast Pacific Ocean. *PeerJ PrePrints* 2, e298v1 (accepted for publication in PeerJ). DOI: 10.7287/peerj.preprints.298v1

Bustamante, C. & Bennett, M.B. (2013). Insights into the reproductive biology and fisheries of two commercially exploited species, shortfin mako (*Isurus oxyrinchus*) and blue shark (*Prionace glauca*), in the south-east Pacific Ocean. *Fisheries Research* 143, 174–183

Bustamante, C., Kyne, P.M., & Bennett, M.B. (2013). Comparative morphology of the egg cases of *Asymbolus analis*, *Asymbolus rubiginosus* and *Figaro boardmani* (Carcharhiniformes: Scyliorhinidae) from southern Queensland, Australia. *Journal of Fish Biology* 83, 133–143. DOI:10.1111/jfb.12155

Bustamante, C., Couturier, L.I.E. & Bennett, M.B. (2012) First record of *Mobula japanica* (Rajiformes, Myliobatidae) from the southeastern Pacific Ocean. *Marine Biodiversity Records* 5, e48. DOI: 10.1017/S1755267212000310

Bustamante, C., Flores, H., Concha-Perez, Y., Vargas-Caro, C., Lamilla, J. & Bennett, M.B. (2012). First record of *Hydrolagus melanophasma* James, Ebert, Long & Didier, 2009 (Chondrichthyes, Chimaeriformes, Holocephali) from southeastern Pacific Ocean. *Latin-American Journal of Aquatic Research* 40, 236–242. DOI: 10.3856/vol40-issue1-fulltext-23

Bustamante, C., Lamilla, J., Concha, F., Ebert, D.A. & Bennett, M.B. (2012). Morphological characters of the thickbody skate *Amblyraja frerichsi* (Krefft 1968) (Rajiformes: Rajidae), with notes on its biology. *PLoS ONE* 7(6), e39963. DOI:10.1371/journal.pone.0039963

Bustamante, C., Vargas-Caro, C., Oddone, M.C., Concha, F., Flores, H., Lamilla, J. & Bennett, M.B. (2012). Reproductive biology of *Zearaja chilensis* (Guichenot 1848) (Chondrichthyes: Rajidae) in the southeast Pacific Ocean. *Journal of Fish Biology* 80(5), 1213–1226. DOI: 10.1111/j.1095-8649.2011.03164.x

Concha, F., Oddone, M.C., Bustamante, C. & Morales, N. (2012). Egg capsules of the yellownose skate *Zearaja chilensis* (Guichenot 1848) and the roughskin skate *Dipturus trachyderma* (Krefft and Stehmann 1974) (Rajiformes: Rajidae) from the south-eastern Pacific Ocean. *Ichthyological Research* 59, 323–327. DOI: 10.1007/s10228-012-0293-z

Lopez, S., Zapata-Hernández, G., Bustamante, C., Sellanes, C., & Meléndez, R. (2013). Trophic ecology of the dusky catshark *Bythaelurus canescens* (Chondrychthyes: Scyliorhinidae) in the southeast Pacific Ocean. *Journal of Applied Ichthyology* 29, 751–756. DOI: 10.1111/jai.12151

Publications included in this thesis

The following publications have been included into my thesis as per UQ policy (PPL 4.60.07 Alternative Thesis Format Options). Detailed contribution of all authors is described below as per the requirements in the UQ Authorship Policy (PPL 4.20.04 Authorship).

Chapter 2

Bustamante, C., Couturier, L.I.E. & Bennett, M.B. (2012) First record of *Mobula japonica* (Rajiformes, Myliobatidae) from the southeastern Pacific Ocean. *Marine Biodiversity Records* 5 (May 2012), e48.

<i>Contributor</i>	<i>Statement of contribution</i>
Bustamante, Carlos (Candidate)	Designed experiments (80%) Wrote the paper (70%)
Couturier, Lydie I. E.	Designed experiments (10%) Wrote and edited paper (20%)
Bennett, Michael B.	Designed experiments (10%) Wrote and edited paper (10%)

Bustamante, C., Flores, H., Concha-Perez, Y., Vargas-Caro, C., Lamilla, J. & Bennett, M.B. (2012) First record of *Hydrolagus melanophasma* James, Ebert, Long & Didier, 2009 (Chondrichthyes, Chimaeriformes, Holocephali) from southeastern Pacific Ocean. *Latin-American Journal of Aquatic Research* 40, 236–242.

<i>Contributor</i>	<i>Statement of contribution</i>
Bustamante, Carlos (Candidate)	Designed experiments (70%) Fieldwork sampling (40%) Wrote the paper (70%)
Flores, Hernán	Fieldwork sampling (20%)
Concha-Perez, Yhon	Fieldwork sampling (20%)
Vargas-Caro, Carolina	Fieldwork sampling (20%) Wrote and edited paper (10%)
Lamilla, Julio	Designed experiments (30%)
Bennett, Michael B.	Wrote and edited paper (20%)

Bustamante, C., Lamilla, J., Concha, F., Ebert, D.A. & Bennett, M.B. (2012) Morphological characters of the thickbody skate *Amblyraja frerichsi* (Krefft 1968) (Rajiformes: Rajidae), with notes on its biology. *PLoS ONE* 7(6), e39963.

<i>Contributor</i>	<i>Statement of contribution</i>
Bustamante, Carlos (Candidate)	Designed experiments (70%) Wrote the paper (70%)
Lamilla, Julio	Designed experiments (20%)
Concha, Francisco	Wrote and edited paper (10%)
Ebert, David A.	Wrote and edited paper (10%)
Bennett, Michael B.	Designed experiments (10%) Wrote and edited paper (10%)

Chapter 3

Bustamante, C., Vargas-Caro, C. & Bennett, M.B. (2014). Not all fish are equal: Functional biodiversity of cartilaginous fishes (Elasmobranchii and Holocephali) in Chile. *Journal of Fish Biology* (early view).

<i>Contributor</i>	<i>Statement of contribution</i>
Bustamante, Carlos (Candidate)	Designed experiments (70%) Wrote the paper (70%)
Vargas-Caro, Carolina	Designed experiments (10%) Wrote and edited paper (15%)
Bennett, Michael B.	Designed experiments (20%) Wrote and edited paper (15%)

Bustamante, C., Vargas-Caro, C. & Bennett, M.B. (2014). Biogeographic patterns in the cartilaginous fauna (Pisces: Elasmobranchii and Holocephali) in the southeast Pacific Ocean. *PeerJ PrePrints* 2, e298v1 (accepted for publication in *PeerJ*)

<i>Contributor</i>	<i>Statement of contribution</i>
Bustamante, Carlos (Candidate)	Designed experiments (70%) Fieldwork sampling (100%) Wrote the paper (70%)
Vargas-Caro, Carolina	Wrote and edited paper (10%)

Bennett, Michael B.	Designed experiments (30%)
	Wrote and edited paper (20%)

Chapter 4

Bustamante, C. & Bennett, M.B. (2013). Insights into the reproductive biology and fisheries of two commercially exploited species, shortfin mako (*Isurus oxyrinchus*) and blue shark (*Prionace glauca*), in the south-east Pacific Ocean. *Fisheries Research* 143, 174–183

<i>Contributor</i>	<i>Statement of contribution</i>
Bustamante, Carlos (Candidate)	Designed experiments (80%) Wrote and edited paper (80%)
Bennett, Michael B.	Designed experiments (20%) Wrote and edited paper (20%)

Bustamante, C., Vargas-Caro, C., Oddone, M.C., Concha, F., Flores, H., Lamilla, J. & Bennett, M.B. (2012) Reproductive biology of *Zearaja chilensis* (Guichenot 1848) (Chondrichthyes: Rajidae) in the southeast Pacific Ocean. *Journal of Fish Biology* 80, 1213–1226.

<i>Contributor</i>	<i>Statement of contribution</i>
Bustamante, Carlos (Candidate)	Designed experiments (50%) Fieldwork sampling (30%) Wrote and edited paper (60%)
Vargas-Caro, Carolina	Fieldwork sampling (20%) Wrote and edited paper (10%)
Oddone, Maria C.	Wrote and edited paper (10%)
Concha, Francisco	Wrote and edited paper (10%)
Flores, Hernán	Fieldwork sampling (30%)
Lamilla, Julio	Designed experiments (40%) Fieldwork sampling (20%)
Bennett, Michael B.	Designed experiments (10%) Wrote and edited paper (10%)

Contributions by others to the thesis

This Ph.D. thesis was undertaken as a result of a collaborative effort between Chilean National Commission for Scientific and Technological Research (CONICYT in Spanish) and The University of Queensland thought the Becas-Chile cooperative scholarship framework. The Chilean government, through the Fisheries Research Fund (FIP in Spanish), provided funds for different research projects where I was involved, and where indirectly data was collected as a collateral effort for the present thesis; proper acknowledgment to each project (and project leader) is mentioned in each related publication.

Additional data was collected through privately funded projects conducted by Universidad Austral de Chile. Julio Lamilla was the principal investigator in all those projects and as such was responsible for project conception. Students and staff of Elasmobranchs Laboratory (ELASMOLAB) from Universidad Austral de Chile and Shark Conservation Program (Programa de Conservación de Tiburones, PCT, in Spanish) provided support during fieldwork, specimens collection and assisted during sampling.

Carolina Vargas-Caro, Astrid Isla, Cynthia Diaz and Yhon Concha-Perez assisted in the dissection and processing of specimens in the laboratory. Pete Kyne, Dave Ebert, Francisco Concha, Lydie Couturier and Maria Cristina Oddone, reviewed and provided editorial comments and methodological support in some chapters. Michael B. Bennett reviewed and provided editorial comments on all chapters herein.

In all instances, however, I was the primary author and responsible for the preparation and writing of the chapters and/or publications herby included, including literature reviews and the collection of available information and data.

Statement of parts of the thesis submitted to qualify for the award of another degree

None.

Acknowledgements

I have to first and foremost acknowledge my parents for their unwavering encouragement and support. My most prized gift in life has been my education and without their selfless commitment. I'm confident that I would not be where I'm today, thanks for your sacrifice and unconditional love. An extension of this sacrifice belongs to my *Tita* who, with a high personal and economic cost, allowed and encouraged me, to start my grown-up life in Chile. I never will find a way to repay this great debt. Part of my work also belongs to my two brothers, who always have supported me in the dream's pursue. Last but not least, I never would find the strength to change my life without the love of Carolina, my wife. She found me in dark places and made me a better man. Her patience and advices will always enlighten my way.

The work would never have been conducted without the sacrifice of thousands of sharks, skates and chimaeras; who died in commercial fishing operations during 2004 and 2010. They gave me a reason, and the means to do my research. The following thesis proves that their death was not in vain and now we, as society, are a little bit closer to end this greedy, senseless slaughter.

I express immense gratitude to all the great scientists who have been on my path, sometimes providing new ones and even walking the road with me. I owe this thesis to Mike Bennett, who gave me the opportunity to realise my dreams and provide new ones. Also, I'm fully grateful for his English lessons and all my 'fancy' words belong to him. As a non-native English speaker, it's not easy to produce a manuscript of this magnitude, especially with all the spelling and grammar confusion made in Australia. Julio Lamilla and Alejandro Bravo taught me what the science means, and how we can do science in a simple daily-basis; they were in charge of my Academic early-life and without them, I would never had discovered and lived the scientific world. Jenny Ovenden, opens my eyes (and made me overcome my prejudices) to the genetics world. I never thought that the DNA was so amazing, thanks for the opportunity to learn from you. During this time, I have shared my opinions and I learned from the best (and have grown thanks to them): John D. Stevens, Enric Cortés, Peter Kyne, Will White, Dave Ebert, Gavin Naylor, and Peter Last.

This thesis could not have been carried out without the continuous help, support and encouragement from friends, family and colleagues that help me in silent and often unaware way.

Academic Supervision

Michael B. Bennett (The University of Queensland)

External and Internal Examiners

Jennifer R. Ovenden, Ian Tibbetts, Ulrike Siebeck, Kerstin Fritsches (The University of Queensland), Steven Taylor (Department of Fisheries, Government of Western Australia).

Financial Support

CONICYT–Becas Chile RHD scholarship; Top-Up Assistance Program (TUAP) of the Graduate School of The University of Queensland.

Assistance with specific methodologies and analyses

Lydie Couturier, Bonnie Holmes (The University of Queensland), Francisco Concha (Universidad de Valparaíso), Pete Kyne (Charles Darwin University); Dave Ebert (Pacific Shark Research Center); Maria Cristina Oddone (Universidade Federal de Rio Grande).

Assistance with samples and sampling

Jeff Johnson (Queensland Museum & Sciencentre), Carolina, Vargas-Caro, Yhon Concha-Perez, Hernán Flores, Astrid Isla (Universidad Austral de Chile), Julio Sanzana, Sebastian Hernandez.

Other

Shannon Rawding and Fiona Gilloway (SMBS Postgraduate Administration Officers), and Deborah McCamley and Don Weerheim (SBMS Finance); for their help and patience surfing through UQ's paperwork. To all doctor-to-be on the Bennett's Lab and SBMS tiffin gang: Adrian Gutteridge, Bonnie Holmes, Chris Glen, Chris Rohner, Deb Bowden, Joanna Stead, Kate Burgess, Lindsay Marshal, Lydie Couturier, Richard Smith, Carolina Vargas-Caro, Sam Williams and Tom Kashiwagi.

Keywords

Chondrichthyan, Elasmobranch, Shark, Skate, Ray, Chimaera, Fisheries, Bycatch, Diversity, Abundance, Life history.

Australian and New Zealand Standard Research Classifications (ANZSRC)

ANZSRC code: 060205 Marine and Estuarine Ecology (incl. Marine Ichthyology), 60%

ANZSRC code: 060809 Vertebrate Biology, 20%

ANZSRC code: 060207 Population Ecology, 20%

Fields of Research (FoR) Classification

FoR code: 0608, Zoology, 60%

FoR code: 0602, Ecology, 30%

FoR code: 0699, Other Biological Sciences, 10%

Cover photo: A juvenile shortfin mako shark, *Isurus oxyrinchus* caught in Caldera, Chile.

Additional photos: Fins of shortfin mako sharks, *Isurus oxyrinchus* (Chapter 1); neonate of the redspotted catshark, *Schroederichthys chilensis* (Chapter 2); closeup to the eye of a spiny dogfish, *Squalus acanthias* (Chapter 3); the egg case of an elephantfish *Callorhinichthys callorynchus* (Chapter 4); a bluntnose sixgill shark, *Hexanchus griseus* caught as bycatch of squat lobsters trawling fishery (chapter 5); a juvenile blue shark *Prionace glauca* cruising off Caldera, Chile (back cover).

Dedication

A mis padres y mi abuela;

A mi Caro

“Sharks have everything a scientist dreams of. They're beautiful—God, how beautiful they are!

They're like an impossibly perfect piece of machinery.

They're as graceful as any bird. They're as mysterious as any animal on earth”

- Peter Benchley

“Sleep my friend and you will see / The dream is my reality”

Hetfield, Hammett, Ulrich

Table of Contents

<i>Abstract</i>	i
<i>Declaration by author</i>	iii
<i>Publications during candidature</i>	iv
<i>Publications included in this thesis</i>	vii
<i>Contributions by others to the thesis</i>	x
<i>Acknowledgements</i>	xi
<i>Dedication</i>	xiv
Table of Contents	xv
List of Figures and Tables	
 Chapter 1 Research context	1
1.1. Introduction	2
Geomorphology of the study area	4
<i>Oceanographic influences</i>	5
<i>Climatic influences</i>	5
<i>Oceanographic variability and its implication in fisheries</i>	7
Aims and significance	9
1.2. General methodology	10
1.3. References	15
 Chapter 2 Taxonomy	21
2.1. First record of <i>Mobula japonica</i> (Rajiformes: Myliobatidae) from the south-eastern Pacific Ocean	22
<i>Abstract</i>	22
<i>Introduction</i>	23
<i>Materials and methods</i>	25
<i>Results and discussion</i>	26
<i>References</i>	29
2.2. Morphological characters of the thickbody skate <i>Amblyraja frerichsi</i> (Krefft 1968) (Rajiformes: Rajidae), with notes on its biology	32
<i>Abstract</i>	32
<i>Introduction</i>	33

<i>Materials and methods</i>	34
<i>Results</i>	37
<i>Discussion</i>	51
<i>References</i>	54
2.3. First record of <i>Hydrolagus melanophasma</i> James, Ebert, Long & Didier, 2009 (Chondrichthyes, Chimaeriformes, Holocephali) from the southeastern Pacific Ocean	59
<i>Abstract</i>	59
<i>Introduction</i>	60
<i>Materials and methods</i>	60
<i>Results and discussion</i>	64
<i>References</i>	68
Chapter 3 Zoogeography	71
3.1. Not all fish are equal: Functional biodiversity of cartilaginous fishes (Elasmobranchii and Holocephali) in Chile	72
<i>Abstract</i>	72
<i>Introduction</i>	73
<i>Materials and methods</i>	73
<i>Results</i>	77
<i>Discussion</i>	88
<i>References</i>	92
3.2. Biogeographic patterns in the cartilaginous fauna (Pisces: Elasmobranchii and Holocephali) in the southeast Pacific Ocean	101
<i>Abstract</i>	101
<i>Introduction</i>	102
<i>Materials and methods</i>	103
<i>Results</i>	106
<i>Discussion</i>	119
<i>References</i>	125
Chapter 4 Life history	130
4.1. Reproductive biology of <i>Zearaja chilensis</i> (Guichenot 1848) (Chondrichthyes: Rajidae) in the southeast Pacific Ocean	131
<i>Abstract</i>	131
<i>Introduction</i>	132

<i>Materials and methods</i>	133
<i>Results</i>	136
<i>Discussion</i>	142
<i>References</i>	146
4.2. Insights into the reproductive biology and fisheries of two commercially exploited species, shortfin mako (<i>Isurus oxyrinchus</i>) and blue shark (<i>Prionace glauca</i>), in the south-east Pacific Ocean	151
<i>Abstract</i>	151
<i>Introduction</i>	152
<i>Materials and methods</i>	154
<i>Results</i>	156
<i>Discussion</i>	166
<i>References</i>	170
Chapter 5 General Discussion	178
<i>Overview</i>	179
<i>Taxonomy</i>	180
<i>Zoogeography</i>	182
<i>Life history</i>	184
<i>Future directions for Chilean cartilaginous fish research</i>	186
<i>References</i>	189

List of Tables

Table 1 Effort and sampling units per locality along the Chilean coast.	11
Table 2 Main artisanal fisheries in Chile with interaction/historical capture of cartilaginous fishes.	13
Table 3 Definition of variables per sampling group used during on-board surveys and landings site visits performed during this research.	14
Table 4 Proportional dimensions as percentage of the disc length for <i>Mobula japonica</i> from North Stradbroke Island, Australia (QMI.38137); and Bahía Ingresa, Chile (IZUA-PM 4058), and range values converted from Notarbartolo-di-Sciara (1987).	28
Table 5 <i>Amblyraja frerichsi</i> catches location, sex and depth by year of historical and recent collections.	36
Table 6 Measurements (mm) of the morphometric characters taken from 35 specimens of	

<i>Amblyraja frerichsi</i> . Range expressed as percentage of total length (TL). Mean value (Mean) and standard deviation (s.d.) are indicated in each case.	40
Table 7 Measurements (mm) of the neurocranium taken from one specimen of <i>Amblyraja frerichsi</i> (adult male 1194 mm TL) expressed as percentage of nasobasal length.	44
Table 8 Measurements (mm) of the egg capsules of <i>Amblyraja frerichsi</i> .	50
Table 9 Geographical position of captured specimens of <i>Hydrolagus melanophasma</i> .	62
Table 10 Body measurements expressed as percentage of the body length (% BDL) for examined material of <i>Hydrolagus melanophasma</i> .	66
Table 11 Morphometric measurements expressed as a proportion of head length (% HDL) of the head lateral line canals of <i>Hydrolagus melanophasma</i> .	68
Table 12 Localities of landing sites and bases for on-board surveys with an indication of relative observer effort. Days-at-sea observed during on-board surveys are indicated in brackets.	74
Table 13 Main fisheries in Chile with interaction and/or catch records of cartilaginous species.	76
Table 14 Cartilaginous fishes reported to Chile, indicating the date of last record and its distribution zone along the country. N= north, C= central, S= south, AS= austral south, OI= oceanic islands. † indicates confirmed, but rarely collected species; ‡ indicates doubtful record for the species.	80
Table 15 Number of cartilaginous fishes in the world by taxonomic order and species reported (and confirmed) to occur in Chile.	89
Table 16 Depth and latitudinal range of cartilaginous fishes caught during surveys.	108
Table 17 Percentage of tows with cartilaginous fishes in the catch, species richness (S) and total number (N) of cartilaginous fishes caught in each zone and depth stratum.	111
Table 18 Abundance, as total CPUE (ind $\text{km}^{-2}\text{h}^{-1}$) of cartilaginous fishes caught during surveys in each zone (geographic location of zones is indicated in Fig. 17).	112
Table 19 Frequency of occurrence of cartilaginous fishes caught during surveys in each zone (geographic location of zones is indicated in Fig. 17).	113
Table 20 Abundance, as total CPUE (ind $\text{km}^{-2}\text{h}^{-1}$) and frequency of occurrence (F_O) of cartilaginous fishes caught in each depth stratum.	114
Table 21 Average abundance (ind $\text{km}^{-2}\text{h}^{-1}$) and percentage of contribution per species in each assemblage (n indicates the number of sites included per assemblage).	117
Table 22 Summary of fitting the Generalised Additive Model (GAM), relating <i>Isurus oxyrinchus</i> and <i>Prionace glauca</i> catches to environmental factors in the artisanal fishery of the south-eastern Pacific Ocean.	164

List of Figures

Figure 1 Main oceanic circulation patterns along the south east Pacific Ocean. CHC: Cape Horn Current; CPC: Chilean-Peruvian Current (Oceanic Humboldt Current) ECC: Equatorial Counter-Current; FC: Fjords Current (Coastal Humboldt Current), WWD: West Wind Drift.	6
Figure 2 Map of Chile indicating the main landing localities and geographic zones surveyed during the projects FIP No. 2004-18, 2005-61, 2006-31 and 2008-60.	12
Figure 3 Map of Chile (A) showing location of Bahía Ingresa (B). † indicates collection site of specimen of <i>Mobula japonica</i> .	24
Figure 4 <i>Mobula japonica</i> (IZUA-PM 4058) from Bahía Ingresa, Chile. (A) pectoral fins and tail projection based on Notarbartolo-di-Sciara (1987); details of (B) head and (C) dorsal fin; (D) specimen from North Stradbroke Island, Australia (Townsend & Kyne, 2010). Arrows indicate the position of spiracles (B), white tip on dorsal fin and spine (C).	27
Figure 5 Map of Chile (A) showing location of study area (inset box), and collecting localities (B) by date.	35
Figure 6 Adult male of <i>Amblyraja frerichsi</i> (1051 mm TL) in dorsal (A) and ventral (B) views. Scale bar 100 mm.	39
Figure 7 Dermal denticles of <i>Amblyraja frerichsi</i> . Dorsal view of the head (A) showing the snout and orbito-spiracular, nuchal and scapular thorns. Detailed view of malar (B), midline (C), and tail (D) thorns. (pre) preorbital, (pos) postorbital, (spi) spiracular, (nuc) nuchal, (sca) scapular, (sup) suprascapular. Scale bar 50 mm (A) or 10 mm (B-D).	41
Figure 8 Coloration of <i>Amblyraja frerichsi</i> subadult male (985 mm TL) in dorsal and ventral views. Scale bar 100 mm.	42
Figure 9 Neurocranium of <i>Amblyraja frerichsi</i> (adult male 1194 mm TL), in dorsal (A), ventral (B), and lateral (C) views. (af) anterior fontanelle, (bp) basal plate, (eb) epiphyseal bridge, (ecf) ethmoidal canal foramen, (ephf) endolymphatic foramen, (hm VII) hyomandibular branch foramen, (ja) jugal arches, (nc) nasal capsules, (of) orbital fissure, (pcf) preorbital canal foramen, (pd) parietal depression, (pf) posterior fontanelle, (phf) perilymphatic foramen, (pof) prootic foramen, (ptc) pteroptic crest, (ptp) pteroptic process, (ra) rostral appendix, (rc) rostral cartilage, (rn) rostral node, (rs) rostral shaft, (sc) supraorbital crest, (II) optic nerve foramen, (III) oculomotor nerve foramen, (IV) trochlear nerve foramen, (IX) glossopharyngeal nerve foramen, (X) vagus nerve foramen. Scale bar 50 mm.	45
Figure 10 General structure of right clasper gland and cartilages of <i>Amblyraja frerichsi</i> in lateral (A) view partially expanded; clasper cartilages in dorsal (B) and ventral (C) views.	47

(at1) accessory terminal 1, (at2) accessory terminal 2, (ax) axial, (cf) cleft, (dm) dorsal marginal, (dt1) dorsal terminal 1, (dt2) dorsal terminal 2, (dt3) dorsal terminal 3, (dt4) dorsal terminal 4, (hp) hypopyle, (pe) pent, (ps) pseudosiphon, (rh) rhipidion, (sh) shield, (sl) slit, (sp) spike, (sr) spur (st), sentinel, (vm) ventral marginal, (vt) ventral terminal. Scale bar 50 mm.	
Figure 11 Dorsal views of clasper cartilages of <i>Amblyraja frerichsi</i> . Abbreviations of clasper cartilages are indicated at Fig. 6. Scale bar 20 mm.	48
Figure 12 Egg capsules of <i>Amblyraja frerichsi</i> in dorsal (A) and lateral (B) views. Scale bar 50 mm.	49
Figure 13 <i>Hydrolagus melanophasma</i> : (a) Male 1175 mm TL (IZUA-PM 4007); (b) female 1277 mm TL (IZUA-PM 4011). Scale bar represents 250 mm.	63
Figure 14 Head lateral line canals of <i>Hydrolagus melanophasma</i> (IZUA-PM 4007) showing the preopercular (POP), oral (O) and infraorbital (IO) canals.	65
Figure 15 Map of South America showing the location of study area (inset boxes), indicating (A) main localities in Chile, zones and biogeographic provinces on the latitudinal gradient; and (A) oceanic islands zone (see text for reference of main points). Contour lines (grey) indicate 2000 m isobath on (A).	75
Figure 16 Composition (%) of the three major cartilaginous fish groups, sharks (grey), rays (white) and chimaeras (black), for six South American countries. Italics numbers represent species richness of confirmed species. CL: Chile; P: Peru; EC: Ecuador; CO: Pacific coast of Colombia; AR: Argentina; UR: Uruguay.	90
Figure 17 Map of (A) Chile showing location of study area (inset box) and (B) location of zones (Z1 to Z8) and sampling sites (circles). Commercial trawl intensity is indicated in (B), in terms of tows per nautical mile (nmi).	104
Figure 18 Latitudinal and bathymetric changes of species richness of sharks (A–B), skates (C–D) and chimaeras (E–F) across the study area. Fitted least-square regression model (solid line) and statistical significance are indicated in each case.	109
Figure 19 Latitudinal and bathymetric changes of relative abundance (Log (CPUE+1)) of sharks (A–B), skates (C–D) and chimaeras (E–F) across the study area. Fitted least-square regression model (solid line) and statistical significance are indicated in each case.	110
Figure 20 Latitudinal and bathymetric changes of Shannon diversity index (H) of sharks (A–B) and skates (C–D) across the study area. Fitted least-square regression model (solid line) and statistical significance are indicated in each case.	115
Figure 21 Agglomerative hierarchical cluster indicating the clustering of the four assemblages. Sites grouping is colour coded and indicate 40% similarity.	118

Figure 22 Ordination in two-dimensions using non-dimensional metric scaling indicating the clustering of the four assemblages. Sites grouping is colour coded and indicate 40% similarity.	119
Figure 23 Latitudinal distribution and abundance (Log CPUE+1) of cartilaginous fishes present in the continental shelf and slope of Chile. Black lines represent species range reported by Acuña <i>et al.</i> (2005).	122
Figure 24 Map of Chile (A) showing location of study area (inset box), and three <i>Zearaja chilensis</i> landings sites (B), indicated by circles.	135
Figure 25 Length absolute frequency distribution of <i>Zearaja chilensis</i> (n=5,477). Black bars represent males (n=3,121) and white bars represent females (n=2,356).	136
Figure 26 Relationships between total length and body mass (a), disc width (b) and disc length (c) of male (●) and female (○) <i>Zearaja chilensis</i> . Circles represent observed values and linear models are presented for males (solid line) and females (dashed line).	137
Figure 27 Monthly variation of maximum ovarian follicle diameter (●) and hepatosomatic index (○) of <i>Zearaja chilensis</i> . Circles indicate observed values along with standard deviation.	138
Figure 28 Relationships between total length and ovary mass (a) and oviducal gland mass (b); ovum diameter and ovum mass (c) and logistic model (line) fitted for the relationship between total length and percentage of mature (d) female <i>Zearaja chilensis</i> . Immature (●) and mature (○) specimens are represented by circles; squares indicate the observed percentage of mature individual in each size interval.	140
Figure 29 Relationships between total length and clasper length (a) and logistic model (line) fitted for the relationship between total length and percentage of mature (b) male of <i>Zearaja chilensis</i> . Immature (●) and mature (○) specimens are represented by circles; squares indicate the observed percentage of mature individual in each size interval.	141
Figure 30 Accumulated size frequencies of <i>Zearaja chilensis</i> females (a) and males (b) by fishing grounds (Modified from Quiroz <i>et al.</i> , 2009). Valdivia, 39.4° S to 40.5° S (—); Chiloé Island, 41.5° S to 43.5° S (.....); Moraleda Channel, 43.8° S to 45.9° S (— · —); and Castro-Magallanes Channel, 51.0° S to 54.0° S (— · ·).	145
Figure 31 Map of (a) Chile showing location of study area (inset box), and (b) position of longline sets sampled in 2005 (white circles) and 2010 (black circles).	157
Figure 32 Length frequency distribution of <i>Isurus oxyrinchus</i> (a) and <i>Prionace glauca</i> (b) in 2005 and in 2010.	159
Figure 33 Relationships between inner clasper length and total length based on reproductive classifications of <i>Isurus oxyrinchus</i> (a) and <i>Prionace glauca</i> (b). Maturity condition is	

indicated as juveniles (•); adolescents (○) and adults (▲).

161

Figure 34 Logistic model (line) fitted for the relationship between total length and percentage of mature *Isurus oxyrinchus* (a) male; and *Prionace glauca* (b) female and (c) male. Circles indicate the observed percentage of mature individual in each size interval. Dashed line indicated 95% confidence interval for the logistic model.

162

Figure 35 Generalised Additive Model (GAM) output for *Isurus oxyrinchus* and *Prionace glauca*; and the influence of the each environmental variable on the CPUE. Grey areas represent 95% confidence intervals.

163

Figure 36 Landings of *Isurus oxyrinchus* and *Prionace glauca* in Chile (a) by fishery type, (b) export of dried shark fins and (c) fishery landing proportion from Chile between 1979 and 2009. Lines in (a) indicates tonnes of sharks landed at overall national (black line), artisanal (grey line), economic exclusive zone industrial (dashed line) and international waters (IW) industrial (dotted line) fisheries.

165

1

CHAPTER 1
RESEARCH CONTEXT



1.1. INTRODUCTION

Cartilaginous fishes are probably the most successful of all fishes if success is measured in terms of historical endurance, based on the ability to survive mass extinctions of the last 400 million years (Grogan & Lund, 2004). Two taxonomic classes encompass all species with a cartilaginous skeleton, namely sharks, rays, skates and chimeras, formerly of the Class Chondrichthyes (Eschmeyer & Fong, 2011). Worldwide, approximately 1,207 living species have been described to date, including at least 50 species in Class Holocephali (Didier, 2004; Eschmeyer & Fong, 2011), and about 1,156 species in Class Elasmobranchii (Ebert *et al.*, 2013; Eschmeyer & Fong, 2011) that comprises sharks and the phylogenetic sister groups, the skates and rays (McEachran & Aschliman, 2004).

Most cartilaginous fishes exhibit slow growth, late maturity and very low fecundity compared to bony fishes (Camhi *et al.*, 1998), and these attributes result in low intrinsic rates of population increase (Smith *et al.*, 1998) and low resilience to fishing mortality (Hoenig & Gruber, 1990). Therefore, most cartilaginous fishes populations can withstand only modest levels of fishing without depletion and stock collapse (Camhi *et al.*, 1998; Musick, 1999; Cortes, 2000).

Although many sharks and rays have a low value in fisheries (compared to other fishing resources), the economic impact of stock collapse may be similar to more productive species because the population recovery time and economic loss last much longer (Musick, 1999). Around the world, the vast majority of cartilaginous fish fisheries display a common depletion pattern (Musick, 1999); and the absence of management, rapid stock decline and collapse are documented in every country that has commercially harvested cartilaginous fishes (Anderson, 1990; Hoff & Musick, 1990; Bonfil, 1994). Successful sustainable fisheries are possible, particularly for smaller species that mature relatively early and have a large number of young, and this success has come through knowledge of species' intrinsic biology and active management measures (Walker, 1998; Stevens, 1999). Although directed fisheries have been the cause of stock collapse, the mortality in mixed-species fisheries and bycatch in fisheries targeting bony fishes seems to be the major threat to cartilaginous fishes (Bonfil, 1994; Musick, 1999). In those fisheries, species of high economic value continues support the fishery, while bycatch species with a lower rebound potential are driven to stock collapse or extirpation (Musick, 1999; Stevens *et al.*, 2000).

The increase of cartilaginous fishes, as target or bycatch has been discussed by international organisations and has been a focus of the scientific community in recent decades (Camhi *et al.*, 1998). The United Nations Food and Agriculture Organization suggested that sharks comprise 60% of the catch of cartilaginous fishes in the world (FAO, 1999). However, not all the catch is landed

and most of the bycatch is discarded dead without any record of the species or capture volume (Stevens *et al.*, 2000).

Chile has one of the largest maritime territories in the world (Cubillos, 2005), and despite a relatively short commercial fishing history of less than 50 years, it is among the top-five fishing countries in the world, measured in terms of landings and exports (Albarrán, 2005). Chile is the second largest producer of fishmeal (Sepúlveda *et al.*, 2005) and has the second largest farmed-fish output in the world (Bustos, 2005). Within Chilean fisheries, the cartilaginous fishes have a relatively low commercial interest and are among the least researched species in national waters, as effort is oriented towards small pelagic fishes (sardines, anchovies and mackerels) and the salmon harvest (Cubillos, 2005). Despite the increased research effort that usually accompanies fisheries exploitation, the basic biology and taxonomy of cartilaginous fishes in Chile is still poorly known. Elasmobranchs and holocephalans are commonly caught as target and bycatch in several trawl, coastal gill-nets and longline fisheries along the Chilean coast, but captured (bycatch and discard) are rarely reported, with the exception of target species (Lamilla *et al.*, 2010).

There is a very significant problem in the interpretation and understanding of elasmobranch catch due to poor landing records, a lack of clear taxonomic identification of the species involved and a paucity of biological information on cartilaginous fish species landed as target and bycatch (Pequeño & Lamilla, 1997).

Until 2000, there was an incentive to increase commercial shark catches in Chilean waters to address international demand; and cartilaginous fish fisheries remained unregulated. An inflection point in fisheries policies occurred in 2000 as a response to pressure from the scientific community; with an increase in management supervision and research conducted by the Chilean Government. The current fishing scene has remained largely unmodified from that time, except for the implementation of the "National Plan of Action" for shark fisheries management and conservation (Lamilla *et al.*, 2010), where research guidelines were proposed for a sustainable exploitation of cartilaginous fishes. Up to the present time, the mako shark fishery is unregulated except for fishing gear restrictions, while a closure was imposed on the yellownose skate and elephantfish fishery although they continued unaffected by these measures. There are no regulations on the bycatch of any cartilaginous fish, finning and discard of sharks, skates and chimaeras in national waters. Recent studies have focused on determining the basic biology of *C. callorynchus* (Alarcon *et al.*, 2011) on models to estimate bycatch (Lamilla *et al.*, 2010) reflecting a large and continuous gap between the fishery and the scientific knowledge.

Geomorphology of the study area

At a large scale, the shape and configuration of the western edge of South America reveal two contrasting geographical settings (Fig. 1). On the one hand, the coastline of southern Peru to Chiloé Island is continuous, relatively smooth with no breaks or major geographical features. On the political borderline between Peru and Chile is located the “Arica’s elbow” (*ca.* 18° 20' S), where the coastline changes direction abruptly from SW facing to predominantly west, and from which the coastline to the south is virtually straight to the Chacao Channel (41° 47' S), constituting one of the four geomorphological units of Chile.

The most notable geographic feature of continental Chile is the 48 latitudinal degrees of coastal extension (18.4° to 56° S), that comprises about 55,000 km of coastline, 95% of which occurs in the Chilean archipelago (Camus, 2001); from Chiloé to Cape Horn. Regarding the configuration of the ocean floor, the South American continental margin is characterized by the presence of a pit that borders the Nazca plate and extends about 5,000 km from the equator (0°) to 46° S (Gulf of Penas), at which point the Chilean submarine ridge reaches the continent and marks the confluence of South American, Nazca and Antarctic tectonic plates (Ahumada *et al.*, 2000). These features demonstrate the role of tectonic processes in the coastal geomorphology, and explain that the Chilean continental shelf is extremely narrow compared to the Atlantic coast, with a maximum width around 45 km in the area of Talcahuano (36°40' S), and a maximum depth of 150 m in general, except for the Valparaíso area (33° S) where it reaches up to 800 m.

Oceanographic influences

Biogeographically, Chile is influenced by three different oceanographic sources. First, the shallow predominant influence of subantarctic water mass, low temperature and salinity, associated with the West Wind Drift, a large surface flow enters Chile from the west and divides before reaching the coast in (a) a northward oceanic flow, usually called the Chilean-Peruvian Current (Bernal *et al.*, 1982); and (b) a southward flow called Cape Horn Current, which borders the southern end of the Chilean archipelago and continues east to join the Falkland Current in the Atlantic. From the Cape Horn Current another flow arises (Fjords Current) and continues to the north and reaches the coast at Chiloé (42° S). The Fjords Current is the coastal branch of the Humboldt Current System and the Chilean-Peruvian current, its oceanic branch, both separated by the equatorial counter-current (Ahumada *et al.*, 2000).

A second important aspect is the role of the coastal upwelling, mainly from the equatorial subsurface water mass. This nutrient-rich water mass is responsible for high primary coastal productivity and, although the upwelling effect on coastal communities is not yet clearly established (Vasquez *et al.*, 1998; Camus & Andrade, 1999), it seems to be an additional factor contributing to cooling surface waters adjacent to the coast (Espinoza *et al.*, 1983). Factors contributing to the cooling of coastal waters along the south-north flow of surface currents seem to be the most important determinants of marine species distributions; and the cold conditions extend to low latitudes to a much greater degree than in other continents. Viviani (1979) estimated that sea temperatures in the north are 10° C lower than expected compared to similar latitudes on other continents.

The third distinctive feature is the "anomalies" related to oceanographic and atmospheric dynamics of the global atmospheric circulation, particularly the Southern Oscillation whose positive and negative phases are associated with "El Niño" and "La Niña", respectively (Philander, 1983). The development of physical and biological consequences of these events has been widely discussed in the literature (Philander, 1983; Zhang *et al.*, 2008; Sarachik & Cane, 2010), but remains unclear its relationship with the history of climate change and regional distribution of biota (Sielfeld *et al.*, 2010).

Climatic influences

Between 18.4° and 27° S, the terrestrial coastal zone is itself a bioclimatic region called the "littoral desert", with dry conditions throughout the year and a strong oceanic influence. Coastal deserts are a particular feature of the western margin of continents near to oceanic gyres, *e.g.* SW Africa, W. Australia; and results from the interaction of descending air masses in the tropics and the winds that move to the mainland after passing over cold water masses resulting in intensified drying of adjacent land (Brown & Lomolino, 1998). Toward higher latitudes, this effect is less severe and arid conditions are reduced, alternating with wet or cold periods progressively. Between 27° and 39° S, is a large area with a succession of Mediterranean bioclimatic regions ranging from perarid features in northern to perhumid conditions further south, where the coast is also differentiated from the interior by the marine influence. Between 39° and 56° S, the oceanic-influenced area can be differentiated into three bioclimatic regions: Oceanic with Mediterranean influence (39° to 44° S); Cold-temperate ocean (44° to 52°) and; Sub-Antarctic ocean (52° to 56° S), the latter characterised by all-year round rainfall that makes it distinct from the transoceanic arid region in the Atlantic. The three major climatic zones are associated with the presence of the South Pacific subtropical anticyclone centred around 30° S and, due to its annual cycle of latitudinal displacement, influences

the Mediterranean area, favouring precipitation during winter and causing the opposite effect in summer (Villagrán, 1995). The influence of the anticyclone continues to the north of 30° S maintaining dry conditions, although it weakens south of 40° S where there is rain all year.

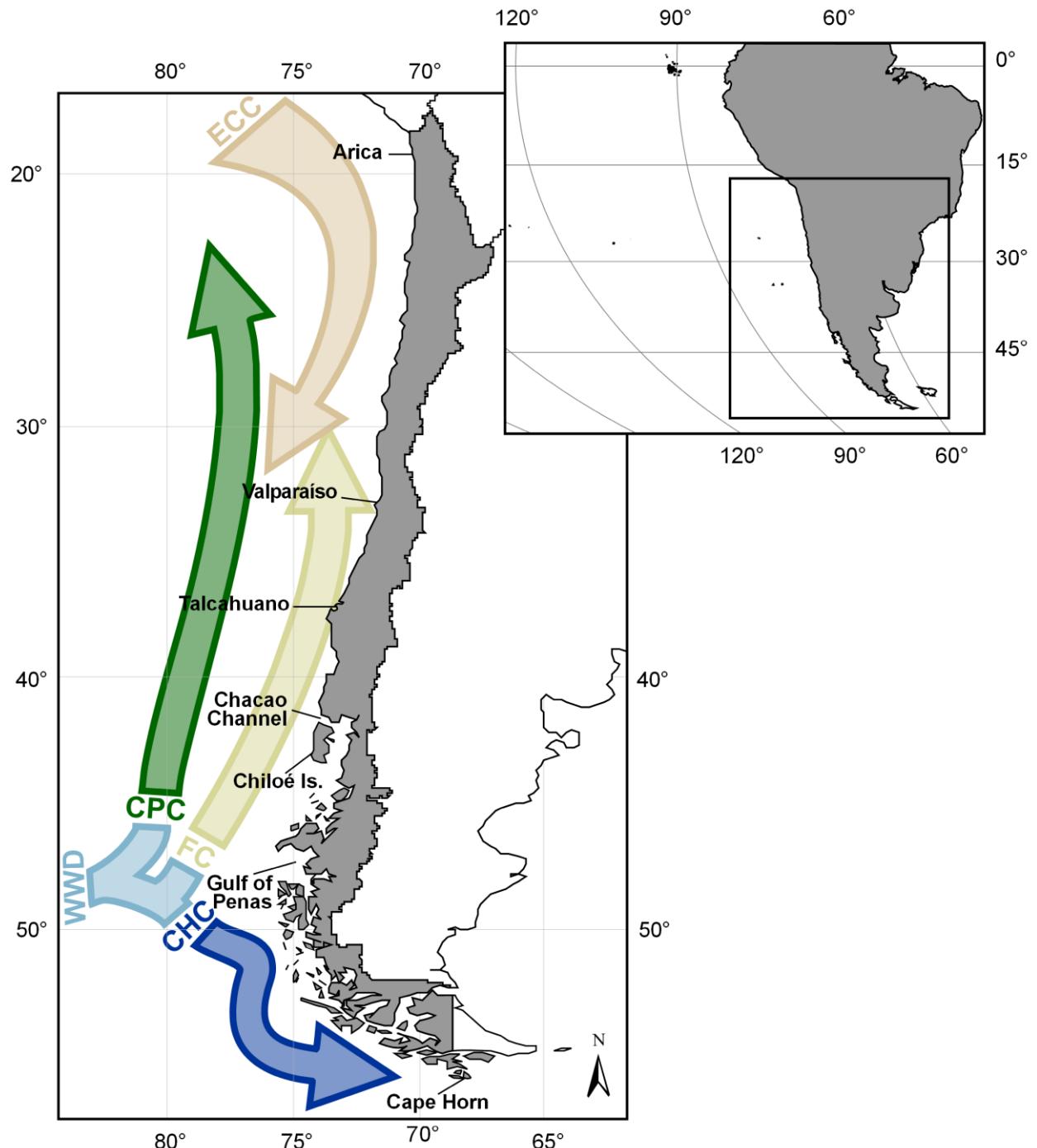


Figure 1 Main oceanic circulation patterns along the southeast Pacific Ocean. CHC: Cape Horn Current; CPC: Chilean-Peruvian Current (Oceanic Humboldt Current) ECC: Equatorial Counter-Current; FC: Fjords Current (Coastal Humboldt Current), WWD: West Wind Drift. Modified after Camus (2001).

Moreover, the afore-mentioned large-scale climatic variations generate a differential interaction pattern between land and sea in terms of freshwater input to the ocean. The desert area is clearly not influenced by this contribution, although it is somewhat more important in the Mediterranean area, but has no real impact beyond near coastal regions. In contrast, the dilution effect of rainfall is highly noticeable in the ocean bioclimatic zone, creating local hydrological conditions with relative independence from oceanographic predominant water mass (Ahumada *et al.*, 2000).

Oceanographic variability and its implication in fisheries

In the oceans, the highest biological productivity centres are located along the eastern basin. In these areas, major upwelling centres are generated by the dominant wind direction, coast orientation and rotation of the earth (Smith, 1995). The upwelling of subsurface water causes a decrease in sea surface temperature and dissolved oxygen and increased nutrients favouring primary productivity (Glantz, 1996; Voituriez & Jacques, 2000). Along the Chilean coast the occurrence of coastal upwelling between latitudes 18° S and 38° S is common due to coast orientation and wind regime dominated by the S and SW winds as result of the subtropical anticyclone (Bakun & Nelson, 1991). Coastal upwelling can occur throughout the north and central coast of Chile (Marín & Olivares, 1999), however, this process has been observed at specific points such as bays, points and capes. Punta Curaumilla (33°05' S) and San Antonio Bay (33°35' S) have been identified as the most important local upwelling centres (Brandhorst, 1971; Strub *et al.*, 1998), with upwelling cold waters that extends to the northwest covering the continental shelf within 3–4 days (Fonseca & Farias, 1987).

The variability of the oceanographic system off the Chilean coast is determined by continuous coastal upwelling events, currents that carry subantarctic water northward and the intrusion of subtropical waters southward (Marín & Olivares, 1999). From the dynamic point of view, this variability affect the currents, the water column mixing, the upwelling intensity as well as the sea surface temperature and sea level on the continental shelf along the Humboldt system (Shaffer *et al.*, 1999).

The physical properties of the Oceans clearly influence all marine biological processes and over all time scales (Mann, 1992). Among the different variables that affect the distribution of pelagic resources, the sea surface temperature is considered one of the most relevant. Its fluctuations often represent disturbance signals that extend deep into the oceans (White & Walker, 1974).

Changes in the physical environment, such as those associated with “El Niño” events, are characterized by displacements of large water masses. Many neritic fish, such as anchovy and sardine, respond to these changes redistributing geographically in relation mainly to temperature (Yáñez *et al.*, 1995). In this sense, synoptic information of physical environmental variables can be useful for understanding the movement of fishes and changes in their geographical ranges. If their food is abundant, fishes may reach higher growth rates when the water temperature is preferred. Evidence shows that when food is scarce, fishes move to the border of their home range seeking temperatures to maximize growth (Csirke & Sharp, 1984).

Understanding and predicting the reactions of fish to changes in the physical environment and ecosystem responses to changes in the abundance of fish, is useful in the decision making process on fisheries management (Bernal *et al.* 1982; Csirke & Sharp, 1984; Yáñez *et al.*, 1995).

Aims and significance

The life history strategy of cartilaginous fishes suggests the need for conservative management of a balanced population and compatible fishery activities. However, most cartilaginous fish fisheries are completely unmonitored or unmanaged (Dulvy *et al.*, 2008). About 50% of the estimated global catch of cartilaginous fish is gathered as bycatch and this is generally not mentioned in official fishery statistics (Stevens *et al.*, 2000, Dulvy *et al.*, 2014).

In general, the contribution of cartilaginous fishes to national markets is low because of the relatively scarce economic value of shark, skate, ray and chimaera flesh. Consequently, these species tend to be low priority for research and management compared to bony fishes, although recently, shark fins (Hernández *et al.*, 2008) and branchial filter-plates of Mobulid rays (Marshall *et al.*, 2011) have become high-value by-products for which there is a thriving international demand.

Management and conservation of cartilaginous fish resources are necessary on fishing countries to maintain biodiversity and ecosystem structures (Agnew *et al.*, 2000; Dulvy *et al.*, 2008). The interactions between species in marine ecosystems, as well as the impact of the removal of top predators on other marine organisms on the functionality of the whole ecosystem are poorly understood (Bonfil, 1994; Camhi *et al.*, 1998) although, there are some well-known examples of cascade effects that perturb whole ecosystems after apex predators are removed (Stevens 1999; Gilman *et al.*, 2007; Ferretti *et al.*, 2008; 2010). Basically, identification guides and basic knowledge regarding abundance, distribution, life history and fishing effort are required for a successful management of cartilaginous fisheries.

The results of the present research provide first step in providing necessary information that may help to build a baseline for sustainable fishery practices with the aim of obtaining a balance between the economic development and maintenance of marine ecosystem health in Chilean waters. The following chapters fill many knowledge gaps in the biology, taxonomy and distribution of cartilaginous fishes in the south-eastern Pacific Ocean, and aim to: **(a)** supplement the taxonomic and systematic information available to date, **(b)** describe zoogeographical patterns of cartilaginous fishes along the coast of Chile, and **(c)** examine the reproductive biology and life history of specific cartilaginous fishes that inhabit Chilean coastal waters.

1.2. GENERAL METHODOLOGY

The present document is separated into chapters, each of which explores a particular aspect of cartilaginous fishes in the south east Pacific Ocean, as a comprehensive approach towards conservation-concerned fisheries management. The research core relays on data and material collected during research surveys made in Chile between 2004 and 2010 conducted by the author and funded by the Chilean Government. Databases analysed included to extracts of four different projects conducted by Universidad Austral de Chile (projects FIP No. 2004-18, 2005-61, 2006-31 and 2008-60). The main aim of these projects was to inform the development of a National Plan of Action for conservation and management of sharks (and relatives), as well to develop a methodological approach for estimation of the shark bycatch from coastal artisanal (medium and small scale) fisheries and semi-industrial oceanic fleets that interact (directly or incidentally) with cartilaginous fish species. During the implementation of these projects, additional biological and fishery-dependent data were collected in order to provide opportunities for future research. All the information included in the following chapters (and hence the research core) is new, unpublished and has not been analysed elsewhere, with the exception of the publications of each chapter *per se*.

To establish quantifiable results from commercial species and bycatch of cartilaginous fishes, 138 landing-site surveys and 206 fishing trips were observed in 24 fisheries with a history of interaction, with interaction defined by Lamilla *et al.* (2008) as “historical or recent record of catch and landing of at least one cartilaginous fish during a commercial trip”. The geographic location of main landing sites along the Chilean coast and sampling effort in each locality are indicated on Fig. 2 and Table 1. Additionally, all fisheries evaluated during surveys are listed in Table 2.

Information on fishes and fisheries, sampling methodology and analysis are described in each chapter separately but follow the procedures and guidelines for the biological monitoring and assessment of the cartilaginous fish bycatch in artisanal vessels prepared by Bustamante *et al.* (2009). This “Observer's Handbook” contains condensed procedures and datasheets to record data regarding the operational design and was designed to improve the reliability of biological information taken by on-board observers in diverse fisheries and fishing gears.

Variables recorded in each on-board survey or landing site visit are indicated in the Table 3 and are related to (a) identify the geometric and functional characteristics of vessels, (b) describe the functional characteristics of fishing gears, (c) perform a census of the catch and (d) execute biological sampling of all cartilaginous fishes caught.

Other information sources where necessary and are indicated in the methodology of each chapter. For example, commercial landings records were extracted from the Fishery National Service database (SERNAP, in Spanish). Additional surveys were developed by the “Shark Conservation Programme” (Programa de Conservación de Tiburones, PCT in Spanish), a flagship initiative of Universidad Austral de Chile, based in Valdivia, Chile which the author founded and directs. The PCT, acts as platform for scientific outreach and coordinates activities that promote responsible and rational use of sharks as fishing resource.

Throughout the document, the terminology proposed by Alverson *et al.* (1994) is used to describe fishing operational definitions: *Target species*, is the catch of a species or group of species that are the main objective of a fishery; *Bycatch*, is the fraction of the total catch does not correspond to target catch; and *Discards*, is the fraction of the catch which is returned to sea as a result of any considerations (legal, economic or personal) and may include commercial and non-commercial species, it also applies when commercial species are retuned in order to keep other species of higher value. The discard may be dead or released alive without knowledge of subsequent mortality related to the capture event.

Table 1 Effort and sampling units per locality along the Chilean coast.

Locality	Zone	Landing site visits	On-board surveys
Iquique	North	26	33
Antofagasta	North	0	9
Caldera	North	7	4
Coquimbo	Central	2	31
Valparaíso	Central	1	39
Concepción	South	70	23
Valdivia	South	18	40
Puerto Montt	South	10	21
Aysén	Austral	0	6
Punta Arenas	Austral	4	0

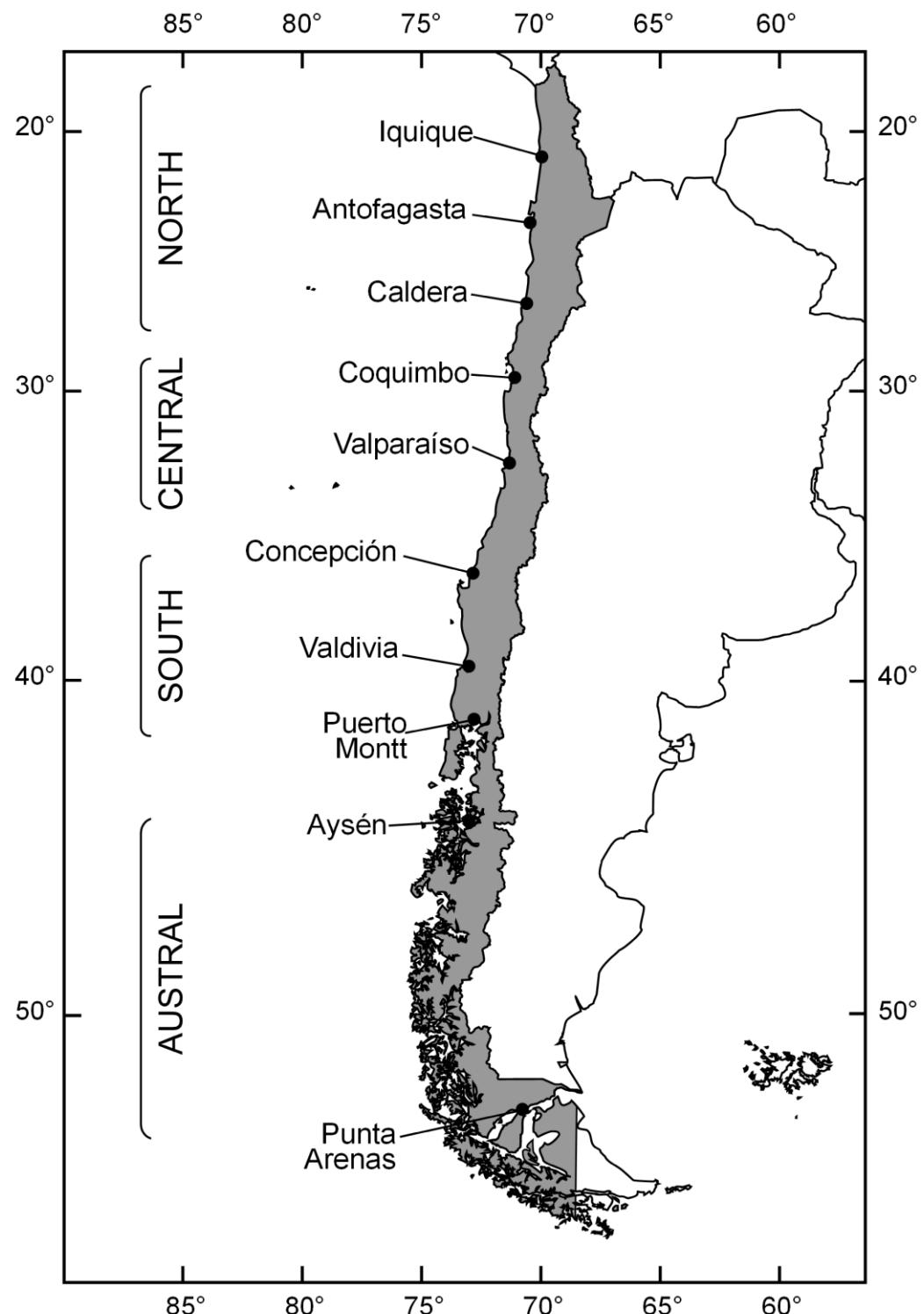


Figure 2 Map of Chile indicating the main landing localities and geographic zones surveyed during the projects FIP No. 2004-18, 2005-61, 2006-31 and 2008-60.

Table 2 Main artisanal fisheries in Chile with interaction/historical capture of cartilaginous fishes.

Target species	Zone	Fishing gear
Swordfish <i>Xiphias gladius</i> Linnaeus 1758	Central	Gillnet/Longline
Albacore <i>Thunnus alalunga</i> (Bonnaterre 1788)	Central	Gillnet
Swimming crab <i>Ovalipes trimaculatus</i> (De Haan 1833)	Central	Gillnet
Chilean jack mackerel <i>Trachurus murphyi</i> Nichols 1920	Central	Gillnet
Blue squat lobster <i>Cervimunida johni</i> Porter 1903	Central	Trawl
Carrot squat lobster <i>Pleuroncodes monodon</i> (Milne Edwards 1837)	Central	Trawl
Chilean nylon shrimp <i>Heterocarpus reedi</i> Bahamonde 1955	Central	Trawl
Smalleye flounder <i>Paralichthys microps</i> (Günther 1881)	Central	Gillnet
Southern rays bream <i>Brama australis</i> Valenciennes 1838	Central	Gillnet
South Pacific hake <i>Merluccius gayi gayi</i> (Guichenot 1848)	Central/South	Gillnet
Yellowtail amberjack <i>Seriola lalandi</i> Valenciennes 1833	North	Longline
Palm ruff <i>Seriolella violacea</i> Guichenot 1848	North	Longline
†Shortfin mako <i>Isurus oxyrinchus</i> Rafinesque 1810	North	Longline
Chilean silverside <i>Odontesthes regia</i> (Humboldt 1821)	North	Gillnet
Pink cusk-eel <i>Genypterus blacodes</i> (Forster 1801)	North/Central/South	Gillnet/Longline
Patagonian toothfish <i>Dissostichus eleginoides</i> Smitt 1898	North/South	Longline
Corvina drum <i>Cilus gilberti</i> (Abbott 1899)	North/South	Gillnet
Red cusk-eel <i>Genypterus chilensis</i> (Guichenot 1848)	South	Longline
Southern hake <i>Merluccius australis</i> (Hutton 1872)	South	Longline
†Elephantfish <i>Callorhinichus callorynchus</i> (Linnaeus 1758)	South	Gillnet
Snoek <i>Thyrsites atun</i> (Euphrasen 1791)	South	Gillnet
Speckled smooth-hound <i>Mustelus mento</i> Cope 1877	South	Gillnet
†Piked dogfish <i>Squalus acanthias</i> Linnaeus 1758	South	Longline
†Yellownose skate <i>Zearaja chilensis</i> (Guichenot 1848)	South/Austral South	Longline

† Cartilaginous fish as target resource.

Table 3 Definition of variables per sampling group used during on-board surveys and landings site visits performed during this research.

Group	Variable
A. Vessel	<ol style="list-style-type: none"> 1. Name and radio signal 2. Date of sail and dock 3. Target fishery 4. Port
B. Fishing gear	<ol style="list-style-type: none"> 1. Longline type (pelagic, demersal, vertical) <ul style="list-style-type: none"> - Number of hooks - Headline - Bait 2. Net type (gillnets, purse seine, trawl) <ul style="list-style-type: none"> - Width and length subunit - Aperture - Number of subunits 3. Number of sets or hauls
C. Capture	<ol style="list-style-type: none"> 1. Geographic position (latitude, longitude) 2. Start and end time 3. Fishing and area depth 4. Wind speed (in Beaufort units) 5. Sea surface temperature (in °C) 6. Capture <ul style="list-style-type: none"> - Species name - Total number of individuals of the species - Intent of use (target, incidental, bycatch, fins, or released alive)
D. Cartilaginous fishes	<ol style="list-style-type: none"> 1. Total and standard length 2. Disc width and length (Batoids only) 3. Sex 4. Clasper length (males only) 5. Reproductive condition <ul style="list-style-type: none"> - Clasper and testes (males) - Ovary, uterus, nidamental gland (females)

1.3. REFERENCES

- Agnew, D.J., Nolan, C.P., Beddington, J.R. & Baranowski, R. (2000) Approaches to the assessment and management of multispecies skate and ray fisheries using the Falkland Islands fishery as an example. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 429–440.
- Ahumada, R.B., Pinto, L. & Camus, P.A. (2000) The Chilean coast. In *Seas at the millennium: an environmental analysis* (Sheppard, C.R.C., ed.), pp. 699–717. Pergamon Press: Oxford, UK.
- Alarcón, C., Cubillos, L.A., & Acuña, E. (2011) Length-based growth, maturity and natural mortality of the cockfish *Callorhinchus callorhynchus* (Linnaeus, 1758) off Coquimbo, Chile. *Environmental Biology of Fishes* 92, 65–78.
- Albarrán, D. (2005) Marco Regulatorio de la Actividad Pesquera en Chile. In *Biodiversidad marina: valoración, usos y perspectivas* (Figueroa, E., ed.), pp. 15–20. Editorial Universitaria: Santiago de Chile.
- Alverson, D.L., Freeberg, M.H., Murawski, S.A. & Pope, J.G. (1994) *A Global Assessment of Fisheries Bycatch and Discards*. Fisheries Technical Paper No. 339. Food and Agriculture Organization: Rome.
- Anderson, E.D. (1990) Fishery models as applied to elasmobranch fisheries. In *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of fisheries* (Pratt, Jr., H.L., Gruber, S.H., Taniuchi, T., eds.), pp. 473–484. NOAA Technical Report NMFS 90. Department of Commerce: US.
- Bakun, A. & Nelson, C. (1991) The seasonal cycle of wind stress curl in sub-subtropical eastern boundary current regions. *Journal of Physical Oceanography* 21, 1815–1834.
- Bernal P., Robles, F.L. & Rojas, O. (1982) Variabilidad física y biológica en la región meridional del sistema de corrientes Chile-Perú. In *Bases biológicas para el uso y manejo de recursos naturales renovables: recursos biológicos marinos* (Castilla, J.C., ed.), pp. 75–102. Monografías Biológicas II, P. Universidad Católica de Chile: Santiago de Chile.
- Bonfil, R. (1994) *Overview of World Elasmobranch Fisheries*. FAO Fisheries Technical Paper No. 341. Food and Agriculture Organization: Rome.
- Brandhorst, W. (1971) Condiciones oceanográficas estivales frente a la costa de Chile. *Revista de Biología Marina, Valparaíso* 14, 45–84.
- Brown, J.H. & Lomolino, M.V. (1998) *Biogeography*. Sinauer Associates, Inc: Sunderland, Massachusetts.

- Bustamante, C., Flores, H., Saldivia, R., Alarcón, M.A. & Lamilla, J. (2009) *Manual del observador científico para las pesquerías de descarte de condriictios*. Programa de Conservación de Tiburones: Universidad Austral de Chile y Subsecretaría de Pesca: Valdivia.
- Bustos, E. (2005) Avances en la Investigación para la Acuicultura en el Sur de Chile. In *Biodiversidad marina: valoración, usos y perspectivas* (Figueroa, E., ed.), pp. 353–364. Editorial Universitaria: Santiago de Chile.
- Camhi, M., Fowler, S.L., Musick, J.A., Bräutigam, A. & Fordham, S.V. (1998) *Sharks and their relatives – Ecology and Conservation*. IUCN/SSC Shark Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK.
- Camus, P.A. (2001) Biogeografía marina de Chile continental. *Revista Chilena de Historia Natural* 74, 587–617.
- Camus, P.A. & Andrade, Y.N. (1999) Diversidad de comunidades intermareales rocosas del norte de Chile y el efecto potencial de la surgencia costera. *Revista Chilena de Historia Natural* 72, 389–410.
- Cortés, E. (2000) Life History Patterns and Correlations in Sharks. *Reviews in Fishery Science* 8, 299–344.
- Cubillos, L. (2005) Diagnóstico, Aspectos Críticos y Propuesta de Sustentabilidad para las Pesquerías Nacionales. In *Biodiversidad marina: valoración, usos y perspectivas* (Figueroa, E., ed.), pp. 27–46. Editorial Universitaria: Santiago de Chile.
- Csirke, J. & Sharp, G.D. (1984) *Reports of the expert consultation to examine changes in abundance and species composition of neritic fish resources*. FAO Fisheries Report 291. Food and Agriculture Organization: Rome.
- Didier, D.A. (2004) Phylogeny and classification of extant Holocephali. In *Biology of sharks and their relatives* (Carrier, J.C., Musick, J.A., Heithaus, M.R., eds.), pp. 115–135. CRC Press: Boca Raton, FL.
- Dulvy, N.K., Baum, J.K., Clarke, S., Compagno, L.J.V., Cortes, E., Domingo, A., Fordham, S., Fowler, S., Francis, M.P., Gibson, C., Martinez, J., Musick, J.A., Soldo, A., Stevens, J.D. & Valenti, S. (2008) You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18, 459–482.
- Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., et al. (2014) Extinction risk and conservation of the world's sharks and rays. *eLife*, 3, e00590.

Ebert, D.A., Fowler, S. & Compagno L.J.V. (2013) *Sharks of the World*. Plymouth: Wild Nature Press.

Espinosa, F.R., Neshyba, S. & Maoxiang, Z. (1983) Surface water motion off Chile revealed in satellite images of surface chlorophyll and temperatures. In *Recursos marinos del Pacífico* (Arana, P., ed.), pp. 41–58. Editorial Universitaria: Santiago, Chile.

Eschmeyer, W.N. & Fong, J.D. (2011) Pisces. In *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness* (Zhang, Z.-Q., ed.). *Zootaxa* 3148, 26–38.

FAO. (1999) *International Plan of Action for the conservation and management of sharks*. Document FI: CSS/98/3, Oct. 1998. Food and Agriculture Organization: Rome.

Ferretti, F., Myers, R.A., Serena, F. & Lotze, H.K. (2008) Loss of large predatory sharks from the Mediterranean Sea. *Conservation Biology* 22, 952–64.

Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R. & Lotze, H.K. (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecology letters* 13, 1055–1071.

Fonseca, T. & Farías, M. (1987) Estudio del proceso de surgencia en la costa chilena utilizando percepción remota. *Investigaciones Pesqueras* 34, 33–46.

Gilman, E., Clarke, S., Brothers, N., Alfaro-Shigueto, J., Mandelman, J., Mangel, J., Petersen, S., Piovano, S., Thomson, N., Dalzell, P., Donoso, M., Goren, M. & Werner, T. (2007) *Shark depredation and unwanted bycatch in pelagic longline fisheries: industry practices and attitudes, and shark avoidance strategies*. Western Pacific Regional Fishery Management Council: Honolulu, USA.

Glantz, M. (1996) *Corrientes de Cambio: El Impacto de “El Niño” sobre el Clima y la Sociedad*. Cambridge University Press: Cambridge.

Grogan, E.D. & Lund, R. (2004) The origin and relationships of early Chondrichthyes. In *Biology of sharks and their relatives* (Carrier, J.C., Musick, J.A., Heithaus, M.R., eds.), pp. 3–31. CRC Press: Boca Raton, FL.

Hernández, S., Haye, P.A. & Shivji, M.S. (2008) Characterization of the pelagic shark-fin trade in north-central Chile by genetic identification and trader surveys. *Journal of Fish Biology* 73, 2293–2304.

Hoenig, J.M. & Gruber, S.H. (1990) Life-history patterns in the elasmobranchs: implications for fisheries management. In *Elasmobranchs as living resources: advances in the biology, ecology,*

- systematics, and the status of fisheries* (Pratt, Jr., H.L., Gruber, S.H., Taniuchi, T., eds.), pp. 1–16. NOAA Technical Report NMFS 90. Department of Commerce: US.
- Hoff, T.B. & Musick, J.A. (1990) Western North Atlantic shark-fishery management problems and informational requirements. In *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of fisheries* (Pratt, Jr., H.L., Gruber, S.H., Taniuchi, T., eds.), pp. 455–472. NOAA Technical Report NMFS 90. Department of Commerce: US.
- Lamilla, J., Roa, R., Barría, P., Bustamante, C., Concha, F., Cortes, E., Acuña, E., Balbontín, F., Oliva, M., Araya, M. & Meléndez, R. (2008) Desarrollo metodológico para la estimación del descarte de Condrictios en las pesquerías artesanales. *Universidad Austral de Chile Informe técnico* No. 2008–60, Valdivia. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 Sep 2013).
- Lamilla J., Bustamante, C., Roa, R., Acuña, E., Concha, F., Meléndez, R., López, S., Aedo, G., Flores, H. & Vargas-Caro, C. (2010) Estimación del descarte de condrictios en pesquerías artesanales. *Universidad Austral de Chile Informe técnico* No. 2008–60, Valdivia. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 Sep 2013).
- Mann, K.H. (1992) Physical influences on biological processes: how important are they? *South African Journal of Marine Sciences* 12, 107–121.
- Marín, V. & Olivares, G.R. (1999) Estacionalidad de la productividad primaria en Bahía Mejillones del Sur (Chile): una aproximación proceso-funcional. *Revista Chilena de Historia Natural* 72, 629–641.
- Marshall A., Bennett M.B., Kodja G., Hinojosa-Alvarez S., Galván-Magaña F., Harding M., Stevens G. and Kashiwagi T. (2011). *Manta birostris*. In *IUCN Red List of Threatened Species*. Version 2011.2. Available at <http://www.iucnredlist.org/> (accessed 25 Sept 2011).
- McEachran, J.D & Aschliman, N. (2004) Phylogeny of Batoidea. In *Biology of sharks and their relatives* (Carrier, J.C., Musick, J.A. & Heithaus, M.R., eds.), pp. 79–113. CRC Press: Boca Raton, FL.
- Musick, J.A. (1999) Criteria to define extinction risk in marine fishes. *Fisheries* 24, 6–14.
- Pequeño, G. & Lamilla, J. (1997) Las pesquerías de condrictios en Chile: primer análisis. *Biología Pesquera* 26, 13–24.
- Philander, S.G.H. (1983) El Niño Southern Oscillation phenomena. *Nature* 302, 295–301.
- Sarachik, E.S., & Cane, M.A. (2010) *The El Niño-Southern Oscillation Phenomenon*. Cambridge University Press: Cambridge.

- Schindler, D.E., Essington, T.E., Kitchell, J.F., Boggs, C. & Hilborn, R. (2002) Sharks and tunas: fisheries impacts on predators with contrasting life histories. *Ecological Applications* 12, 735–748.
- Sepúlveda, A., Cubillos, L. & Arcos, D. (2005) Pesquerías Pelágicas Chilenas: Una Síntesis sobre la Incertidumbre Biológica. In *Biodiversidad marina: valoración, usos y perspectivas* (Figueroa, E., ed.), pp. 91–108. Editorial Universitaria: Santiago de Chile.
- Shaffer, G., Hormazábal, S., Pizarro, O. & Salinas, S. (1999) Seasonal and interannual variability of current and temperature off center Chile. *Journal of Geophysical Research* 104, 29951–29961.
- Sielfeld, W., Laudien, J., Vargas, M., & Villegas, M. (2010) El Niño induced changes of the coastal fish fauna off northern Chile and implications for ichthyogeography. *Revista de Biología Marina y Oceanografía* 45, 705–722.
- Smith, R. (1995) The Physical processes of coastal ocean upwelling systems. In *Upwelling in the ocean: Modern processes and ancient records* (Summerhayes, C., Emeis, K., Angel, M., Smith, R., Zeitzschel, B., eds.), pp. 39–64. John Wiley & Sons: NY.
- Smith, S.E., Au, D.W. & Show, C. (1998) Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research* 41, 663–678.
- Stevens, J.D. (1999) Variable resistance to fishing pressure in two sharks: The significance of different ecological and life history parameters. In *Life in the Slow Lane: Ecology and Conservation of Long-Lived Marine Animals* (Musick, J.A., ed.), pp. 11–15. American Fisheries Society: Bethesda, MD.
- Stevens, J.D., Bonfil, R., Dulvy, N.K. & Walker, P.A. (2000) The effects of fishing on shark, rays, and chimaeras (Chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Sciences* 57, 476–494.
- Strub, T., Mesías, M., Montecino, V., Rutlland, J. & Salinas, S. (1998) Coastal ocean circulation off western South America. In *The Sea* (Robinson, A., Brink, K., eds.), pp. 273–313. John Wiley & Sons: NY.
- Vásquez, J.A., Camus, P.A. & Ojeda, F.P. (1998) Diversidad, estructura y funcionamiento de ecosistemas costeros rocosos del norte de Chile. *Revista Chilena de Historia Natural* 71, 479–499.
- Villagrán, C. (1995) El Cuaternario en Chile: evidencias de cambio climático. In *Cambios cuaternarios en América del Sur* (Argollo, J., Mourguíart, P.H., eds.), pp. 191–214. ORSTOM: La Paz.

- Viviani, C.A. (1979) Ecogeografía del litoral chileno. *Studies on Neotropical Fauna and Environment* 14, 65–123.
- Voituriez, B. & Jacques, G. (2000) *El Niño: Fact and Fiction*. UNESCO: France.
- Yáñez, Y., González, A. & Barbieri, M.A. (1995) Estructura térmica superficial del mar asociada a la distribución espacio-temporal de sardina y anchoveta en la zona norte de Chile entre 1987 y 1992. *Investigaciones Marinas, Valparaíso* 23, 123–147.
- Walker, T.I. (1998) Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries. *Marine and Freshwater Research* 49, 553–572.
- White, W. & Walker, A.E. (1974) Time and depth scales of anomalous subsurface temperatures of Ocean Weather Stations P, N and V in the North Pacific. *Geophysical Research* 79, 4517–4522.
- Zhang, Q., Guan, Y. & Yang, H. (2008) ENSO amplitude change in observation and coupled models. *Advances in Atmospheric Science* 25, 361–366.

CHAPTER 2
TAXONOMY



2.1. First record of *Mobula japanica* (Rajiformes: Myliobatidae) from the south-eastern Pacific Ocean

Originally published in Marine Biodiversity Records (eISSN: 1755-2672)

Copyright © Marine Biological Association of the United Kingdom, 2012

Published online: 25 May 2012

License Number: 3216930517601

Abstract

The spinetail devilray Mobula japanica was recorded for the first time in the south-eastern Pacific Ocean, from a single beach washed specimen examined at Bahía Ingresa, Chile. The presence of this temperate-tropical species at about 27° south of its previously recorded range in the eastern Pacific Ocean may be explained by the absence of rigorous species-specific landing reports along the coasts of Peru and Chile. Alternatively, a strong warm phase of El Niño Southern Oscillation may have facilitated conditions allowing this epipelagic species to travel towards higher latitudes. This record increases the known range of M. japanica and the occurrence of mobulids in Chilean waters to three species. Photographs and morphometrics of the specimen are provided.

INTRODUCTION

The spinetail devilray *Mobula japanica* (Müller & Henle 1841) is a large zooplanktivorous ray circum-globally distributed within tropical to warm temperate waters (Notarbartolo-di-Sciara, 1987; White *et al.*, 2006; Couturier *et al.*, 2012). However, detailed information on its distribution and biology remain scarce. This species belongs to the family Myliobatidae, which includes the largest living rays, and among it can be found the manta (*Manta* Bancroft, 1829) and devil (*Mobula* Rafinesque, 1810) rays. The genus *Mobula* is currently represented by nine recognised species (Notarbartolo-di-Sciara, 1987) and *Manta* by two species (Marshall *et al.*, 2009). The genera are separated by the position of the mouth, which is located ventrally in *Mobula* and is terminal in *Manta*. *Mobula japanica* is a highly mobile epipelagic ray that reaches 3.1 m disc width (Notarbartolo-di-Sciara, 1987) and occurs in both shallow-inshore and deeper offshore environments, with seasonal aggregations in highly productive areas, such as the Gulf of California (Notarbartolo-di-Sciara, 1988).

Although the fishing effort in the southeastern Pacific Ocean has increased significantly over the last 20 years (Lamilla *et al.*, 2010), the distribution patterns of myliobatid rays in this region are poorly known. While eagle rays (*Myliobatis*, Cuvier 1816) and devil rays have been reported in trawl, coastal gill nets and longline catches, relatively little is known about these specimens (Pequeño, 1989; Lamilla *et al.*, 2005).

Four mobulid species have been confirmed in the southeastern Pacific Ocean: *Mobula munkiana* Notarbartolo-di-Sciara 1987 can be found from Ecuador to Peru (Bizzarro *et al.*, 2006); *Manta birostris* (Walbaum 1792) occurs between 0° (Ecuador) and 18° S (south Peru) and, although not reported in the literature, the presence of the species in southern locations is possible as *M. birostris* occurs up to 34° S in the southwestern Atlantic (Marshall *et al.*, 2011) and 35° S in the southwestern Pacific Oceans (Kashiwagi *et al.*, 2011); *Mobula thurstoni* (Lloyd 1908) and *Mobula tarapacana* (Philippi 1892) are the only mobulid species reported within Chilean waters, with the southernmost record for *M. thurstoni* at 37° S (Clark *et al.*, 2006). Historical records of these two *Mobula* species suggest a small distribution range in the Peru-Chile border region (Beebe & Tee-Van, 1941; Fowler, 1945; Mann, 1954; De Buen, 1959; Pequeño, 1989). The absence of fishery specimens for these *Mobula* species has resulted in a paucity of verified biodiversity records for this species, despite unconfirmed anecdotal reports by coastal fishermen (Lamilla *et al.*, 2010).

This article presents the first record of *M. japanica* in the southeastern Pacific, with one specimen from Bahía Inglesa, Chile.

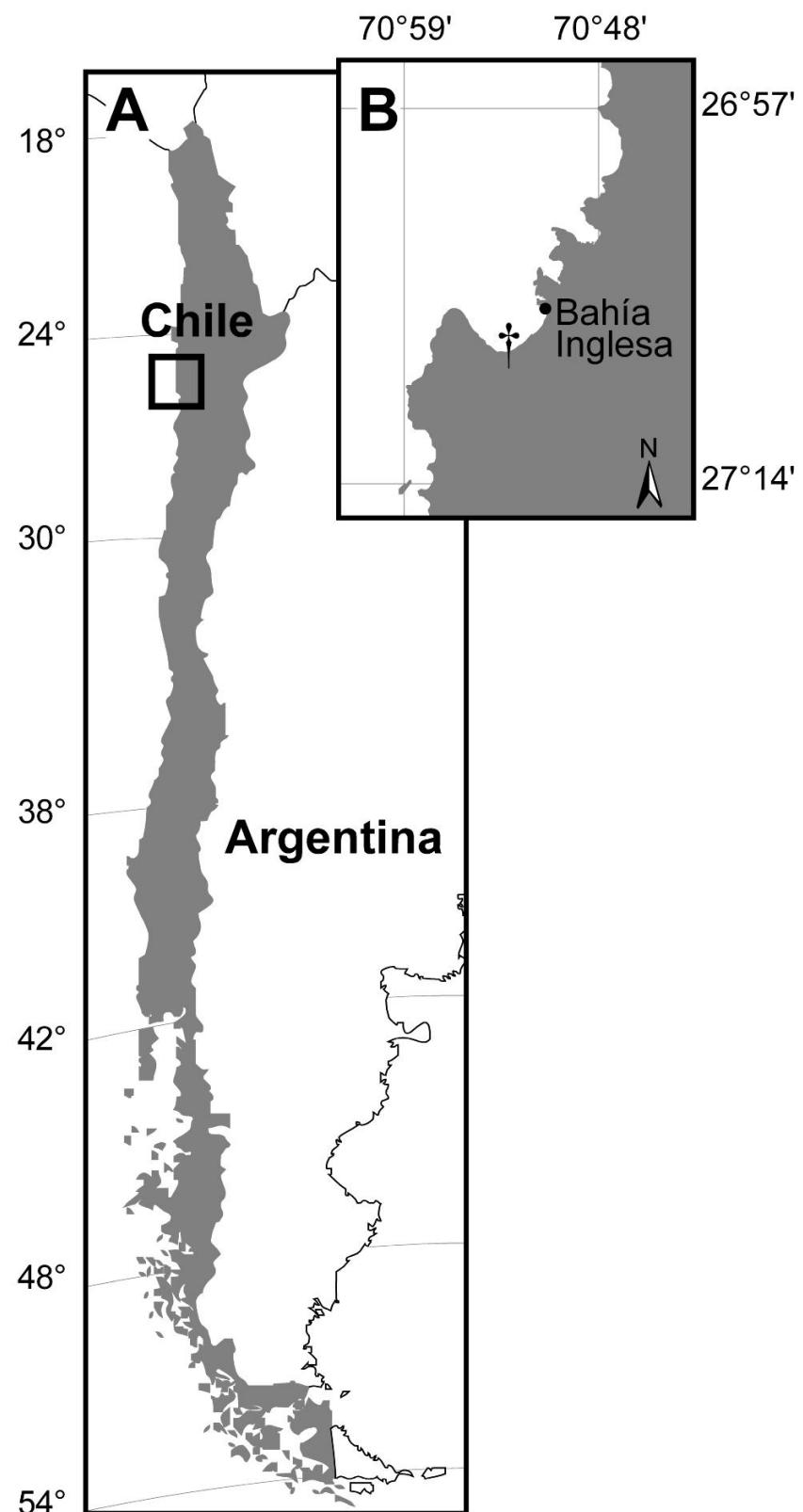


Figure 3 Map of Chile (A) showing location of Bahía Ingresa (B). † indicates collection site of specimen of *Mobula japonica*.

MATERIALS AND METHODS

One beached-washed *M. japanica* was collected near Bahía Ingresa, Chile ($27^{\circ}08' 32''$ S $70^{\circ} 53' 03''$ W), in February 2010 (Fig. 3). At the time of examination, the specimen was dead, gutted and finned (both pectoral fins removed). No evidence of any fishing gear was observed. Twenty-two morphometric measurements were made on the carcass to the nearest 1 mm following Notarbartolo-di-Sciara (1987), and the lateral lobes of the left-side gill filter-plates were counted. The sex was determined by the absence of claspers, but no observations were made of internal organs.

The body proportions of the specimen is presented as a percentage of disc length, and compared with those of 19 museum specimens from the Eastern Central Pacific (converted from disc width values provided by Notarbartolo-di-Sciara, 1987) and a specimen from North Stradbroke Island, Australia (Museum accession number QMI.38137 extracted from Townsend & Kyne, 2010). Due to the large size of the carcass, only the head and the first gill filter-plates were preserved and deposited in the Marine Fishes Collection of the Universidad Austral de Chile (IZUA-PM 4058).

Characteristic features of *Mobula japanica* were extracted from Notarbartolo-di-Sciara (1987) and Last & Stevens (2009), and include: disc broad; dark blue dorsal coloration with occasional lighter shoulder patches; caudal spine; white tip on dorsal fin; very long tail; and spiracles positioned above the plane of pectoral fins.

SYSTEMATICS

Order RAJIFORMES Berg 1940

Family MOBULIDAE Bonaparte 1838

Genus *Mobula* Rafinesque 1810

Mobula japanica (Müller & Henle 1841)

(Figure 4; Table 4)

Cephaloptera japanica Müller & Henle (1841:185); *Cephaloptera japonica* Gray (1851: 134);

Aodon japonicus Jordan & Snyder (1901: 43); *Mobula rancureli* Cadenat (1959: 1326)

RESULTS AND DISCUSSION

A mid-size (1065 mm disc length) female ray (Fig. 4A) was found dead on the beach. The cause of death could not be determined. Morphological measurements of the specimen fell within the ranges provided by Notarbartolo-di-Sciara (1987), with the exception of the preoral length in spite of the differing states of preservation between the specimens (Table 4).

Distinctive features could be identified from the remains, such as the elliptical spiracles located above the level of pectoral fins (Fig. 4B), gill filter-plates with 20–24 lateral lobes, the white tip to dorsal fin and an oval-based stinging spine in the base of tail (Fig. 4C). Together, these features allow the specimen to be clearly differentiated from other *Mobula* species reported in the southeastern Pacific Ocean. *Mobula thurstoni* has small and circular spiracles, fused gill filter-plates with 15–20 lateral lobes and lacks a caudal spine. *Mobula tarapacana* has elongated longitudinal spiracles, 50–65 lateral lobes to the gill filter-plates and no caudal spine. *Mobula munkiana* is the smallest mobulid species, reaching up to 1 m disc width, and has small subcircular spiracles, 50–60 lateral lobes to the gill filter-plates and no caudal spine.

The presence of *M. japanica* at c. 27° southward of its reported distribution may be explained by the absence of rigorous species-specific fishery reports of landings along the coast of Peru and Chile, making it difficult to differentiate between mobulid species in the area (CPPS, 2010). However, the absence of capture or sighting records in landing statistics, technical reports or local newspapers suggests that *M. japanica* is rare in Chilean waters. It is possible, however, that this species is caught in gillnet fisheries that target anchovies and sardines in the region. Bycatch of other large elasmobranchs, such as the smooth hammerhead *Sphyrna zygaena* (Linnaeus 1758) and the Chilean eagle ray *Myliobatis chilensis* Philippi 1892, has been observed previously in these fisheries (C. Bustamante, *unpublished data*). Such large species are usually finned and the carcasses discarded. Whether the specimen examined represents bycatch discard or was stranded on the beach is unknown.

An alternative explanation to the lack of fishery records may be the presence of a strong warm phase of El Niño Southern Oscillation (ENSO) during 2010 (Montecinos *et al.*, 2011). The coastal fringe off northern Chile and southern Peru is characterised by upwelling processes (Arntz *et al.*, 2006), fuelling the ecosystem with cold waters and high levels of primary production (Barber & Smith, 1981). This cold water mass, normally present all year, may act as a natural barrier to southerly movements of tropical and subtropical fauna (Smith, 1992; Figueroa 2002). A disruption of this barrier, as occurs with warm phases of the ENSO, can facilitate a latitudinal displacement of tropical fauna allowing migrant species of Panamic origin to invade the Peruvian and Chilean

coastal waters (Sielfeld *et al.* 2010). At least 100 tropical fishes labelled as “septentrional invaders of the Peru Current” have been documented as ‘alien’ species in latitudes south of their natural distribution range (Mann, 1954; Sielfeld *et al.* 2010).

Based on our observations, we confirm the presence of *Mobula japonica* for the first time in the southeastern Pacific Ocean. This record from Chilean waters increases the known range of *M. japonica*, and raises the number of mobulid species recorded in Chilean waters to three along with *M. tarapacana* and *M. thurstoni* (Pequeño, 1989).

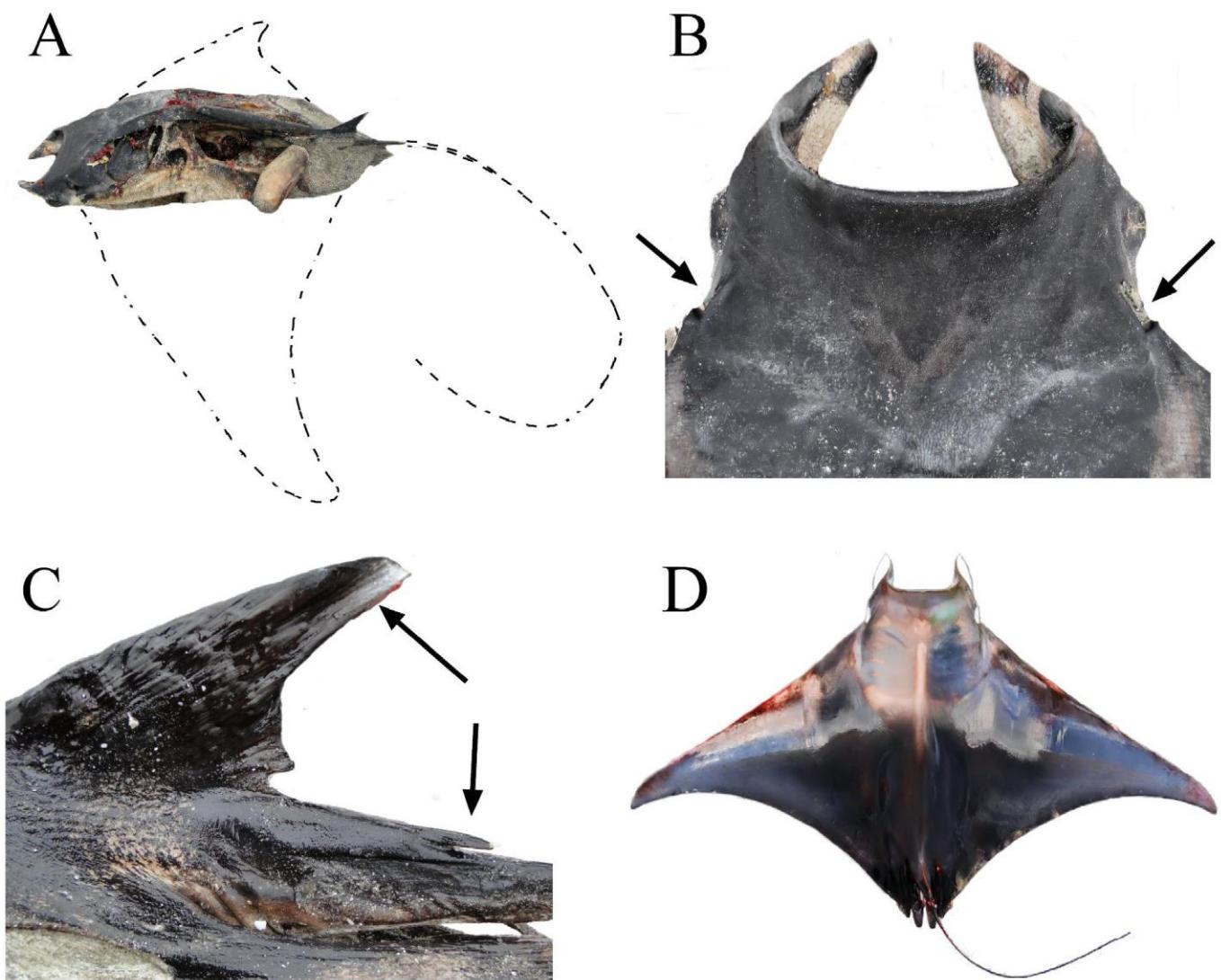


Figure 4 *Mobula japonica* (IZUA-PM 4058) from Bahía Ingresa, Chile. (A) pectoral fins and tail projection based on Notarbartolo-di-Sciara (1987); details of (B) head and (C) dorsal fin; (D) specimen from North Stradbroke Island, Australia (Townsend & Kyne, 2010). Arrows indicate the position of spiracles (B), white tip on dorsal fin and spine (C).

Table 4 Proportional dimensions as percentage of the disc length for *Mobula japonica* from North Stradbroke Island, Australia (QMI.38137); and Bahía Inglesa, Chile (IZUA-PM 4058), and range values converted from Notarbartolo-di-Sciara (1987).

Measurement	Range	North	Bahía Inglesa
	(North Pacific Ocean)	Stradbroke Is.	
Disc length (mm)	1074–2443	2446	1065
Rostrum to pelvic fin	0.919–1.128	1.029	1.028
Predorsal distance	0.750–0.887	0.847	0.868
Dorsal fin base length	0.078–0.111	0.077	0.095
Dorsal fin height	0.070–0.094	0.083	0.075
Precloacal distance	0.738–0.864	0.811	0.821
1st gill opening length	0.094–0.115	0.103	0.094
2nd gill opening length	0.103–0.125	0.110	0.109
3rd gill opening length	0.099–0.123	0.112	0.110
4th gill opening length	0.088–0.117	0.107	0.111
5th gill opening length	0.068–0.088	0.081	0.078
1st interbranchial distance	0.217–0.239	0.224	0.219
5th interbranchial distance	0.092–0.139	0.103	0.103
Rostrum to 1st gill openings	0.207–0.243	0.224	0.222
Rostrum to 5th gill openings	0.388–0.444	0.414	0.403
Cephalic fin length	0.235–0.255	0.235	0.236
Diameter of eye ball	0.042–0.052	0.039	0.047
Cranial width	0.298–0.340	0.346	0.311
Preoral length	0.076–0.086	0.107	0.071
Head length	0.265–0.328	0.281	0.292
Mouth width	0.221–0.253	0.228	0.228
Internarial distance	0.199–0.221	0.199	0.207

REFERENCES

- Arntz, W.E., Gallardo, V.A., Gutiérrez, D., Isla, E., Levin, L.A., Mendo, J., Neira, C., Rowe, G.T., Tarazona, J. & Wolff, M. (2006) El Niño and similar perturbation effects on the benthos of the Humboldt, California, and Benguela Current upwelling ecosystems. *Advances in Geosciences* 6, 243–265.
- Barber, R.T. & Smith R.L. (1981) Coastal upwelling ecosystems. In *Analysis of marine ecosystems* (Longhurst, A.R., ed.), pp. 31–68. Academic Press: London.
- Beebe W. & Tee-Van J. (1941) Fishes from the tropical eastern Pacific. Rays, mantas and chimaeras. *Zoologica* 26, 245–280.
- Bizzarro, J.J., Smith, W.D. & Clark, T.B. (2006) *Mobula munkiana*. In *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.2. Available at <http://www.iucnredlist.org>. (accessed 25 Sept 2011).
- Clark, T.B., Smith, W.D. & Bizzarro J.J. (2006) *Mobula thurstoni*. In *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.2. Available at <http://www.iucnredlist.org>. (accessed 25 Sept 2011).
- Couturier, L.I.E., Marshall, A.D., Jaine, F.R.A., Kashiwagi, T., Pierce, S.J., Townsend, K.A., Weeks, S.J., Bennett, M.B. & Richardson, A.J. (2012) Biology, ecology and conservation of mobulid rays, the Mobulidae (Gill 1893). *Journal of Fish Biology* 80, 1075–1119.
- CPPS (2010) *Plan de Acción Regional para la Conservación de tiburones, rayas y quimeras en el Pacífico Sudeste*. Comisión Permanente del Pacífico Sur (CPPS), Guayaquil, Ecuador, Res. No 8.
- De Buen, F. (1959) Notas preliminares sobre la fauna marina preabismal de Chile, con descripción de una familia de rayas, dos géneros y siete especies nuevas. *Boletín del Museo de Historia Natural, Chile* 27, 171–202.
- Eschmeyer, W.N. & Fong, J.D. (2011) Pisces. In *Animal biodiversity: An outline of higher-level classification and survey of taxonomic richness* (Zhang, Z.-Q., ed.). *Zootaxa* 3148, 26–38.
- Figueroa, D. (2002) Forcing of physical exchange in the nearshore Chilean Ocean. In *The oceanography and ecology of the nearshore and bays in Chile* (Castilla, J.C. & Largier J.L., eds.), pp. 31–43. Ediciones Universidad Católica de Chile: Santiago de Chile.
- Fowler, H.W. (1945) Fishes of Chile, Systematic Catalog. *Apartado Revista Chilena de Historia Natural* Parts I and II, 36–171.

- Kashiwagi, T., Marshall, A.D., Bennett, M.B. & Ovenden, J.R. (2011) Habitat segregation and mosaic sympatry of the two species of manta ray in the Indian and Pacific Oceans: *Manta alfredi* and *M. birostris*. *Marine Biodiversity Records* 4, e53.
- Lamilla, J., Acuña, E., Araya, M., Oliva, M., Kong, I., Villaroel, J.C., Hernández, S., Concha, F., Vögler, R., Bustamante, C. & Mutche E. (2005) Lineamientos básicos para desarrollar el Plan de Acción Nacional de Tiburones. *Universidad Austral de Chile Informe técnico No. 2004-18, Valdivia*. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 Sept 2013).
- Lamilla, J., Bustamante, C., Roa, R., Acuña, E., Concha, F., Meléndez, R., López, S., Aedo, G., Flores, H. & Vargas-Caro C. (2010). Estimación del descarte de condriictios en pesquerías artesanales. *Universidad Austral de Chile Informe técnico No. 2008-60, Valdivia*. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 Sept 2013).
- Last, P.R. & Stevens, J.D. (2009) *Sharks and rays of Australia*, 2nd Ed. CSIRO Marine and Atmospheric Research: Hobart.
- Mann, G. (1954) *La vida de los peces en aguas chilenas*. Instituto de Investigaciones Veterinarias. Universidad de Chile: Santiago.
- Marshall, A.D., Bennett, M.B., Kodja, G., Hinojosa-Alvarez, S., Galván-Magaña, F., Harding, M., Stevens, G. & Kashiwagi T. (2011) *Manta birostris*. In *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.2. Available at <http://www.iucnredlist.org>. (accessed 25 Sept 2013).
- Marshall, A.D., Compagno, L.J.V. & Bennett, M.B. (2009) Redescription of the genus *Manta* with resurrection of *Manta alfredi* (Krefft, 1868) (Chondrichthyes; Myliobatoidei; Mobulidae). *Zootaxa* 2301, 1–28.
- Montecinos, A., Kurgansky, M.V., Muñoz, C. & Takahashi, K. (2011) Non-ENSO interannual rainfall variability in central Chile during austral winter. *Theoretical and Applied Climatology* 106, 557–568.
- Notarbartolo-di-Sciara, G. (1987) A revisionary study of the genus *Mobula* Rafinesque, 1810 (Chondrichthyes: Mobulidae) with the description of a new species. *Zoological Journal of the Linnean Society* 91, 1–91.
- Notarbartolo-di-Sciara, G. (1988) Natural history of the rays of the genus *Mobula* in the Gulf of California. *Fishery Bulletin* 86, 45–66.
- Pequeño, G. (1989) Peces de Chile. Lista sistemática revisada y comentada. *Revista de Biología Marina, Valparaíso* 24, 1–132.

- Sielfeld, W., Laudien, J., Vargas, M. & Villegas M. (2010) El Niño induced changes of the coastal fish fauna off northern Chile and implications for ichthyogeography. *Revista de Biología Marina y Oceanografía* 45, 705–722.
- Smith, R.L. (1992) Coastal upwelling in the modern ocean. In *Upwelling systems: evolution since the early Miocene* (Summerhayes, C.P., Prell, W.L. & Emeis K.C., eds.), pp. 9–28. Geological Society Special Publication 64.
- Townsend, K.A. & Kyne, P.M. (2010) New records of the Japanese devilray *Mobula japonica* (Müller & Henle 1841) for Australian waters. *Memoirs of the Queensland Museum-Nature* 55, 225–230.
- White, W.T., Clark, T.B., Smith, W.D. & Bizzarro, J.J. (2006). *Mobula japonica*. In *IUCN 2011. IUCN Red List of Threatened Species*. Version 2011.2. Available at <http://www.iucnredlist.org>. (accessed 25 Sept 2013).

2.2. Morphological characters of the thickbody skate *Amblyraja frerichsi* (Krefft 1968) (Rajiformes: Rajidae), with notes on its biology

Originally published in PLoS ONE (eISSN: 1932-6203)

Copyright © Carlos Bustamante, 2012

Published online: 29 June 2012

License Number: open-access article

Abstract

Detailed descriptions of morphological features, morphometrics, neurocranium anatomy, clasper structure and egg case descriptions are provided for the thickbody skate Amblyraja frerichsi; a rare, deep-water species from Chile, Argentina and Falkland Islands. The species diagnosis is complemented from new observations and aspects such as colour, size and distribution are described. Geographic and bathymetric distributional ranges are discussed as relevant features of this taxon's biology. Additionally, the conservation status is assessed including bycatch records from Chilean fisheries.

INTRODUCTION

The genus *Amblyraja* Malm 1877 (Rajiformes: Rajidae) is a group of wide-ranging, circumglobal, stout bodied skates that are found mostly at higher latitudes (Kyne & Simpfendorfer, 2010) and in deep tropical waters (Ebert & Winton, 2010), mostly on outer continental shelves, insular shelves and slopes, and around seamounts (Ebert & Compagno, 2007). The genus as currently includes ten nominal species with perhaps two additional undescribed species. In the south-east Pacific Ocean three poorly known species are recognized (Lamilla & Bustamante, 2005): *Amblyraja doellojuradoi* (Pozzi 1935), *A. frerichsi* (Krefft 1968) and *A. georgiana* (Norman 1938).

Amblyraja doellojuradoi occurs from off Argentina and the Falkland Islands through the Magellan Strait to off Punta Arenas, Chile at a reported depth range of 51 to 642 m (Menni & Stehmann, 2000). *Amblyraja georgiana*, a morphologically similar species to *A. frerichsi*, is an Antarctic species known from the Antarctic Peninsula (Pequeño, 1997; Pequeño & Lamilla, 1985) and South Georgia Island from a depth range of 150 to about 800 m. Perhaps the least known species in the region is the thickbody skate *A. frerichsi*. Originally described from a type series of 35 subadult and immature specimens (Krefft, 1968) collected between 800 and 1000 m off the Rio de la Plata, Argentina/Uruguay common fishing zone; this species has been reported as a rare species in deepwater off Brazil, Argentina and the Falkland Islands (Krefft, 1968; Bizikov *et al.*, 2004; Cousseau *et al.*, 2007). Recently, high bycatch rates of *A. frerichsi* have been reported from the Magellan Strait (Reyes & Torres-Florez, 2009). However, due to a lack of adult descriptive material and proper field guides, this species largely went unnoticed in Chile and Argentina deep-sea fisheries. The absence of comparative material and a species-specific description of adults have lead to unregulated bycatch landings and a lack of capture records due to misidentification (Lamilla *et al.*, 2010), due in part, to a relatively high degree of variability of morphological characters for this family of elasmobranchs (Ebert & Compagno, 2007; Ebert & Winton, 2010).

Complementary descriptions of the anatomy are usually made to clarify the taxonomic status of an important fishery species, which enabled on-board observers to determine species-specific landings (Walsh & Ebert, 2007). Skates worldwide are taken in considerable numbers either as a directed fishery or indirectly as bycatch (Ebert & Sulikowski, 2007) and given that many of skates are landed in large numbers and in a mixture of species, it is critically important that accurate morphological descriptions of both adult and subadult fish are available.

The aim of this research is to provide a detailed morphological description of *A. frerichsi* from specimens taken as bycatch in Chilean waters. The neurocranium, clasper, dermal denticles and egg case morphology are presented as characters to facilitate identification among other

Amblyraja species in the area. New information on the habitat and fisheries, together with a discussion of the related conservation implications for this species for the south-east Pacific are also provided.

MATERIAL AND METHODS

The specimens used in this study came from historical and recent bycatch records in the Patagonian toothfish (*Dissostichus eleginoides* Smitt 1898) fishery from southern Chile (Fig. 5, Table 5). A total of 13 males with sizes between 705 to 1201 mm total length (TL) (mean and standard deviation; 1068 ± 163 mm), were caught between 1989 and 1993, and donated by artisanal fishermen to ELASMOLAB: two specimens were from off Valdivia (1989), four specimens were from Arauco (1990), and seven specimens were captured between Isla Guamblin and Golfo Ladrilleros (1993). In addition, 26 females ranging in size from 442 to 1762 mm TL (905 ± 368 mm) and 26 males ranging between 404 and 1114 mm TL (835 ± 193 mm) were caught in the same fishery during 2009 within the research project FIP No. 2008-60, five from off Arauco and 47 from off Valdivia, and for which sample collection permits were obtained from the Maritime and Fisheries Authority.

Morphometric measurements and description of key characters were made in 35 specimens. All measurements were made to the nearest millimeter (mm), and follow recent recommendations in the literature (Last *et al.*, 2008). Terminology was adapted from recent literature for dermal denticles (Gravendeel *et al.*, 2002), egg capsules (Oddone *et al.*, 2004; Concha *et al.*, 2009), and clasper (Ishiyama, 1958; Stehmann, 1970) descriptions. The right clasper was removed from two adult males (1194 mm and 1201 mm TL) and both external and internal structures are described. The neurocranium was dissected and described from an adult male (1194 mm TL).

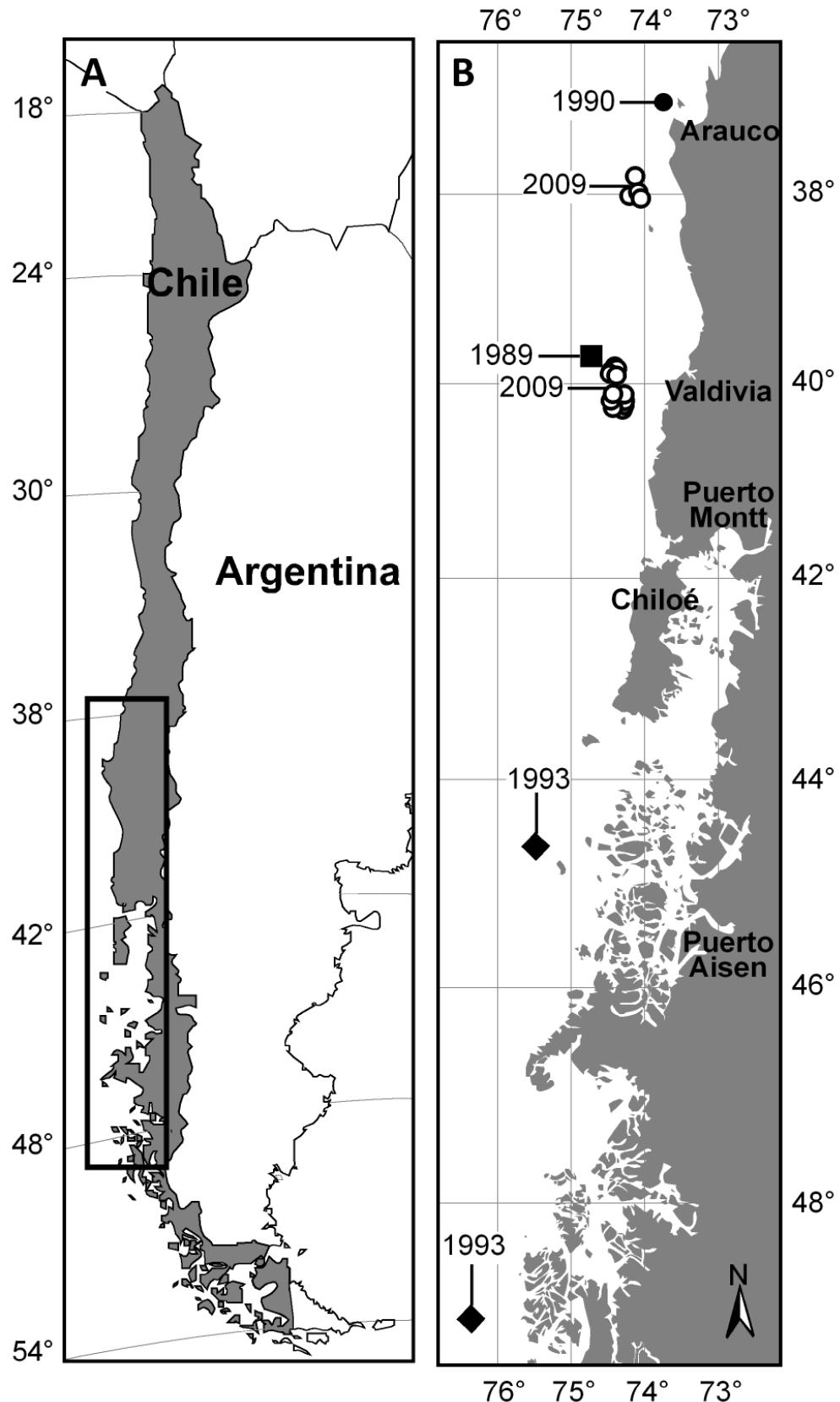


Figure 5 Map of Chile (A) showing location of study area (inset box), and collecting localities (B) by date.

Table 5 *Amblyraja frerichsi* catches location, sex and depth by year of historical and recent collections.

Year	Depth (m)	Sex	Geographical position
1993	1,900	4 Male	44° 40' S; 75° 30' W
1993	2,200	3 Male	49° 01' S; 76° 20' W
1989	1,300	2 Male	39° 49' S; 74° 24' W
1990	1,990	4 Male	37° 00' S; 73° 45' W
2008	2,200	3 Female	37° 57' S; 74° 12' W
2008	2,200	1 Female	38° 01' S; 74° 14' W
2008	2,200	1 Female	37° 48' S; 74° 12' W
2009	1,280	1 Male	40° 08' S; 74° 17' W
2009	1,550	1 Female	40° 07' S; 74° 23' W
2009	1,520	1 Male	40° 05' S; 74° 22' W
2009	1,253	3 Male; 3 Female	40° 06' S; 74° 23' W
2009	1,150	6 Male; 5 Female	40° 02' S; 74° 24' W
2009	1,445	1 Male	40° 06' S; 74° 18' W
2009	1,317	2 Female	40° 06' S; 74° 17' W
2009	1,614	3 Male; 3 Female	40° 06' S; 74° 26' W
2009	1,075	1 Male	40° 06' S; 74° 23' W
2009	1,037	1 Female	40° 10' S; 74° 18' W
2009	1,414	1 Male; 2 Female	40° 08' S; 74° 24' W
2009	1,419	1 Male	40° 07' S; 74° 26' W
2009	1,729	5 Male; 1 Female	40° 05' S; 74° 23' W
2009	1,168	1 Male	39° 52' S; 74° 26' W
2009	1,168	1 Male; 1 Female	39° 52' S; 74° 26' W
2009	1,168	1 Male; 1 Female	39° 50' S; 74° 22' W
2009	1,168	1 Female	39° 53' S; 74° 22' W

General biological data were also recorded to estimate the size at maturity, females were considered mature when yellow ovarian follicles and/or egg capsules were present (Oddone & Velasco, 2004). Males were considered mature if sperm were present in their seminal vesicles, and their claspers were calcified and rigid (Sosebee, 2005).

Two adult specimens, one male (1094 mm LT) and one female (1213 mm LT, were preserved and deposited in the Marine Fishes Collection of Universidad Austral de Chile (Museum accession number IZUA-PM 4064 and IZUA-PM 4065). Egg capsules were extracted from a 1445 mm LT female and deposited at Universidad de Valparaíso Marine Fishes Collection (Museum accession number CCM-173 and CCM-174).

RESULTS

Amblyraja frerichsi (Krefft 1968)

Thickbody skate (Figures 6–12; Tables 5–8)

Raja frerichsi (Krefft, 1968; Pequeño, 1997; Thiel *et al.*, 2009)

Raja (Amblyraja) frerichsi (Stehmann, 1970)

Amblyraja frerichsi (McEachran & Dunn, 1998; Compagno, 1999; Menni & Stehmann, 2000)

Diagnosis

A relatively large species of *Amblyraja* with the following combination of characters: quadrangular disc, 1.3 times its length and width 77% TL; tail evenly tapering and robust, width at base 1.3 times first dorsal-fin origin; snout length 23% disc length. Ventral and dorsal disc uniformly dark-brown to grey-brown colouration. Dorsal surface densely cover with small dermal denticles on the head, fins and tail; large hook-shaped denticles on the orbital series, one preorbital, one postorbital and one postspiracular; also one nuchal, one scapular and three suprascapular are present in the scapular series; and 8–26 in the midline of disc, from behind the scapula to tail. Adult clasper relatively large, 49% caudal length; and distal lobe extremely spatulate. Violin-shaped neurocranium with large and bulbous nasal capsules, with a relatively large rostral shaft ending in a widened rhomboidal rostral node. Dark brown and finely striated egg capsules with posterior horns longer than the anterior, both tapering towards the tips. Horns of egg capsules without lateral fibrils and coiled terminal tendrils.

Description

Disc quadrangular, 1.28 times as wide as long in adult specimens, width 77.4% TL, maximum disc width 59.1% TL (Fig. 6). Anterior margin of disc concave behind head, convex at eye level and concave at spiracle level. Outer margin of disc is acute angled and posterior margin is slightly convex almost straight. Snout short, preorbital snout length 0.9 times snout to spiracle length, 1.9 times interorbital space, 23.7% disc length (DL). Snout tip pointed, lacking distal process or filament. Orbit length 2.5 times interorbital space. Spiracle small, 0.9 times orbit length, 4.9% DL; opening subcircular in shape. Nostril sub-triangular to oval; anterior nasal flap forms an opening, posterior lobes not developed meeting medially to form nasal curtain; distal end sub-rectangular with curved fringe on the posterior margin. Internarial distance 2.2 times distance between first gill slits, 1.5 times distance between fifth gill slits. Mouth slightly arched in subadult males and females, curved in adult males; mouth width 1.2 times internarial distance. Teeth with a flat oval base and acute single cusp, arranged in quincunx without sexual dimorphism. Total tooth count in upper jaw 36 (42) arranged in four rows and in lower jaw 37 (40) arranged in five rows. Bilobed pelvic fins thin and tapering toward distal end; anterior lobe length 5.7% DL, with a broad posterior lobe with concave external margin. Strong tail broad, depressed, tapers from broad base to first dorsal fin. Tail moderately long, length 43.3% TL; width at insertions of pelvic fins 1.3 times width at first dorsal-fin origin. Lateral tail fold long and well developed, length 38% TL, origin after dorsal fins and extending to tail tip. Dorsal fins strongly acute with long bases and similar shape. First dorsal fin base length 2.2 times height; second dorsal fin base length 2.6 times height. Both fin apices angular; straight posterior inner margins and anterior margins convex. Dorsal fins sometimes separated by a space, with interdorsal distance 13% first dorsal-fin base length. Second dorsal fin continues to a short, undeveloped epichordal caudal lobe, 0.7 first dorsal-fin base length. Main morphometric characters expressed as a percentage of total length are found in Table 6.

Dermal denticles

Dorsal surface with a wide variety of dermal denticles, thornlets and thorns, but ventral surface with no squamation (Fig. 7A). Small dermal denticles (myrmecoid type), less than 2 mm in height on subadults and adults, have radial symmetry and cover the surface of eyelids, pelvic fins and tail, including dorsal and caudal fins. Basal plate (BP) edge serration of dermal denticles resembles a 4–6 ridged star (Fig. 7B). Thornlets are dermal denticles usually more than 3 mm height (in subadults and adults), similar in shape but larger and more robust than dermal denticles. Thornlets have a small BP with 7–9 straight furrows and elongated ridges; BP with a saddle-like

fold and crown curved backward staying within the BP. Thornlets are densely distributed in rostral and malar zones beside pectoral fins and parallel, lateral rows in tail. Additionally, larger denticles that double in size and height thornlets (usually 60–80 mm height in subadults and adults) are called thorns, and are distributed around head (Fig. 7C) and tail (Fig. 7D). The orbital series has three thorns, two in the inner orbit proximal (preorbital) and distal (postorbital) margins, one behind spiracle (postspiracular); suprascapular series has one nuchal, one scapular and three suprascapular thorns, the latter forming a triangle. In the midline 18–26 thorns are present from the disc, behind the scapula at level of the maximum disc width, to the tail. Thorns BP have fine radial ridges; wavy-lined lobed edges in a regular elliptic shape without elongated ridges or furrows. Thorns acute and curved crown is only one third of BP height and reaches BP margin. Alar hooks (thorns-like) found only in adult males in six to eight longitudinal rows near the edge of pectoral fins. When an interdorsal space is present, one or two thornlets of variable size present.

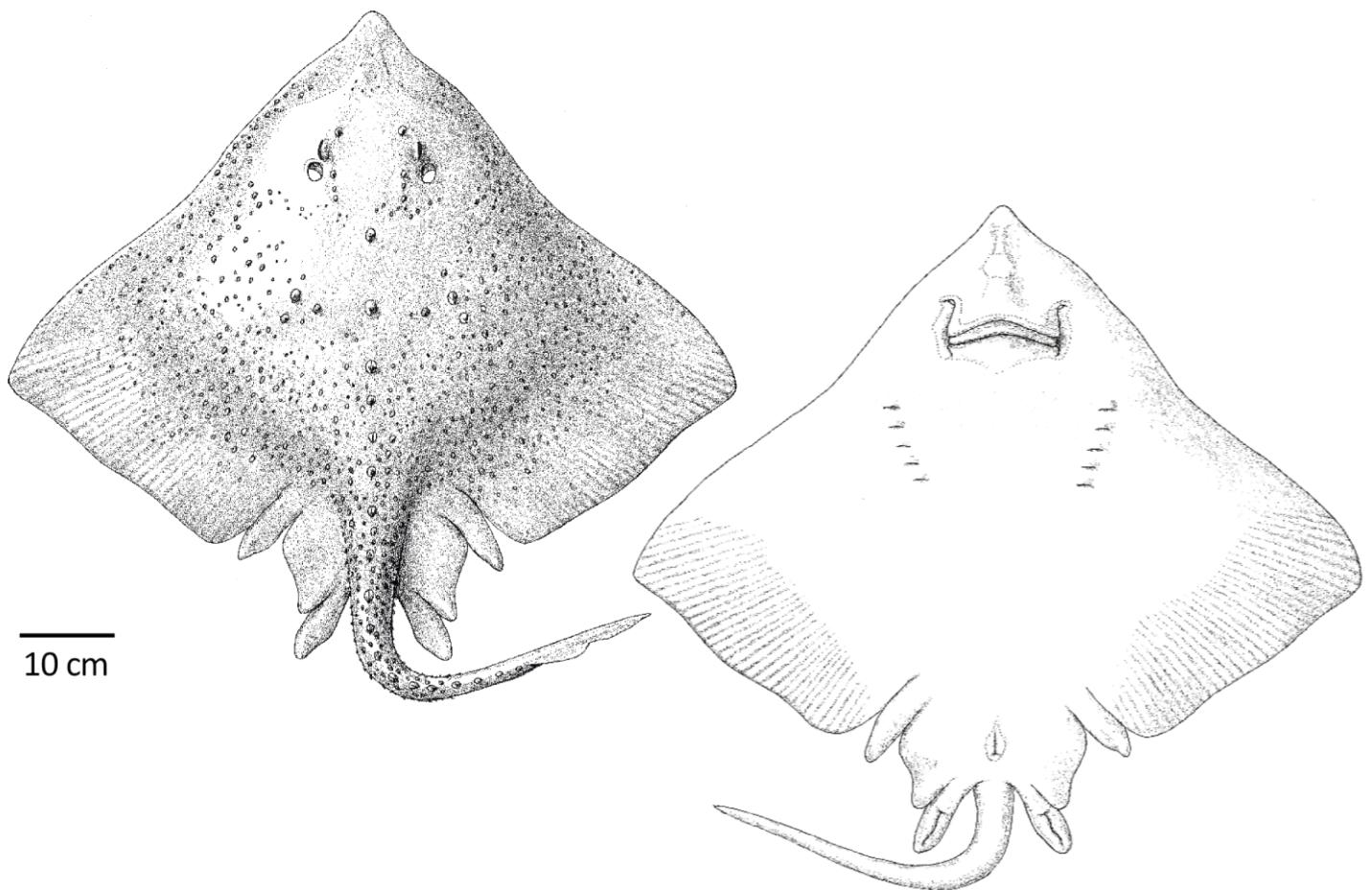


Figure 6 Adult male of *Amblyraja frerichsi* (1051 mm TL) in dorsal (A) and ventral (B) views.
Scale bar 100 mm.

Table 6 Measurements (mm) of the morphometric characters taken from 35 specimens of *Amblyraja frerichi*. Range expressed as percentage of total length (TL). Mean value (Mean) and standard deviation (s.d.) are indicated in each case.

Morphometric character	Min.	Max.	Mean	s.d.
Disc width (DW)	70.77	80.74	77.39	2.54
Disc length (DL)	55.42	59.08	56.73	1.04
Snout length (preorbital direct)	12	14.78	13.46	0.91
Snout to spiracle	13	15.61	14.32	0.87
Head (dorsal length)	18.37	21.84	19.90	1.02
Eye diameter	2.47	3.16	2.87	0.22
Orbit diameter	2.91	5.07	4.35	0.57
Orbit and spiracle length	4.63	6.38	5.29	0.49
Spiracle length (main aperture)	2.57	3.27	2.81	0.23
Distance between orbits	6.47	8.04	7.10	0.40
Distance between spiracles	5.83	10.69	8.92	1.20
Snout to cloaca (1st hemal spine)	50.77	54.96	53.41	1.24
Distance-cloaca to caudal-fin tip	38.55	43.85	41.41	1.56
Ventral snout length (pre upper jaw)	10.59	15.49	12.66	1.44
Prenasal length	9.61	12.16	10.88	0.75
Ventral head length (to fifth gill)	26.3	30.81	29.26	1.29
Mouth width	9.66	12.33	11.23	0.74
Distance between nostrils	8.87	10.56	9.79	0.57
Nasal curtain (total width)	12.8	14.64	13.77	0.64
Width of first gill opening	1.48	2.16	1.76	0.22
Width of fifth gill opening	1.2	2.2	1.63	0.27
Distance between first gill openings	19.4	23.14	21.16	1.17
Distance between fifth gill openings	13.66	15.78	14.59	0.74
Length of anterior pelvic lobe	8.34	11.89	9.92	1.07
Tail at axil of pelvic fins (width)	3.22	4.65	3.88	0.38
Tail at first dorsal-fin origin (width)	2.5	3.36	2.94	0.28
D1 base length	3.63	4.87	4.35	0.43
D2 base length	3.53	5.69	4.89	0.63
D1 height	1.7	2.44	1.97	0.21
D2 height	1.57	2.13	1.86	0.20
Interdorsal space	0	1.77	0.60	0.56
Caudal-fin length	1.75	3.87	3.15	0.61
Tail lateral folding	35.52	41.93	38.31	1.89

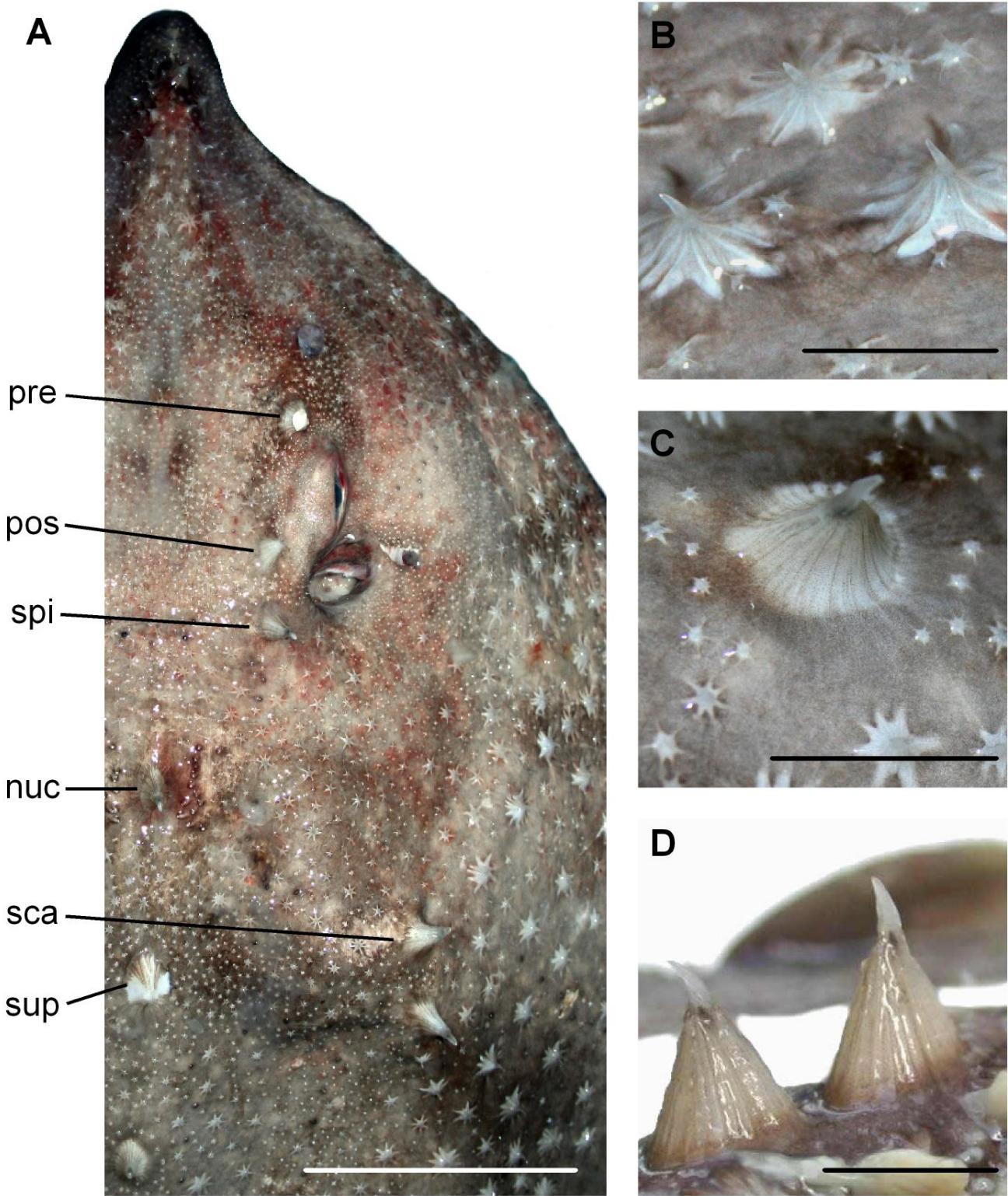


Figure 7 Dermal denticles of *Amblyraja frerichi*. Dorsal view of the head (**A**) showing the snout and orbito-spiracular, nuchal and scapular thorns. Detailed view of malar (**B**), midline (**C**), and tail (**D**) thorns. (pre) preorbital, (pos) postorbital, (spi) spiracular, (nuc) nuchal, (sca) scapular, (sup) suprascapular. Scale bar 50 mm (**A**) or 10 mm (**B–D**).

Colour

Dorsal disc of fresh adult and subadult male is dark-brown except blackish-brown distal edges, pelvic fins, tail, dorsal and caudal fins. Ventral surface uniformly dark-brown (Fig. 8). Dorsal colouration of female is greyish-brown; disc margins, scapulae and pelvic fins darker. Tail, dorsal and caudal fins are blackish-brown. In adult males, dorsal and ventral surface is grey-brown with disc margins, scapulae, pelvic fins, tail and snout a darker shade. Anterior lobe of pelvic fins, mouth edges, nasal curtain, cloaca and gill slits are white in all individuals. Sensory pores clearly visible on the ventral side around the snout and mouth margins. Sometimes there is a white triangular patch, where the first two vertices point to the fifth gill slit and the third vertex to the cloaca. Another oval spot can be seen usually at the end of the nose. Immature specimen (<400 mm TL) may have white blotches between gill slits.



Figure 8 Coloration of *Amblyraja frerichsi* subadult male (985 mm TL) in dorsal and ventral views.
Scale bar 100 mm.

Neurocranium

Neurocranium is violin-shaped (Fig. 9). Nasal capsules (**nc**) are large and bulbous, orientated 70° forward midline rostral cartilage. Ethmoidal canal foramen (**ecf**) is located beneath rostral base, between rostral cartilage (**rc**) and nasal capsules (**nc**). Preorbital canal foramen (**pcf**) is located in the distal margin of nasal capsules in the same longitudinal line of the jugal arches (**ja**). Strong, angular jugal arches surrounding the parietal fossa (**pfs**), with perilymphatic (**phf**) and endolymphatic (**eph**) foramina located in the inner margins. Rostral node (**rn**) is rhomboidal in shape with a pronounced concavity at the anterior margin. Rostral appendices (**ra**) have two small foramina, the larger with an inverted triangular-shape. Rostral appendices are c. 37% of rostral shaft (**rs**) length. Fontanelles separated by a small epiphyseal bridge (**eb**). Anterior fontanelle (**af**) is oval with a high resemblance to a blunt arrowhead; while posterior fontanelle (**pf**) is ovoid. Posterior fontanelle c. 68% of anterior fontanel length. Openings of nasal capsules are kidney-shaped with larger length in same orientation of nasal capsule. The lateral cranial roof is dorsally limited by the supraorbital crest (**sc**), with no visible foramina on surface. Neurocranium basal plate (**bp**) is short and narrow at orbit level. Dorsolateral and delimiting the otic capsule, is located the rounded pterotic process (**ptp**) which is continuous towards a low pterotic crest (**ptc**). Optic nerve foramen (**II**) is elliptic and rounded, located in mid-orbital wall. Dorsal to the optic nerve foramen are two small openings for the passage of the trochlear nerve (**IV**). Posteroventral to the optic nerve foramen is the foramen for the oculomotor nerve (**III**). Prootic foramen (**pof**) is located in distal margin near orbital fissure (**of**) and hyomandibular branch of facial nerve foramen (**hm VII**). The remaining branches of the trigeminal and facial nerves (**V+VII**) cannot be observed at naked eye. Morphometric measurements, expressed in mm and percentage of nasobasal length are shown in Table 7.

Clasper

Mature males of have moderately long, solid and distally widened claspers. Clasper length can reach 49% (36–50%) of caudal length in mature males, and all surfaces lack dermal denticles. In the dorsal surface (Fig. 10A), the pseudosiphon (**ps**) is located in the distal half of clasper and is continued by the cleft (**cf**), a narrow longitudinal fissure at same line with the rhipidion (**rh**). The slit (**sl**), a tissue infolding made by the division of axial cartilage and the proximal end of dorsal terminal cartilage 2, is located in the proximal half of clasper between **ps** and **cf**. In the outer lateral margin of dorsal lobe and in same line with **rh**, the spur (**sr**) is formed by the distal end of dorsal cartilage terminal 3. The shield (**sh**) is an elongated plate located in the internal ventral lobe,

dorsally convex with sharp edges extending from the hypopyle (**hp**) up to the pent (**pe**) and the sentinel (**st**) on its distal margin. The rhipidion (**rh**) is observed as a fan-shaped protruding structure which extends parallel to the clasper longitudinal axis and continues to **pe**, a structure deeply folded and covered with tissue. In its distal inner margin **st** is located, a thick structure, dorsally convex, funnel-like composed by the distal margin the terminal accessory cartilage 1. The spike (**sp**) is a small tab covered by tissue, with the tip pointing towards the dorsal lobe.

Table 7 Measurements (mm) of the neurocranium taken from one specimen of *Amblyraja frerichsi* (adult male 1194 mm TL) expressed as percentage of nasobasal length.

	mm	%
Nasobasal length	128.9	100
Cranial length	225	174.6
Rostral cartilage length	112.5	87.3
Prefontanelle length	71.6	55.5
Cranial width	129.4	100.4
Interorbital width	58.35	45.3
Rostral base	40.4	31.3
Anterior fontanelle length	63.5	49.3
Posterior fontanelle length	20.7	16.1
Anterior fontanelle width	43.2	33.5
Posterior fontanelle width	20	15.5
Rostral cleft length	94.2	73.1
Rostral appendix length	44.8	34.8
Rostral appendix width	32.7	25.4
Posterior foramen of rostral appendix length	33.15	25.7
Cranial height	32.8	25.4
Rostral cartilage height	24.2	18.8
Width across otic capsules	90.5	70.2
Least width of basal plate	38.25	29.7
Greatest width of nasal capsule	50.65	42.2
Internasal width	33.5	26.0

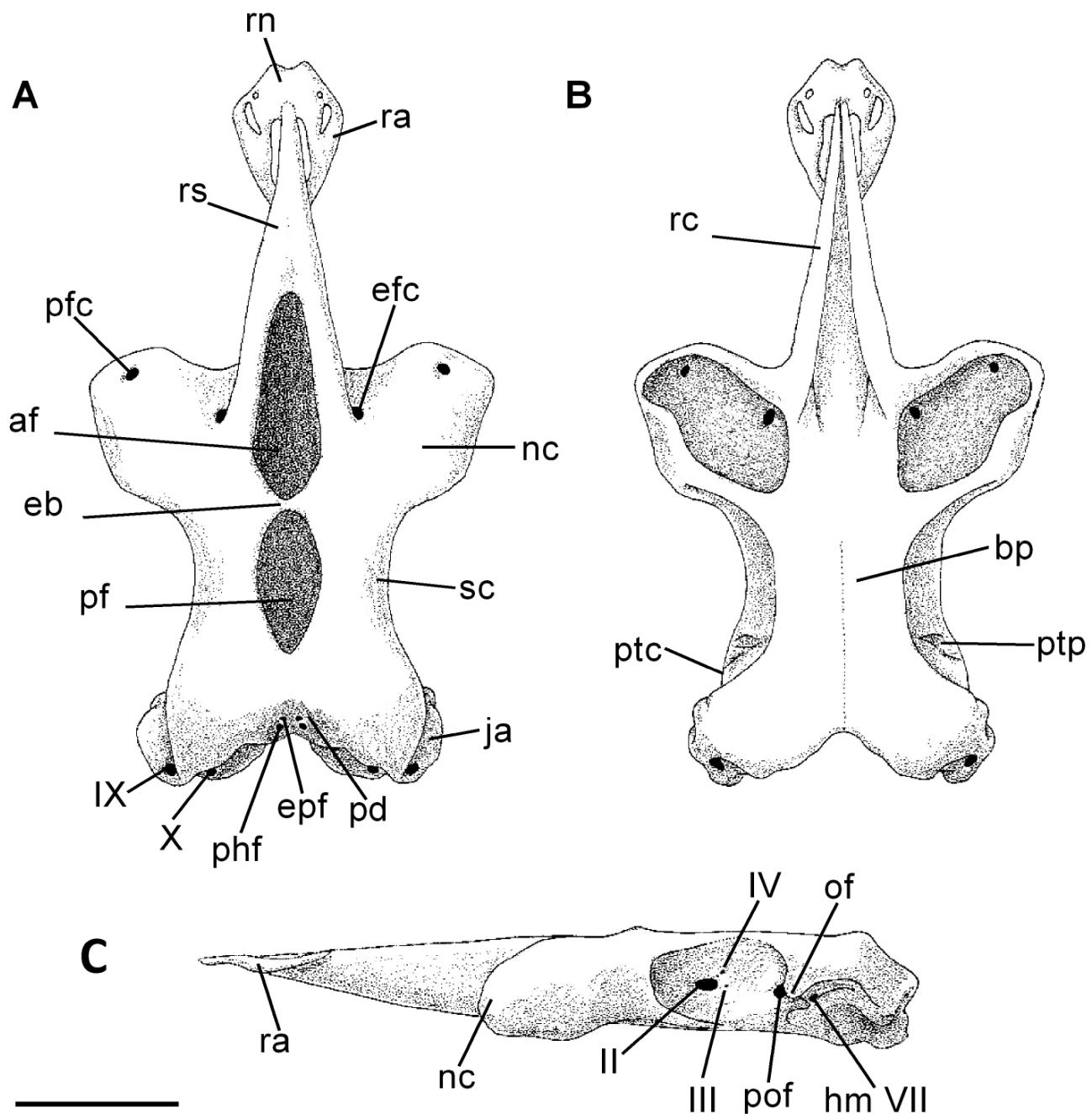


Figure 9 Neurocranium of *Amblyraja frerichsi* (adult male 1194 mm TL), in dorsal (A), ventral (B), and lateral (C) views. (af) anterior fontanelle, (bp) basal plate, (eb) epiphyseal bridge, (ecf) ethmoidal canal foramen, (ephf) endolymphatic foramen, (hm VII) hyomandibular branch foramen, (ja) jugal arches, (nc) nasal capsules, (of) orbital fissure, (pcf) preorbital canal foramen, (pd) parietal depression, (pf) posterior fontanelle, (phf) perilymphatic foramen, (pof) prootic foramen, (ptc) pteroptic crest, (ptp) pteroptic process, (ra) rostral appendix, (rc) rostral cartilage, (rn) rostral node, (rs) rostral shaft, (sc) supraorbital crest, (II) optic nerve foramen, (III) oculomotor nerve foramen, (IV) trochlear nerve foramen, (IX) glossopharyngeal nerve foramen, (X) vagus nerve foramen. Scale bar 50 mm.

The clasper skeleton (Fig. 10B) consists of the ellipsoidal axial cartilage (**ax**), that flattens dorso-ventrally towards distal margin where is spatulate; the **ax** is attached at two-thirds of its length to the dorsal marginal (**dm**) and ventral marginal (**vm**) cartilages. In the distal margin **ax** continues to the dorsal terminal cartilage 4 (**dt4**). Dorsal marginal cartilage (**dm**) is subrectangular, flattened and concave, tapering toward distal end and it expands abruptly to the joint to axial cartilage (Fig. 10B–11). Dorsal terminal cartilage 1 (**dt1**) is long, curved and flattened, with sharp edges (Fig. 11). The small curved t-shaped dorsal terminal cartilage 2 (**dt2**) is located at **dt1** proximal end; while the dorsal terminal cartilage 3 (**dt3**), is a flat triangle connected to **dt2** in the distal margin (Fig. 10B–11). Long, spatulated dorsal terminal cartilage 4 (**dt4**) joins **dt3** in the middle dorsal proximal end. Ventral marginal cartilage (**vm**) elongated with straight edges, ventrally curled and acute in the distal end (Fig. 10C – 11). Hook-shaped ventral terminal cartilage (**vt**) has a wide-base projection in middle of the inner edge. Distal half of **vt** surrounds accessory terminal cartilage 1 (**at1**) and is connected to **dtr1** distal end. Proximal half of **at1** has an acute, strongly curved appendix (Fig. 11), located below the **vmg** and connecting to **ax**. Accessory terminal cartilage 2 (**at2**) is small, curved claw-like, located below **at1** while proximal end is located under inner edge of **vm** and **at1** junction (Fig. 11).

Egg capsules

Capsules *in uteri* were non-translucent, dorsoventrally flattened and thick walled. Dark brown coloration in the centre of the capsule faded to light-brown in the outer margins (Fig. 12A). Surface is finely and longitudinal striated, giving a smooth surface texture. These striations, hard to distinguish to the naked eye, are present on the entire capsule surface including horns. In a lateral view, the dorsal face is convex, while the ventral face is flattened (Fig. 12B). Anterior and posterior margins of the egg capsules are secured by a thick apron while lateral borders exhibited strong lateral keels. Anterior apron is concave and against transmitted light, only the last c. 7 mm of the anterior margin looks translucent. Posterior apron have a straight posterior margin, which last c. 10 mm is translucent. Thick and strong lateral keels were also present the almost full length of the capsule, extending onto the base of anterior and posterior horns, wider in the middle of the egg capsules and thinner towards both anterior and posterior margins. Outer margins of lateral keels are slightly rounded giving the egg capsules a typical barrel shape. Egg capsules do not have any lateral or any other accessory adhesion fibres. Anterior horns are thick, dorsoventrally flattened and inwardly curved thought not long enough for crossing over. The inner margin of the horn is united to the anterior apron. The tips of these horns are fibrous showing a very little coiled end. Posterior horns are straighter and longer than anterior, and also inwardly curved on the tips. The inner side of

posterior horns are fused with the posterior apron and became thinner with a tendril-like final portion. Nevertheless, only the tips are thin and like the anterior horns, posterior horns have the same terminal entanglement. Measurements for egg capsules are presented in Table 8.

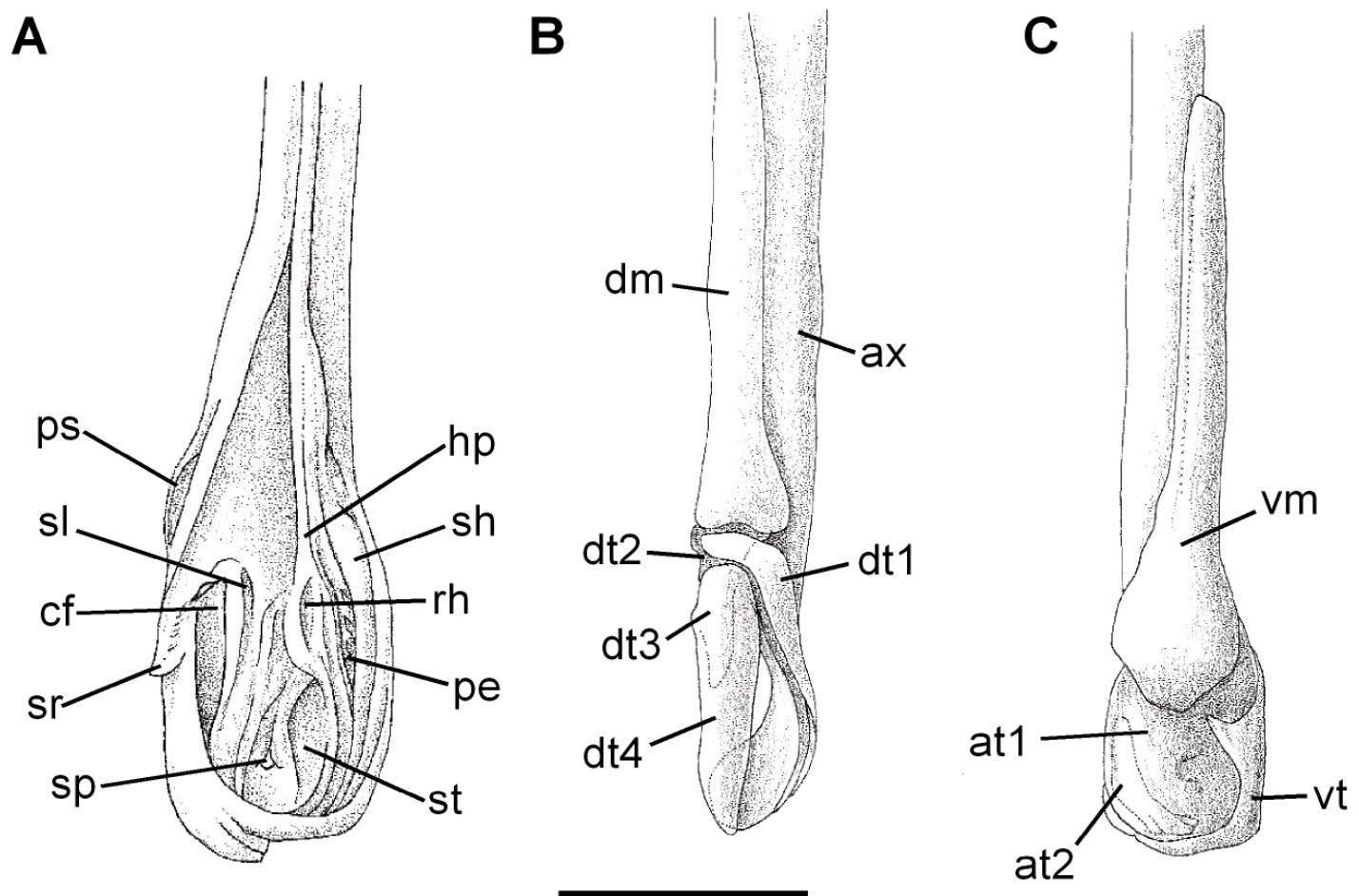


Figure 10 General structure of right clasper gland and cartilages of *Amblyraja frerichsi* in lateral (A) view partially expanded; clasper cartilages in dorsal (B) and ventral (C) views. (at1) accessory terminal 1, (at2) accessory terminal 2, (ax) axial, (cf) cleft, (dm) dorsal marginal, (dt1) dorsal terminal 1, (dt2) dorsal terminal 2, (dt3) dorsal terminal 3, (dt4) dorsal terminal 4, (hp) hypopyle, (pe) pent, (ps) pseudosiphon, (rh) rhipidion, (sh) shield, (sl) slit, (sp) spike, (sr) spur, (st) sentinel, (vm) ventral marginal, (vt) ventral terminal. Scale bar 50 mm.

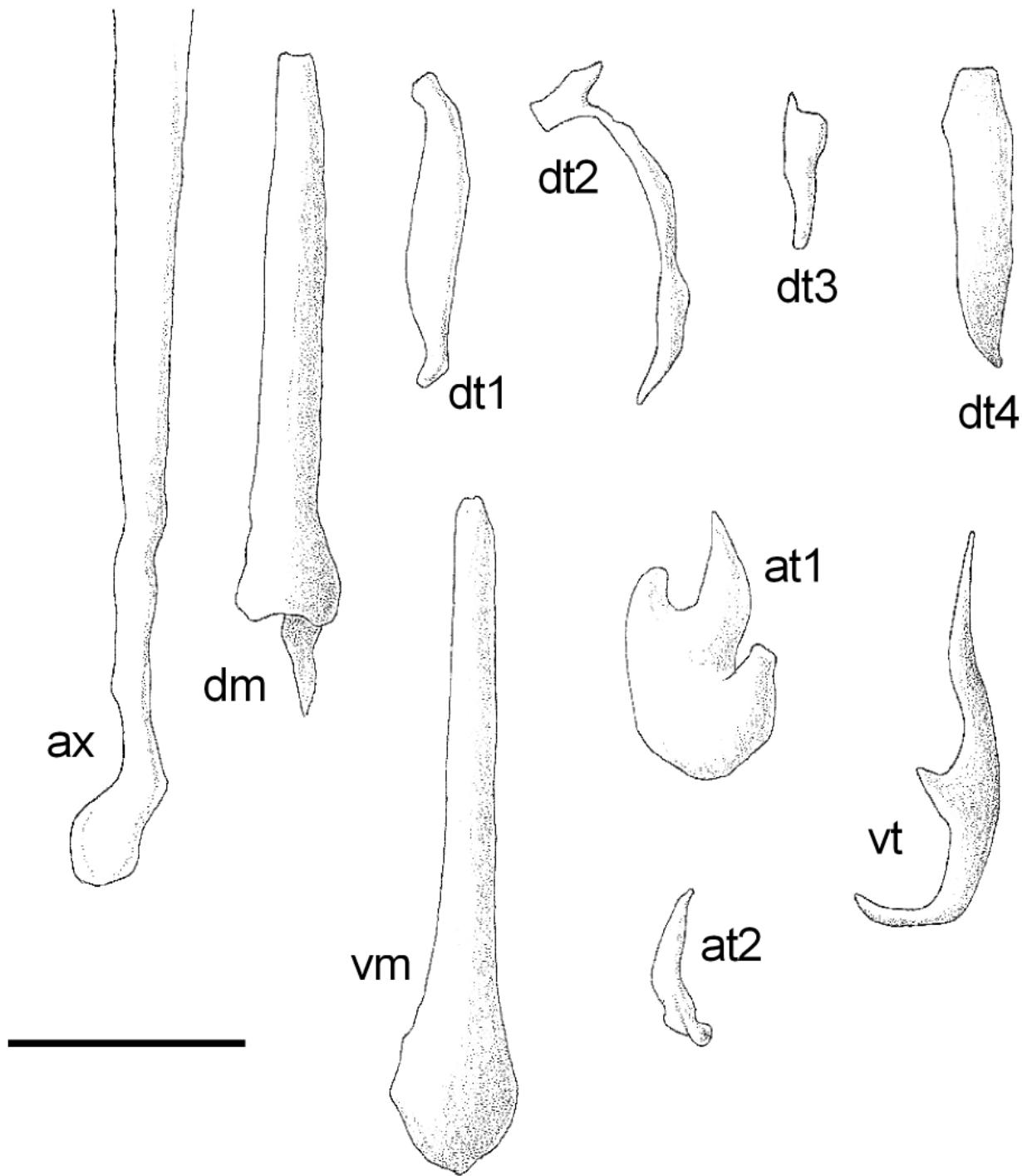


Figure 11 Dorsal view of clasper cartilages of *Amblyraja frerichsi*. Abbreviations of clasper cartilages are indicated at Figure 6. Scale bar 20 mm.

A



B



Figure 12 Egg capsules of *Amblyraja frerichsi* in dorsal (A) and lateral (B) views. Scale bar 50 mm.

Table 8 Measurements (mm) of the egg capsules of *Amblyraja frerichsi*.

	CCM-173	CCM-174
Central capsule length	115.5	112.3
Central capsule width	88.5	90.5
Capsule height	15	12.6
Anterior apron length	22.3	17.9
Right anterior horn length	59	59
Left anterior horn length	59	56
Posterior apron length	21.8	20.5
Right posterior outer horn length	54	59
Left posterior outer horn length	53.8	53
Right lateral keel	9.9	10.3
Left lateral keel	13.4	11.6

Size

Specimens examined range in size from 404 to 1762 mm TL. No individuals with umbilical scars were observed but based on the egg capsules' maximum size and the smallest skate specimens recorded, the size at birth seems to be about 216 mm TL. Immature specimens range from 216 to 817 mm TL (Krefft 1968). Adult females (mature or egg-bearing) ranged from 965 to 1731 mm TL. Males over 855 mm TL had fully calcified claspers suggesting maturity is attained between 775 and 907 mm LT. No apparent sexual dimorphism were observed in size and disc shape.

Distribution

Known distribution on both sides of southern South America, from Rio de Janeiro, Brazil (22° S) through the Magellan Strait to Arauco, Chile (37° S). Recorded at depths of 600 to 2,609 m in the Atlantic Ocean (Krefft, 1968; Gomes *et al.*, 2010; Kyne & Simpfendorfer, 2010) and 1,037 to 2,200 m in the Pacific Ocean.

DISCUSSION

The geographical range of *Amblyraja frerichsi*, based on verified records in the literature, extends southwards from Rio de la Plata (35° S) (Krefft, 1968) to the Falkland Islands (Bizikov *et al.*, 2004) and Cape Horn (57.3° S) in the south-west Atlantic; and northwards in the south-east Pacific, from Cape Horn through the Patagonian Archipelago to 52° S (Reyes & Torres-Florez, 2009). Our observations extend the latitudinal range in the south-east Pacific to Arauco (37° S); about 1,700 km north of the previous confirmed records. It should be noted, however, unverified records of single specimens have been reported from Coquimbo (30° S) (Acuña & Rodríguez, 1987) and the Tarapacá Region (23° S) (Vargas & Sielfeld, 1989) in the south-east Pacific and Rio de Janeiro, Brazil (22° S) in the south-west Atlantic. These isolate records may indicate a more extensive northerly range on each side of South America than is currently accepted.

No major differences in the anatomy were found when compared to the original description (Krefft, 1968). However, differences were found in the spinulation pattern with 16–26 midline thorns found in comparison to the original description (16–22 thorns). Colour pattern was also similar to that provided in the original description, although this character is sensitive to environmental influences (Leible, 1988) and colour is known to vary in this genus with immature individuals often darker than adults (Zorzi & Anderson, 1988). No ontogenetic growth differences were observed in size and disc shape between sex and maturity stage.

Internal and external morphology of claspers may help to define the genus assignment in species specific complex (Ishiyama, 1958; Hulley, 1970; Stehmann, 1970) as has been documented for deep-water skates, *i.e.* the *Zearaja* and *Dipturus* complex (Last & Gledhill, 2007). Recently, a comprehensive study of the clasper in three *Amblyraja* species have been published (Delpiani *et al.*, 2012) contributing to enhance the species diagnosis as a major component of genus morphology.

Structural consistencies can be detected in the clasper internal cartilages within *A. frerichsi* and *A. doellojuradoi*, *A. hyperborea* (Collett 1879) and *A. radiata* (Donovan 1808) (Stehmann, 1970; Hulley, 1972; Delpiani *et al.*, 2012); especially in the shape of the dorsal terminal 2 (**dt2**) and 4 (**dt4**); the ventral terminal and the accessory terminal 1 (**at1**) and 2 (**at2**) cartilages. But the shape and disposition of dorsal terminal 1 (**dt1**) and 2 (**dt2**) cartilages are slightly different; and these differences together may be used in the species diagnosis.

As seen in other skates, the reproductive mode of *A. frerichsi* is single oviparity, in which two egg capsules are produced simultaneously, one in each nidamental gland. Previous descriptions of the egg capsules of *Amblyraja* species are restricted to a few species: egg capsules of *A. hyperborea* and *A. robertsi* (Hulley 1970) are bigger than the mean size of those described in this

study (Treloar *et al.*, 2006; Ebert *et al.*, 2008); in contrast to the egg capsules of *A. radiata* that appear to be smaller (Parent *et al.*, 2008). Nevertheless, all share some common features, such as colouration pattern, texture, apron thickness and lateral keels. The absence of accessory lateral adhesion fibres and long non tendril-like horns are features shared with *A. robertsi* and *A. hyperborea*. Egg capsules of *A. radiata* have a dense and entangled bundle of fine adhesion fibres at the top of each anterior horn, which makes them longer than the posterior horns. In all *Amblyraja* egg cases, the posterior horns are longer than the anterior ones, and taper towards their tips. The general absence of lateral fibrils or long terminal tendrils suggest that *Amblyraja* species deposit egg capsules on the sea floor, rather than attach them to debris or any other types of substrata.

Amblyraja frerichsi could be potentially confused with other *Amblyraja* species present south-east Pacific Ocean because of similarities in the distribution patterns of dermal denticles and its general morphology. However, it can be distinguished from *A. doellojuradoi* who have white ventral colouration and 12–15 midline thorns (Lamilla & Sáez, 2003; Reyes & Torres-Florez, 2009). Also it can be differentiated from *A. georgiana*, who have large white blotches on the ventral surface and 20–28 midline thorns (Lamilla & Sáez, 2003; Bizikov *et al.*, 2004).

An important aspect of this taxon is the geographical and bathymetric range expansion in the Chilean coast. Capture records in south Chile (southwards of 40° S) were made at shallower depths (800–1,300 m) than in northern locations (1,900–2,200 m). These depth variations could be evidence of a relationship between latitudinal ranges, catch depths and water mass temperature; a hypothesis proposed for *Rajella nigerrima* (De Buen 1960) (Pequeño & Lamilla, 1993) on the continental slope of Chile. The environmental homogeneity due the Antarctic Intermediate Water mass that flows at depths of 700 to 1200 m along the Chilean continental slope (González *et al.*, 2006), may explain the depth range variation along the latitudinal gradient in the south-east Pacific.

In the south-west Atlantic, capture records of *Amblyraja frerichsi* are scarce and restricted to deep waters outside the continental shelf between 600 and 1,000 m (Menni & Stehmann, 2000; Gomes *et al.*, 2010). In the same area, off Rio de la Plata, only immature specimens have been captured predicting that adults would be at greater depths (Krefft, 1968). In Chile, *A. frerichsi* specimens were captured over the continental slope at depths between 800 and 2,200 m. All female captured shallower than 1,300 m were immature. Sexually mature female were caught at greatest depths while mature males were observed over the whole depth range. Such depth-segregation by maturity occurs in a number of elasmobranch species (Springer, 1967; Frisk, 2010). Spatial and sexual segregation in *A. frerichsi* could be related to reproductive events, such as oviposition (Hoening & Gruber, 1990; Cedrola *et al.*, 2005). Chilean egg-bearing females were caught in deeper zones as well as deep-water corals (genus *Antipathes* and *Bathyphathes*), showing a positive

correlation in the bycatch. Similarly, in the area it is thought that the dusky catshark *Bythaelurus canescens* (Günther 1878) use deep-water coral branches as a substrate for egg-laying (Concha *et al.*, 2010). But as in other *Amblyraja* species, *A. frerichsi* may deposits its egg capsules on the sea bed and potentially use the coral gardens as oviposition shelter zones. Tendrils and curved horns are usually associated with oviposition into complex three-dimensional substrates, whereas egg cases without tendrils are generally deposited on bare substrate (Francis *et al.*, 2001; Concha *et al.*, 2010). The reason for female's apparent preference for deeper water is uncertain, but mature females could have a male-avoidance strategy (Sims, 2003) going deeper to lay eggs, with young skates migrating to relatively shallow waters to reduce intraspecific competition (Sims *et al.*, 2001). Sex-specific habitat use has been reported previously for batoid species (Hoening & Gruber, 1990; Frisk, 2010).

Sexual segregation may compromise the integrity of the population if only a mature or immature fraction is caught or incidentally harvested (Dulvy & Forrest, 2010). A high abundance and bycatch interaction of *A. frerichsi* have been reported (Reyes & Torres-Florez, 2009) in the *D. eleginoides* fishery around the Patagonian coast of the south-east Pacific Ocean (52° S to 57° S). In this area, *A. frerichsi* represents 97% of the elasmobranch bycatch by species and 57% of the elasmobranch biomass caught in this fishery. In the same fishery but offshore from Valdivia (40° S), have been reported a low interaction/abundance of *A. frerichsi*, comprising just 1% of the total catch (Lamilla *et al.*, 2010). In this fishery while only 8% of the hauls were made below 1,200 m (between 1,200 and 1,800 m), 65% of the *A. frerichsi* catch comprised mature females. The high effort and pressure made by the fleets in the Patagonian Region greatly exceeds the few artisanal vessels that continue catching *D. eleginoides* (Guerrero & Arana, 2009); therefore, more immature skates are caught and discarded than the mature fraction maintaining an ephemeral population balance until bycatch has been evaluated over the entire fisheries distribution range. The relatively higher abundance in the southern records, regarding the capture depth range extension, supports the observation that *A. frerichsi* prefers cold waters, as do almost all species of this genus, except *A. reversa* (Lloyd 1906) which inhabits deepwater of Arabian Sea (McEachran & Miyake, 1990).

The present study extends the distributional range in the south Pacific Ocean from 36° S to the Patagonian Channels (54° S), with a continuous presence along the lower continental slope of Chile. Besides this geographical extension, the bathymetric distributional range is also extended, inhabiting between 800 and 2,200 m depth. It is urgent to focus research on *A. frerichsi* population sex and maturity structure, especially in the area where it occurs as bycatch in the Patagonian toothfish (*D. eleginoides*) fishery from the southern channels of Chile, where overfishing could threaten the integrity and balance of this skate's population.

REFERENCES

- Acuña, E. & Rodríguez, M. (1987) Contribución al estudio de las rayas de profundidad (Familia Rajidae) del Norte de Chile. In *VII Jornadas de Ciencias del Mar* (Anon., ed.), pp. 124. Sociedad Chilena de Ciencias del Mar: Concepción, Chile.
- Bizikov, V., Arkhipkin, A.I., Laptikhovsky, V.V. & Pompert, J.H.W. (2004) *Identification guide and biology of the Falkland skates*. Fisheries Department, Falkland Island Government: Stanley, Falkland Islands.
- Cedrola, P., Gonzalez, A. & Pettovello, A. (2005) Bycatch of skates (Elasmobranchii: Arhyncho-batidae, Rajidae) in the Patagonian red shrimp fishery. *Fisheries Research* 71, 141–150.
- Compagno, L.J.V. (1999) An overview of chondrichthyan systematics and biodiversity in southern Africa. *Transactions of the Royal Society of South Africa* 54, 75–120.
- Concha, F., Hernández, S. & Oddone, M.C. (2009) Egg capsules of the raspthorn sandskate, *Psammobatis scobina* (Philippi, 1857) (Rajiformes, Rajidae). *Revista de Biología Marina y Oceanografía* 44, 253–256.
- Concha, F., Bustamante, C., Oddone, M.C., Hernández, S. & Lamilla, J. (2010) Egg capsules of the dusky catshark *Bythaelurus canescens* (Carcharhiniformes, Scyliorhinidae) from the south-eastern Pacific Ocean. *Journal of Fish Biology* 77, 963–971.
- Cousseau, M.B., Figueroa, D.E., Díaz de Astarloa, J.M., Mabragaña, E. & Lucifora, L.O. (2007) *Rayas, chuchos y otros batoideos del Atlántico sudoccidental (34°S–55° S)*. Instituto Nacional de Investigación y Desarrollo Pesquero INIDEP: Mar del Plata.
- Delpiani, G., Figueroa, D.E. & Mabragaña, E. (2012) Description of the clasper of the Southern Thorny Skate *Amblyraja doellojuradoi* (Pozzi, 1935) (Chondrichthyes: Rajidae). *Zootaxa* 3182, 57–64.
- Dulvy, N.K. & Forrest, R.E. (2010) Life histories, population dynamics, and extinction risks in Chondrichthyans. In *Biology of Sharks and their Relatives II: Biodiversity, Adaptive Physiology, and Conservation* (Carrier, J.C., Musick, J.A. & Heithaus, M.R., eds.), pp. 639–680. CRC Press: Boca Raton, FL.
- Ebert, D.A. & Compagno, L.J.V. (2007) Biodiversity and systematics of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environmental Biology of Fishes* 80, 111–124.
- Ebert, D.A. & Sulikowski, J.A. (2007) *Biology of Skates*. Springer Science+Business Media BV: Dordrecht, Netherlands.

- Ebert, D.A., Compagno, L.J.V. & Cowley, P.D. (2008) Aspects of the reproductive biology of skates (Chondrichthyes: Rajiformes: Rajoidei) from southern Africa. *ICES Journal of Marine Science* 65, 81–102.
- Ebert, D.A. & Winton, M.W. (2010) Chondrichthyans of High Latitude Seas. In *Biology of Sharks and their Relatives II: Biodiversity, Adaptive Physiology, and Conservation* (Carrier, J.C., Musick, J.A., Heithaus, M.R., eds.), pp. 115–158. CRC Press: Boca Raton, FL.
- Francis, M.P., Maolagáin, C.O. & Stevens, J.D. (2001) Age, growth, and sexual maturity of two New Zealand endemic skates, *Dipturus nasutus* and *D. innominatus*. *New Zealand Journal of Marine and Freshwater Research* 35, 831–842.
- Frisk, M.G. (2010) Life History Strategies of Batoids. In *Biology of Sharks and their Relatives II: Biodiversity, Adaptive Physiology, and Conservation* (Carrier, J.C., Musick, J.A., Heithaus, M.R., eds.), pp 283–318. CRC Press: Boca Raton, FL.
- Gomes, U.L., Signori, C.N., Gadig, O.B.G. & Santos, H.R.S. (2010) *Guia de Identificação de Tubarões e Raias do Rio de Janeiro*. Technical Books Editora: RJ, Brazil.
- González, H.E., Daneri, G., Menschel, E., Marchant, M., Pantoja, S., Hebbeln, D., Barria, C., Vera, R. & Iriarte, J. (2006) Downward fluxes of particulate organic matter in coastal and oceanic areas off Chile: The role of the OMZ and functional groups of the plankton. *Gayana (Concepción)* 70, 26–28.
- Gravendeel, R., Van Neer, W. & Brinkhuizen, D. (2002) An identification key for dermal denticles of Rajidae from the North Sea. *International Journal of Osteoarchaeology* 12, 420–441.
- Guerrero, A. & Arana, P. (2009) Fishing yields and size structures of Patagonian toothfish (*Dissostichus eleginoides*) caught with pots and long-lines off far southern Chile. *Latin American Journal of Aquatic Research* 37, 361–370.
- Hoening, J.M. & Gruber, S.H. (1990) Life history patterns in the elasmobranchs: implications for fisheries management. In *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics and the Status of the Fisheries* (Pratt, H.L., Gruber, S.H. & Tanuichi, T., eds.), pp. 1–16. NOAA Technical Report NMFS 90, US Department of Commerce.
- Hulley, P.A. (1970) An investigation of the Rajidae of the west and south coast of southern Africa. *Annals of the South African Museum* 55, 151–220.
- Hulley, P.A. (1972) The origin, interrelationships and distribution of South African Rajidae (Chondrichthyes, Batoidei). *Annals of the South African Museum* 60, 1–103.

- Ishiyama, R. (1958) Studies on the rajid fishes (Rajidae) found in the waters around Japan. *Journal of the Shimonoseki College of Fisheries* 7, 193–394.
- Krefft, G. (1968) Neue und erstmaling nachgewiesene Knorpelfische aus dem Archibenthal des Südwestantlantiks, einschlieszlich einer Diskussion einiger *Etomopterus* - Arten südlicher Meere. *Archiv fuer Fischereiwissenschaft* 19, 1–42.
- Kyne, P.M. & Simpfendorfer, C.A. (2010) Deepwater Chondrichthyans. In *Biology of Sharks and their Relatives II: Biodiversity, Adaptive Physiology, and Conservation* (Carrier, J.C., Musick, J.A., Heithaus, M.R., eds.), pp 37–114. CRC Press: Boca Raton, FL.
- Lamilla, J. & Sáez, S. (2003) Clave taxonómica para el reconocimiento de especies de rayas chilenas (Chondrichthyes, Batoidei). *Investigaciones Marinas, Valparaíso* 31, 1–16.
- Lamilla, J. & Bustamante, C (2005) Guía para el reconocimiento de tiburones, rayas y quimeras de Chile. *Oceana* 18, 1–80.
- Lamilla, J., Bustamante, C., Roa, R., Acuña, E., Concha, F., Meléndez, R., López, S., Aedo, G., Flores, H. & Vargas-Caro C. (2010) Estimación del descarte de condriictios en pesquerías artesanales. *Universidad Austral de Chile Informe técnico No. 2008-60, Valdivia*. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 Sept 2011).
- Last, P.R. & Gledhill, D. (2007) The Maugean skate, *Zearaja maugeana* sp. nov. (Rajiformes: Rajidae) – a micro endemic Gondwanan relict from Tasmanian estuaries. *Zootaxa* 1494, 45–65.
- Last, P.R., White, W.T., Pogonoski, J. & Gledhill, D.C. (2008) New Australian skates (Batoidea: Rajoidei): background and methodology. In *Descriptions of new Australian skates (Batoidea: Rajoidea)* (Last, P.R., White, W.T., Pogonoski, J. & Gledhill, D.C., eds.), pp. 1–8. CSIRO Marine and Atmospheric Research: Hobart, Australia.
- Leible, M. (1988) Revisión de métodos para estudios taxonómicos de rayas (Rajiformes, Rajidae). *Gayana (Zoología)* 52, 15–93.
- McEachran, J.D. & Miyake, T. (1990) Zoogeography and bathymetry of Skates (Chondrichthyes, Rajoidei). In *Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics and the Status of the Fisheries* (Pratt, H.L., Gruber, S.H. & Tanuichi, T., eds.), pp. 305–326. NOAA Technical Report NMFS 90, US Department of Commerce.
- McEachran, J.D. & Dunn, K.A. (1998) Phylogenetic analysis of skates, a morphologically conservative clade of Elasmobranchs (Chondrichthyes: Rajidae). *Copeia* 2, 271–290.

- Menni, R.C. & Stehmann, M. (2000) Distribution, environment and biology of batoid fishes off Argentina, Uruguay and Brazil. A review. *Revista del Museo Argentino de Ciencias Naturales Bernardino Rivadavia* 2, 69–109.
- Oddone, M.C. & Velasco, G. (2004) Size at maturity of the smallnose fanskate *Sympterygia bonapartii* (Müller & Henle, 1841) (Pisces, Elasmobranchii, Rajidae) in the SW Atlantic. *ICES Journal of Marine Science* 61, 293–296.
- Oddone, M.C., Marçal, A. & Vooren, C.M. (2004) Egg capsules of *Atlantoraja cyclophora* (Regan, 1903) and *A. platana* (Gunther, 1880) (Pisces, Elasmobranchii, Rajidae). *Zootaxa* 426, 1–4.
- Parent, S., Pépin, S., Genet, J.P., Misserey, L. & Rojas, S. (2008) Captive breeding of the Barndoor Skate (*Dipturus laevis*) at the Montreal Biodome, with comparison notes of two other captive-bred skate species. *Zoo Biology* 27, 145–153.
- Pequeño, G. (1997) Peces de Chile. Lista sistemática revisada y comentada: addendum. *Revista de Biología Marina, Valparaíso* 32, 77–94.
- Pequeño, G. & Lamilla, J. (1985) Estudio sobre una colección de rayas del sur de Chile (Chondrichthyes, Rajidae). *Revista de Biología Marina, Valparaíso* 21, 225–271.
- Pequeño, G. & Lamilla, J. (1993) Batoideos comunes a las costas de Chile y Argentina-Uruguay (Pisces: Chondrichthyes). *Revista de Biología Marina, Valparaíso* 28, 203–217.
- Reyes, P.R. & Torres-Florez, J.P. (2009) Diversidad, distribución, riqueza y abundancia de condrictios de aguas profundas a través del archipiélago patagónico austral, Cabo de Hornos, Islas Diego Ramírez y el sector norte del paso Drake. *Revista de Biología Marina y Oceanografía* 44, 243–251.
- Sims, D.W. (2003) Tractable models for testing theories about natural strategies: Foraging behaviour and habitat selection of free-ranging sharks. *Journal of Fish Biology* 63, 53–73.
- Sims, D.W., Nash, J.P. & Morritt, D. (2001) Movements and activity of male and female dogfish in a tidal sea lough: Alternative behavioural strategies and apparent sexual segregation. *Marine Biology* 139, 1165–1175.
- Sosebee, K.A. (2005) Maturity of skates in northeast United States waters. *Journal of Northwest Atlantic Fisheries Science* 35, 141–153.
- Springer, S. (1967) Social organization of shark populations. In *Sharks, Skates, and Rays* (Gilbert, P.W., Mathewson, R.F. & Rall, D.P., eds.), pp. 149–174. Johns Hopkins Press: Baltimore.

- Stehmann, M. (1970) Vergleichend morphologische und anatomische Untersuchungen zur Neueordnung der Systematik der nordostatlantischen Rajidae (Chondrichthyes, Batoidei). *Archiv fuer Fischereiwissenschaft* 21, 73–164.
- Thiel, R., Eidus, I. & Neumann, R. (2009) The Zoological Museum Hamburg (ZMH) fish collection as a global biodiversity archive for elasmobranchs and actinopterygians as well as other fish taxa. *Journal of Applied Ichthyology* 25, 9–32.
- Treloar, M.A., Laurenson, L.J.B. & Stevens, J.D. (2006) Descriptions of rajid egg cases from southeastern Australian waters. *Zootaxa* 1231, 53–68.
- Vargas, M. & Sielfeld, W. (1989) Nuevos antecedentes sobre Rajiformes presentes en la costa norte de Chile (Primera Región: Tarapacá). In *IX Jornadas de Ciencias del Mar* (Anon., ed.), pp.87. Sociedad Chilena de Ciencias del Mar: Antofagasta, Chile.
- Walsh, J.H. & Ebert, D.A. (2007) A review of the systematics of western North Pacific angel sharks, genus *Squatina*, with redescriptions of *Squatina formosa*, *S. japonica*, and *S. nebulosae* (Chondrichthyes: Squatiniformes, Squatinidae). *Zootaxa* 1551, 31–47.
- Zorzi, G.D. & Anderson, M.O. (1988) Records of the deep-sea skates, *Raja* (*Amblyraja*) *badia* Garman, 1899 and *Bathyraja abyssicola* (Gilbert, 1896) in the eastern north Pacific, with a new key to California skates. *California Fish and Game* 74, 87–105.

2.3. First record of *Hydrolagus melanophasma* James, Ebert, Long & Didier, 2009 (Chondrichthyes, Chimaeriformes, Holocephali) from the southeastern Pacific Ocean

Originally published in Latin American Journal of Aquatic Research (ISSN: 0718-560X)

Copyright © Carlos Bustamante, 2012

Published online: 15 March 2012

License Number: open-access article

Abstract

The eastern Pacific black ghost shark, *Hydrolagus melanophasma* is reported from deep waters off Chile and is described from specimens collected off Valdivia at depths of 1150 to 1720 m. This species is distinguished from all other members of the genus by its large, curved dorsal fin spine, which extends beyond the dorsal fin apex; a second dorsal fin of uniform height along the caudal peduncle; large pectoral fins extending beyond the pelvic fin insertion; and a uniform black colour of the body. Catch records of this species in Chile suggest a discontinuous distribution along the continental slope of the eastern Pacific Ocean, restricted to the Middle America and Atacama trenches. These observations elevate the number of chimaeroid fishes inhabiting Chile to five species.

INTRODUCTION

Three families of chimaerid fishes (Chimaera: Holocephali) are currently recognized with at least 43 extant species (Didier, 2008). The Family Callorhinchidae with three species restricted to the Southern Hemisphere is the least numerous. The Family Rhinochimaeridae known as "longsnout" or "long-nosed" chimaera, contains three genera and eight species distributed discontinuously in the great oceans. The Family Chimaeridae, with two genera distinguished by the presence, in *Chimaera*, or absence, in *Hydrolagus*, of an anal fin. The *Chimaera* genus contains 11 extant species, and *Hydrolagus* contains 21 valid species to date (Eschmeyer & Fricke, 2010). Fourteen of the *Hydrolagus* species are known to occur in the Pacific Ocean, of which ten have a distribution restricted to the western Pacific (Didier, 2004; Andrade & Pequeño, 2006; Barnett *et al.*, 2006; Quaranta *et al.*, 2006). In the eastern Pacific by comparison only six species of *Hydrolagus* has been reported: two possibly endemic to the Galapagos Islands; two restricted to the coast of Chile and Peru, and two inhabiting the north Pacific off the coast of Mexico and California (Didier, 2008).

In Chile, the number of holocephalans has increased from one, prior to 1950, to four in the present. The first species described for Chile was the elephantfish *Callorhinchus callorynchus* (Linnaeus 1758) by Philippi (1893). The bigeye chimaera *Hydrolagus macrophthalmus* De Buen 1959, was described from the continental slope of central Chile and the Pacific spookfish *Rhinochimaera pacifica* (Mitsukuri 1895), was reported by Pequeño (1989) from the deep continental slope in central Chile. Recently Andrade & Pequeño (2006) reported the pale ghost shark *Hydrolagus pallidus* Hardy & Stehmann 1990, from the Juan Fernández seamounts (ca. 33° S, 77° W) in the bycatch of the orange roughy *Hoplostethus atlanticus* Collett 1889, trawl fishery.

Despite the increased fishing effort in the last 20 years, distribution patterns of chimaerid fishes in the south eastern Pacific are poorly known. Along the Chilean coast are caught as bycatch in trawl, coastal gill-nets or longline fisheries; but its capture never is reported or landed (Lamilla *et al.*, 2008) with exception of the artisanal, coastal gillnet fishery targeting *C. callorhynchus* (Cubillos *et al.*, 2009).

MATERIAL AND METHODS

In June 2009, three chimaerid fishes, one male and two females, were incidentally caught during commercial bottom longline fishery targeting the Patagonian toothfish (*Dissostichus*

eleginoides Smitt 1898) on board L/M Pamela II. Seventeen hauls were made during the cruise, but chimaeroid fishes were caught in three separate occasions along with 121 specimens of eleven elasmobranch species (Lamilla *et al.*, 2010). Additionally, four specimens were bycatch from one haul by the same vessel during November 2009, as indicated in Table 9

Specimens were recognized preliminarily as members of the Family Chimaeridae (Didier, 2004). 30 body measurements and eight lateral-line canal measurements were taken point to point using a dial caliper (0.01 mm) or measuring tape (1 mm). Definition of measurements and their acronyms are based on Compagno *et al.* (1990), Didier & Nakaya (1999) and Didier & Séret (2002): total length (TL), precaudal length (PCL), body length (BDL), snout-vent length (SVL), trunk length (TRL), head length (HDL), preoral length (POR), prenarial length (PRN), preorbital length (POB), eye length (EYL), eye height (EYH), pre-first dorsal length (PD1), pre-second dorsal length (PD2), length of first dorsal fin base (D1B), dorsal spine height (DSA), maximum height of first dorsal fin (D1H), maximum height of second dorsal fin (D2H), interdorsal space (IDS), dorsal caudal margin length (CDM), maximum height of dorsal lobe of caudal fin (CDH), total caudal length (CTL), ventral caudal margin (CVM), maximum height of ventral lobe of caudal fin (CVH), caudal peduncle height (CPH), pectoral fin anterior margin (P1A), posterior base of pectoral fin to anterior base of pelvic fin (P2P), pelvic-caudal space (PCA), origin of first dorsal fin to origin of pectoral fin (D1P1), origin of first dorsal fin to origin of pelvic fin (D1P2), origin of second dorsal fin to origin of pelvic fin (D2P2). In the lateral-line canals of head: distance from anterior oronasal fold to center of nasal canal (ONC), length of the rostral canal (LRC), length of the nasal canal measured as a straight line distance from right to left side (LNC), distance between infraorbital and angular canal measured as the straight line distance from junction of the oral and infraorbital canal to the junction of the oral and angular canal (IOA), distance between preopercular canal and main trunk canal measured from their junction with the infraorbital canal (OTM), distance between main trunk canal and supratemporal canal measured from their junctions with the infraorbital and postorbital canals, respectively (OCL), length of supratemporal canal measured across the head from its junctions with the postorbital canal (STL), distance from anterior base of spine to the center of the supratemporal canal (SPS).

Sexual maturity in males was determined by its secondary sexual characteristics (Didier, 2004) such as, the emergence of the frontal tenaculum, hardened pelvic claspers and denticles present on frontal tenaculum, prepelvic tenacula and pelvic claspers. Females were considered mature when vitellogenic (yellow) ovarian follicles or distended oviductal openings were present (Ebert, 2003). Specimens were fixed in 10% formaldehyde, stored in 70% ethanol and deposited at the Ichthyology Collection (IZUA-PM) belonging to the Universidad Austral de Chile (UACH) and

contrasted with descriptions provided by James *et al.* (2009). For comparison purposes, the specimen described by Andrade & Pequeño (2006) identified as *H. pallidus* (PM-IZUA 341), was examined due to similarities in its external morphology.

All chimaerid fishes were assigned to the genus *Hydrolagus* on the basis of a ventral caudal fin that was not deeply indented at its origin to form a separate anal fin. All specimens were consistent with the diagnosis for *H. melanophasma* (Fig. 13), according James *et al.* (2009). The shape and arrangement of the lateral-line canals of the head; the slightly curved spine of the first dorsal fin, serrated in the posterior margin and greater than the height of the fin; the uniform height of the second dorsal fin; the size of pectoral fins extending beyond insertion of pelvic fins; the trifid clasper which forks about a quarter of the total length and a black uniform coloration which differentiates this species from others described in the region.

Freshly-caught specimens had a uniform dark purple-black body coloration that turned pale after fixation, darker on ventral part of snout, head and trunk. Paired and unpaired fins were black even after fixation. Morphometric measurements are presented in Table 10 and are expressed as percentage of body length (BDL).

Table 9 Geographical position of captured specimens of *Hydrolagus melanophasma*.

Date	GPS Position	Depth (m)	Specimen
19-06-2009	39° 52' 20" S	74° 18' 10" W	1280 IZUA-PM 4007
22-06-2009	40° 02' 27" S	74° 24' 30" W	1150 IZUA-PM 4010
23-06-2009	40° 07' 23" S	74° 24' 29" W	1720 IZUA-PM 4011
04-11-2009	39° 51' 35" S	74° 22' 42" W	1528 Four mature male

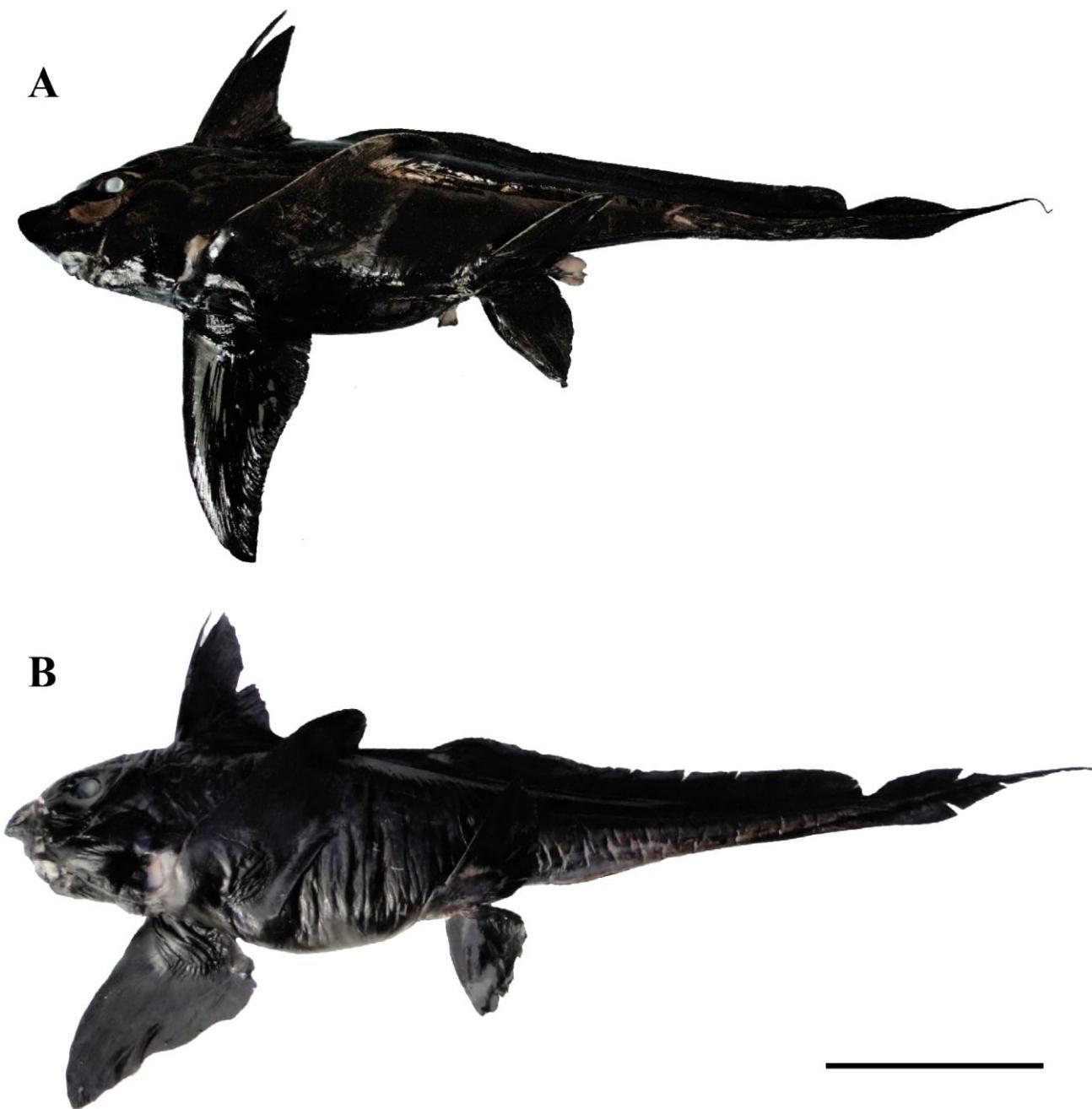


Figure 13 *Hydrolagus melanophasma*: (A) Male 1175 mm TL (IZUA-PM 4007); (B) female 1277 mm TL (IZUA-PM 4011). Scale bar represents 250 mm.

RESULTS AND DISCUSSION

Hydrolagus melanophasma is characterized by large-bodied specimens (adults BDL > 705 mm) with a blunt snout that continues the line from the orbit to the tip of the snout; eyes of moderate size, length 19.5% of head length. Snout-vent length is short, 64.6% BDL, slightly bigger than the pelvic-caudal space, 58.2% BDL. Pectoral-pelvic space, 36% BDL, is one-half snout-vent length. Skin firm and robust, not deciduous as in some *Hydrolagus* (Didier, 2002; 2008). Pectoral fins large, triangular, anterior margin 41.3% BDL that extends to or beyond pelvic fin insertion. Straight anterior margin of pelvic fins and posterior margin strongly convex. First dorsal fin preceded by prominent, slightly curved dorsal spine attached to the first dorsal fin; dorsal fin spine long, 28.5% BDL, larger than first dorsal fin apex. Posterior edge of spine serrated for last 6.3% of spine length. Dorsal spine and first dorsal fin overlap with the second dorsal fin when laid flat. First dorsal fin triangular, base short 20.9% BDL with concave posterior margin. Second dorsal fin long and uniform in height throughout body. Depth of second dorsal fin, 4.5% BDL, is greater than depth of dorsal lobe of caudal fin, 3.0% BDL. There is no measurable separation between insertion of the second dorsal fin and the origin of the caudal fin dorsal lobe. Depth of dorsal and ventral caudal fin lobes is nearly equal. Ventral lobe of caudal fin extends beyond the insertion of the dorsal lobe of caudal fin. No anal fin.

Trifid claspers present in mature males along with frontal tenaculum and prepelvic tenacula. Claspers forked and extend beyond distal edge of pelvic fins. The prepelvic tenacula have four to five denticles along the medial edge. Frontal tenaculum with indistinct rows of 32 pointed, needle-like denticles.

The head lateral line canals are open grooves with wide dilation on the snout. There is a distinct space between the preopercular and oral canals where they branch separately from the infraorbital canal (Fig. 14). The preopercular canal is discontinuous after it branches from the oral or infraorbital before breaking into consecutively smaller pieces. Lateral line canal measurements are presented in Table 9. Trunk lateral line extends the length of the body from junction with post-orbital to whip-like filament and is generally straight with no regular undulations.

Chimaerid fishes, especially species of *Hydrolagus*, are often difficult to distinguish because they look very similar and their geographic range often overlaps. The morphological characteristics of *H. melanophasma* clearly differentiate it from two other species of this genus occurring in the southeastern Pacific. The combination of characters, such as body colouration, length and serrations of dorsal spine, and lateral-line canals of the head; constitute useful means for a quick and easy distinction among *Hydrolagus* species.

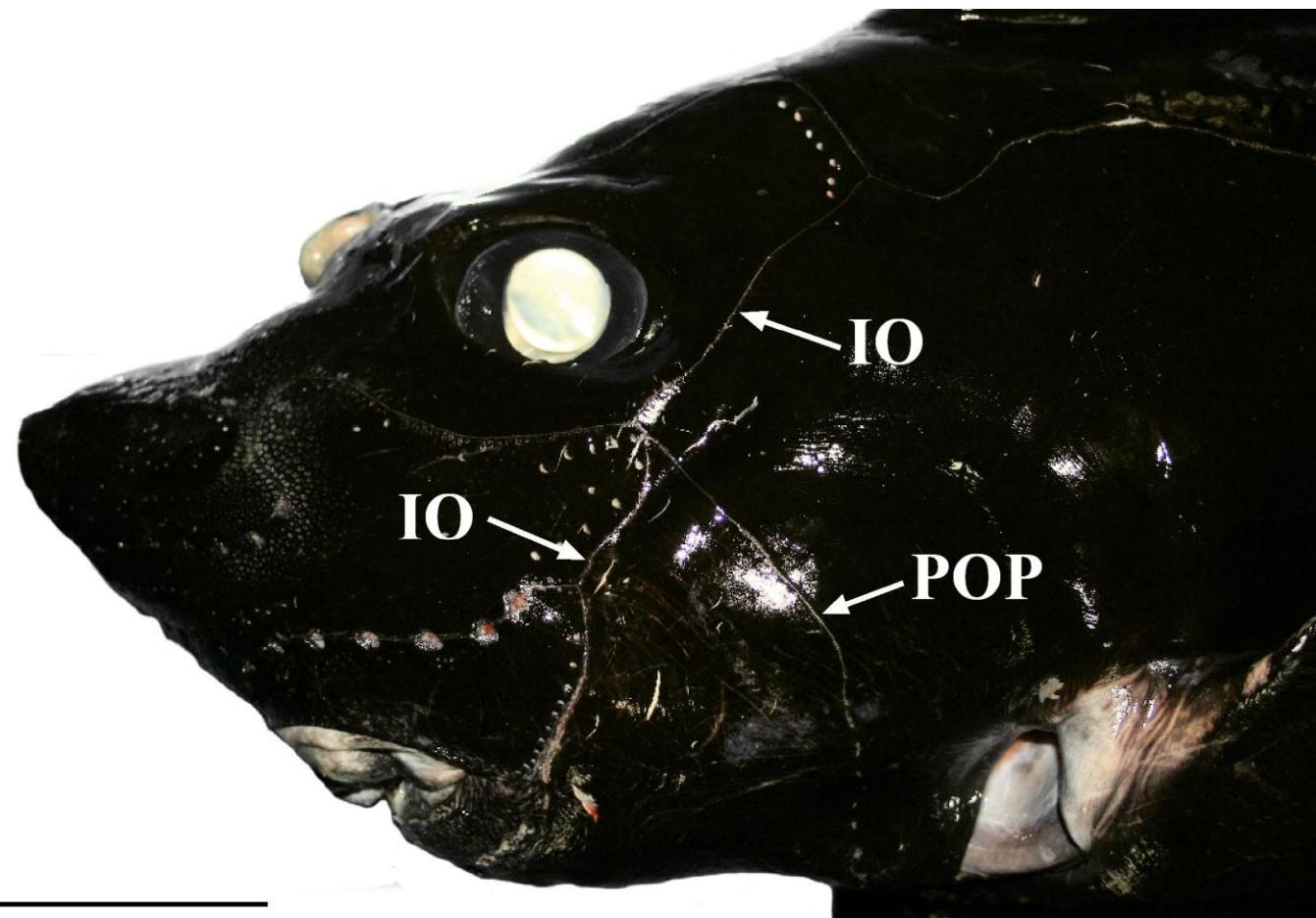


Figure 14 Head lateral line canals of *Hydrolagus melanophasma* (IZUA-PM 4007) showing the preopercular (POP), oral (O) and infraorbital (IO) canals.

Hydrolagus macrourus differs from the *H. melanophasma* by a number of characters being most conspicuous, such as (a) the length of the dorsal spine, usually shorter or equal than length of the first dorsal fin; (b) larger eyes, 30% HDL; (c) preopercular and oral canals shares a short common branch from the infraorbital canal; and its (d) pale brown body coloration. *H. melanophasma* differs slightly from the *H. pallidus* specimen reported from Juan Fernandez seamounts; by its pale-grey coloration and morphometrics (Table 8). Observations on the head lateral line canals and measurement of precaudal (PCL), pre-second dorsal (PD2), pre-oral (POR) length and the space between the pectoral and pelvic fins (P2P); considerably exceed the size range of the *H. melanophasma* original description and our observations.

Hydrolagus pallidus have been reported to island slopes of north-east Atlantic (Hardy & Stehmann, 1990) but this geographical divergence, its unusual discrepancy in distribution and the fact that no additional specimens of *H. pallidus* have been caught or reported from the Pacific allows us to recognize that the first assignment was inadequate. The only specimen (IZUA-PM

2341) reported by Andrade & Pequeño (2005), by its colour and morphometrics, could correspond to the pointy-nose blue chimaera *Hydrolagus trolli* Didier & Séret 2002 (D. Didier *comm. pers.*); described from the south-western Pacific. Recent observations of *H. trolli*, from deep seamounts around Hawaii and off southern coast of California, raise questions about the species designation by Andrade & Pequeño (2005), which needs to be revised and supported by a comparative analysis to argue species identification.

Table 10 Body measurements expressed as percentage of the body length (% BDL) for examined material of *Hydrolagus melanophasma*. † Original measurements of Andrade & Pequeño (2006); * measurement not indicated.

	<i>H. melanophasma</i> (James <i>et al.</i> , 2009)	<i>H. pallidus</i> IZUA-PM 2341†	IZUA-PM 4007	IZUA-PM 4010	IZUA-PM 4011
Sex	Male	Male	Male	Female	Female
BDL (mm)	577 – 631	660	705	733	918
TL	155.6 – 160.5	129.8	166.7	162.9	138.9
PCL	121.9 – 126.9	115.8	127.7	130.6	121.8
SVL	56.9 – 60.1	*	64.7	73.1	56.1
TRL	35.5 – 37.3	*	31.9	34.7	35.1
HDL	25.0 – 29.5	29.8	27.7	30.6	21.8
POR	10.6 – 11.5	16.3	14.5	13.4	8.3
PRN	7.1 – 8.2	12.6	11.2	11.9	7.1
POB	13.2 – 13.7	17.7	11.8	14.2	10.5
EYL	6.5	6.7	5.4	7.1	5.7
EYH	4.1 – 4.4	4.7	4.4	4.6	3.7
PD1	27.4 – 27.7	28.6	29.1	27.3	26.7
PD2	47.4 – 47.8	86.0	44.3	48.3	53.4
D1B	13.9 – 15.3	13.2	20.9	18.4	16.9
DSA	25.9	*	28.5	29.9	17.6
D1H	19.0 – 19.5	*	24.5	25.2	18.1
D2H	4.0 – 4.1	4.6	4.5	4.8	5.8
IDS	6.4 – 9.0	*	3.0	10.6	5.4
CDM	20.5 – 23.1	16.1	20.1	22.5	18.5

Table 10 continued

	<i>H. melanophasma</i> (James <i>et al.</i> , 2009)	<i>H. pallidus</i> IZUA-PM 2341†	IZUA-PM 4007	IZUA-PM 4010	IZUA-PM 4011
CDH	2.0 – 3.3	3.0	3.0	2.9	2.4
CTL	33.3 – 34.5	*	40.7	31.1	30.5
CVM	26.0 – 28.8	32.1	34.2	39.0	43.6
CVH	2.4 – 2.9	2.6	2.7	2.5	2.8
CPH	2.4	2.6	3.8	2.9	2.4
P1A	38.5 – 40.9	37.7	41.3	41.5	32.0
P2P	29.8 – 32.2	19.3	36.0	40.2	38.6
PCA	57.9 – 60.1	*	58.2	50.2	51.2
D1P1	16.4 – 19.6	*	21.0	22.1	19.2
D1P2	39.5 – 42.5	*	46.1	48.4	41.0
D2P2	20.3 – 24.6	*	30.5	31.2	27.2

Abbreviation: total length (TL), precaudal length (PCL), body length (BDL), snout-vent length (SVL), trunk length (TRL), head length (HDL), preoral length (POR), prenarial length (PRN), preorbital length (POB), eye length (EYL), eye height (EYH), pre-first dorsal length (PD1), pre-second dorsal length (PD2), length of first dorsal fin base (D1B), dorsal spine height (DSA), maximum height of first dorsal fin (D1H), maximum height of second dorsal fin (D2H), interdorsal space (IDS), dorsal caudal margin length (CDM), maximum height of dorsal lobe of caudal fin (CDH), total caudal length (CTL), ventral caudal margin (CVM), maximum height of ventral lobe of caudal fin (CVH), caudal peduncle height (CPH), pectoral fin anterior margin (P1A), posterior base of pectoral fin to anterior base of pelvic fin (P2P), pelvic-caudal space (PCA), origin of first dorsal fin to origin of pectoral fin (D1P1), origin of first dorsal fin to origin of pelvic fin (D1P2), origin of second dorsal fin to origin of pelvic fin (D2P2).

Based on direct observations, we confirm the presence of *H. melanophasma* for first time in the South Pacific Ocean. The eastern Pacific black ghost shark, *H. melanophasma*, was described from southern California (USA), along the Pacific coast of Baja California (Mexico) and into the Gulf California. Capture records of *H. melanophasma* in the southeastern Pacific from Caldera (25° S) (J. Lamilla *unpublished data*) to Valdivia (40° S) suggests a continuous distribution along the deep continental slope of the southeastern Pacific ocean, restricted to the Middle America and Atacama oceanic trenches. The identification of *H. melanophasma* from Chilean waters increases the known Chimaeroid fish species of Chile to five: *Hydrolagus macrophthalmus* (Pequeño, 1989), *H. cf. trolli* (as *H. pallidus* in Andrade & Pequeño, 2005), *H. melanophasma* (as *H. affinis* in Lamilla & Bustamante, 2005), *Callorhinichus callorynchus* and *Rhinochimaera pacifica* (Pequeño, 1989).

Table 11 Morphometric measurements expressed as a proportion of head length (% HDL) of the head lateral line canals of *Hydrolagus melanophasma*.

<i>H. melanophasma</i> (James <i>et al.</i> , 2009)	IZUA-PM 4007	IZUA-PM 4010	IZUA-PM 4011
HDL (mm)	170	195	224
ONC	8.2	11.3	9.4
LRC	3.8	5.1	5.8
LNC	26.0	23.6	29.5
IOA	14.9	14.4	12.9
OTM	30.6	30.3	28.1
OCL	11.1	12.3	11.2
STL	14.5	23.6	22.3
SPS	16.9	14.9	18.3
			15.0

Abbreviation: head length (HDL), distance from anterior oronasal fold to center of nasal canal (ONC), length of the rostral canal (LRC), length of the nasal canal measured as a straight line distance from right to left side (LNC), distance between infraorbital and angular canal measured as the straight line distance from junction of the oral and infraorbital canal to the junction of the oral and angular canal (IOA), distance between preopercular canal and main trunk canal measured from their junction with the infraorbital canal (OTM), distance between main trunk canal and supratemporal canal measured from their junctions with the infraorbital and postorbital canals, respectively (OCL), length of supratemporal canal measured across the head from its junctions with the postorbital canal (STL), distance from anterior base of spine to the center of the supratemporal canal (SPS)

REFERENCES

- Andrade, I. & Pequeño, G. (2006) First record of *Hydrolagus pallidus* Hardy & Stehmann, 1990 (Chondrichthyes: Chimaeridae) in the Pacific Ocean, with comments on Chilean holocephalians. *Revista de Biología Marina y Oceanografía, Valparaíso* 41, 111–115.
- Barnett, L.K., Didier, D.A., Long, D.J. & Ebert, D.A. (2006) *Hydrolagus mccoskeri* sp. nov., a new species of chimaeroid fish from the Galapagos Islands (Holocephali: Chimaeriformes: Chimaeridae). *Zootaxa* 1328, 27–38.

Compagno, L.J.V., Stehmann, M. & Ebert, D.A. (1990) *Rhinochimaera africana*, a new longnose chimaera from Southern Africa, with comments on the systematics and distribution of the genus *Rhinochimaera* Garman, 1901 (Chondrichthyes, Chimaeriformes, Rhinochimaeridae). *South African Journal of Marine Science* 9, 201–222.

Cubillos, L., Aedo, G., Araya, M., Meléndez, R., Galleguillos, R. & Pedraza, M. (2009) Estudio biológico-pesquero del recurso pejegallo entre la IV y X Regiones. *Departamento de Oceanografía, Universidad de Concepción, Informe técnico* No. 2006-18. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 Sep 2011).

Didier, D.A. (2004) Phylogeny and classification of extant Holocephali. In *Biology of sharks and their relatives* (Carrier, J.C., Musick, J.A., Heithaus, M.R., eds.), pp. 115–135. CRC Press: Boca Raton, FL.

Didier, D.A. (2008) Two new species of the genus *Hydrolagus* Gill (Holocephali: Chimaeridae) from Australia. In *Descriptions of New Australian Chondrichthyans* (Last, P.R., White, W.T. & Pogonoski, J.J., eds.). pp. 349-356. CSIRO Marine and Atmospheric Research Paper 22: Hobart, Australia.

Didier, D.A. & Seret, B. (2002) Chimaeroid fishes of New Caledonia with description of a new species of *Hydrolagus* (Chondrichthyes, Holocephali). *Cybium* 26, 225–233.

Didier, D.A. & Nakaya, K. (1999) Redescription of *Rhinochimaera pacifica* (Mitsukuri) and first record of *R. africana* Compagno, Stehmann & Ebert from Japan (Chimaeriformes: Rhinochimaeridae). *Ichthyological Research* 46, 139–152.

Ebert, D.A. (2003) *Sharks, Rays, and Chimaeras of California*. University of California Press: Berkeley, California.

Eschmeyer, W.N. & Fricke, R. (2010) Catalog of Fishes, electronic version Available at: <http://researcharchive.calacademy.org/research/Ichthyology/catalog/fishcatmain.asp> (accessed 25 Sep 2011).

Hardy, G.S. & Stehmann, M. (1990) A new deep- water ghost shark, *Hydrolagus pallidus* n.sp. (Holocephali, Chimaeridae), from the Eastern North Atlantic, and redescription of *Hydrolagus affinis* (Brito Capello, 1867). *Archiv fuer Fischereiwissenschaft* 40, 229–248.

James, K.C., Ebert, D.A., Long, D.J. & Didier, D.A. (2009) A new species of chimaera, *Hydrolagus melanophasma* sp. nov. (Chondrichthyes: Chimaeriformes: Chimaeridae), from the eastern North Pacific. *Zootaxa* 2218, 59–68.

Lamilla, J., Roa, R., Barría, P., Bustamante, C., Concha, F., Cortes, E., Acuña, E., Balbontín, F., Oliva, M., Araya, M. & Meléndez, R. (2008) Desarrollo metodológico para la estimación del descarte de Condrictios en las pesquerías artesanales. *Universidad Austral de Chile Informe técnico* No. 2008–60, Valdivia. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 Sep 2011).

Lamilla J., Bustamante, C., Roa, R., Acuña, E., Concha, F., Meléndez, R., López, S., Aedo, G., Flores, H. & Vargas-Caro, C. (2010) Estimación del descarte de condrictios en pesquerías artesanales. *Universidad Austral de Chile Informe técnico* No. 2008–60, Valdivia. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 Sep 2011).

Pequeño, G. (1989) Peces de Chile. Lista sistemática revisada y comentada. *Revista de Biología Marina y Oceanografía, Valparaíso* 24, 1–132.

Philippi, R.A. (1892) Algunos peces de Chile: Las rayas, *Callorhynchus* i *Orthagoriscus* Chilenos. *Anales del Museo Nacional de Chile, Primera sección, Zoología* 3, 1–16.

Quaranta, K.L., Didier, D.A., Long, D.J. & Ebert, D.A. (2006) A new species of chimaeroid, *Hydrolagus alaphus* sp. nov. (Chimaeriformes: Chimaeridae) from the Galapagos Islands. *Zootaxa* 1377, 33–45.

CHAPTER 3
ZOOGEOGRAPHY



3.1. Not all fish are equal: Functional biodiversity of cartilaginous fishes (Elasmobranchii and Holocephali) in Chile

Originally published in Journal of Fish Biology (ISSN: 1095-8649)

Copyright © Carlos Bustamante, 2014

Published online: 26 September 2014

License Number: 3477960616609

Abstract

A review of the primary literature on the cartilaginous fishes (sharks, skates, rays and chimaeras), together with new information suggests that 106 species occur in Chilean waters, comprising 58 sharks, 30 skates, 13 rays and five chimaeras. The presence of 93 species was confirmed, although 30 species were encountered rarely, through validated catch records and sightings made in artisanal and commercial fisheries and on specific research cruises. Overall, only 63 species appear to have a range distribution that normally includes Chilean waters. Actual reliable records of occurrence are lacking for 13 species. Chile has a cartilaginous fish fauna that is relatively impoverished compared to the global species inventory, but conservative compared to countries in South America with warm-temperate waters. The region of highest species richness occurs in the mid-Chilean latitudes of c. 30–40°S. This region represents a transition zone with a mix of species related to both the warm-temperate Peruvian province to the north and cold-temperate Magellan province to the south. This study provides clarification of species occurrence and the functional biodiversity of Chile's cartilaginous fish fauna.

INTRODUCTION

The influence of sharks, rays, skates (class Elasmobranchii) and chimaeras (class Holocephali) in ecosystems is under increasing threat due to continuing population declines of many species as a result of overfishing and by-catch mortality (Stevens *et al.*, 2000; Ferretti *et al.*, 2010). Knowledge of national and regional elasmobranch and holocephalan biodiversity is necessary to formulate management plans and conservation actions (Compagno, 1999; CPPS, 2009). Species richness is one of the most commonly used indices for assessing biodiversity in ecological studies (Whittaker, 1972; Magurran, 2003; Sahney *et al.*, 2010), but in some cases even this basic information lacks scientific rigour and leads to interpretation errors when management and conservation measures are implemented (Novacek, 2001; Mejía-Falla *et al.*, 2007; Rozzi *et al.*, 2008).

This paper reviews Chile's national elasmobranch and holocephalan species inventory. Existing records, new descriptions and recent taxonomic changes at the species level are examined through application of specific criteria, to assess the functional diversity and distributions of these cartilaginous fishes within the south-eastern Pacific Ocean. Species are highlighted where there are taxonomic issues, or records are rare or of uncertain validity. The resulting validated species inventory contributes to an understanding of the diversity of cartilaginous fishes off the coast of South America, which should aid future management and conservation planning.

MATERIAL AND METHODS

Historic and recent literature was reviewed for any reference to cartilaginous fishes (Class Elasmobranchii and Holocephali, *sensu* Eschmeyer & Fong, 2011) in Chilean waters that would complement the species inventories of Pequeño (1989, 1997) and Lamilla&Bustamante (2005). Additionally, an extensive survey comprising 10 localities along the Chilean coast was conducted in 2009 to assess cartilaginous fish by-catch in coastal artisanal (medium and small scale) fisheries and semi-industrial oceanic fleets. Descriptions of the variables surveyed and a detailed sampling methodology are provided by Lamilla *et al.* (2010). On-board operations and landings were observed in commercial fisheries with a history of interaction; where interaction is defined as a 'historical or recent record of catch and landing of at least one cartilaginous fish during a commercial trip' (Lamilla *et al.*, 2010). For each landing site and on-board survey, all cartilaginous fishes caught and landed were recorded and identified to species. Localities along the Chilean coast

(Fig. 15A) and the sampling effort for landing site visits and on-board surveys are provided in Table 12. Table 13 presents information about each fishery evaluated during this research.

Table 12 Localities of landing sites and bases for on-board surveys with an indication of relative observer effort. Days-at-sea in relation to on-board surveys are indicated in brackets.

Locality	Zone	Landing site visits	On-board surveys
Iquique	North	26	33 (46)
Antofagasta	North	0	9 (15)
Caldera	North	7	30 (69)
Coquimbo	Central	2	48 (68)
Valparaíso	Central	1	39 (45)
Concepción	South	70	24 (36)
Valdivia	South	18	76 (88)
Puerto Montt	South	10	21 (52)
Aysén	Austral South	0	6 (27)
Punta Arenas	Austral South	4	0

The 10 localities span c. 33° of latitude and represent four zones (north, central, south and austral south) which are independent of bathymetric reference and the biographic provinces described by Camus (2001). North includes localities between Iquique (20.2° S) and Caldera (27° S), central localities between Coquimbo (29.9° S) and Valparaiso (33° S), south localities between Concepción (36.9° S) and Puerto Montt (41.5° S) and austral south includes localities between Aysén (45.4° S) and Punta Arenas (53.1° S). The oceanic islands zone is treated separately and includes species reported around insular territories within the Chilean Economic Exclusive Zone, such as Nazca and Sala y Gómez submarine ridges, Juan Fernández Islands, Desventuradas Islands and Easter Island (Fig. 15B).

To assess cartilaginous fishes of Chile on a meaningful basis, specific criteria are used to ensure that only those species reported and confirmed within circumscribed geographical areas within the political boundaries are considered (Mejía-Falla *et al.*, 2007). For this purpose, confirmed species are defined as those that meet the following criteria: (1) identification has been validated scientifically, and there are no reasonable doubts about a species' identity, (2) there are

reports of its presence, capture and sale from fishing or scientific expeditions and (3) records do not indicate a haphazard or anecdotal encounter of a species that has a low natural abundance.

The modern classification of extant Elasmobranchii and Holocephali and comparative values of global biodiversity were extracted from Eschmeyer & Fong (2011) and Ebert *et al.* (2013).

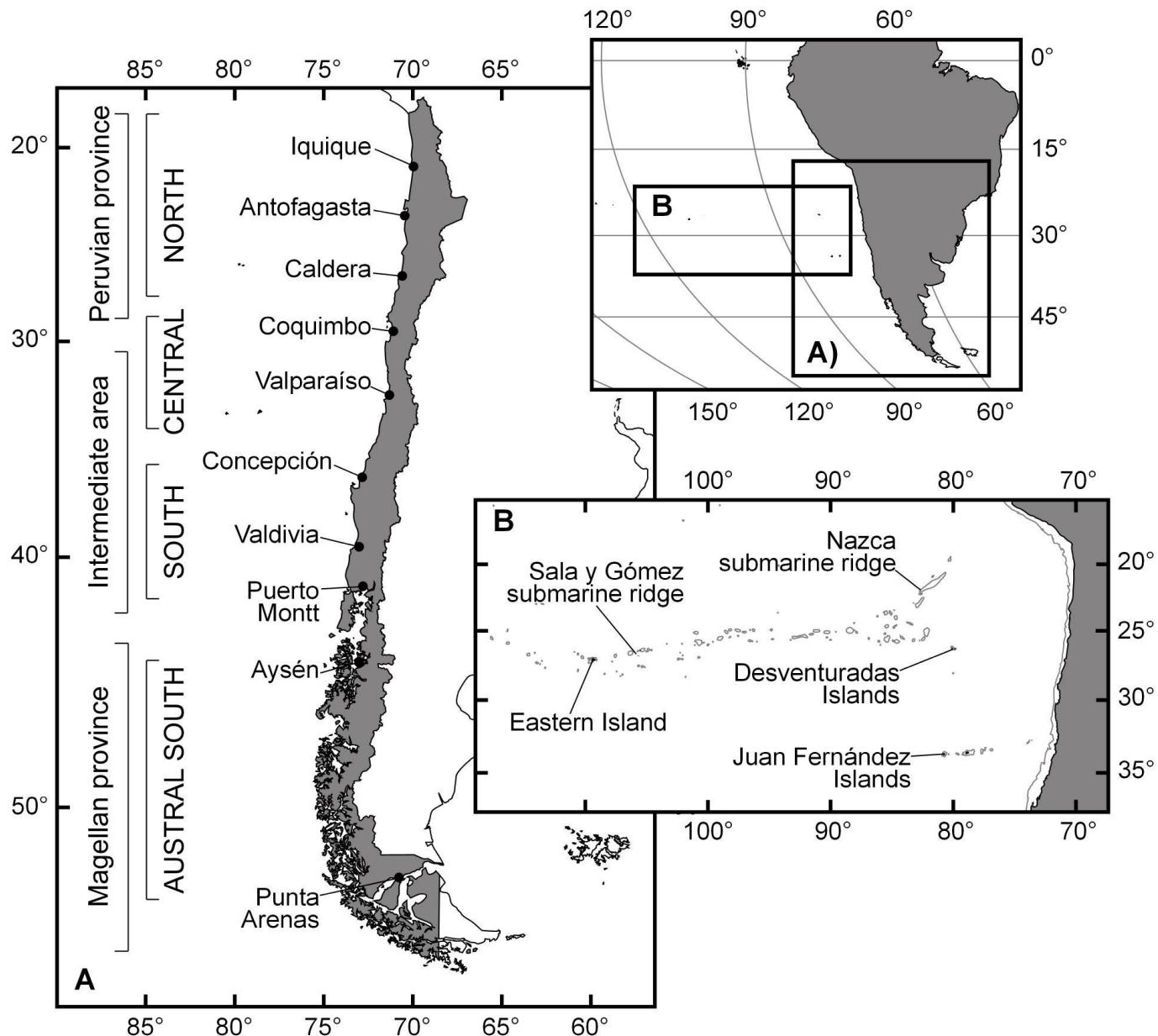


Figure 15 Map of South America showing the location of study area (inset boxes), indicating (A) main localities in Chile, zones and biogeographic provinces on the latitudinal gradient; and (B) oceanic islands zone (see text for reference of main points). Contour lines (grey) indicate 2000 m isobath on (B)

Table 13 Main fisheries in Chile with interaction and/or catch records of cartilaginous species.

Target species	Zone	Fishing gear
Swordfish <i>Xiphias gladius</i> L. 1758	Central	Gillnet/Longline
Albacore <i>Thunnus alalunga</i> (Bonnaterre 1788)	Central	Gillnet
Swimming crab <i>Ovalipes trimaculatus</i> (De Haan 1833)	Central	Gillnet
Chilean jack mackerel <i>Trachurus murphyi</i> Nichols 1920	Central	Gillnet
Blue squat lobster <i>Cervimunida johni</i> Porter 1903	Central	Trawl
Carrot squat lobster <i>Pleuroncodes monodon</i> (H. Milne Edwards 1837)	Central	Trawl
Chilean nylon shrimp <i>Heterocarpus reedi</i> Bahamonde 1955	Central	Trawl
Smalleye flounder <i>Paralichthys microps</i> (Günther 1881)	Central	Gillnet
Southern rays bream <i>Brama australis</i> Valenciennes 1838	Central	Gillnet
South Pacific hake <i>Merluccius gayi gayi</i> (Guichenot 1848)	Central/South	Gillnet
Yellowtail amberjack <i>Seriola lalandi</i> Valenciennes 1833	North	Longline
Palm ruff <i>Seriolella violacea</i> Guichenot 1848	North	Longline
†Shortfin mako <i>Isurus oxyrinchus</i> Rafinesque 1810	North	Longline
Chilean silverside <i>Odontesthes regia</i> (Humboldt 1821)	North	Gillnet
Pink cusk-eel <i>Genypterus blacodes</i> (Forster 1801)	North/Central/South	Gillnet/Longline
Patagonian toothfish <i>Dissostichus eleginoides</i> Smitt 1898	North/South	Longline
Corvina drum <i>Cilus gilberti</i> (Abbott 1899)	North/South	Gillnet
Red cusk-eel <i>Genypterus chilensis</i> (Guichenot 1848)	South	Longline
Southern hake <i>Merluccius australis</i> (Hutton 1872)	South	Longline
†Elephantfish <i>Callorhinus callorynchus</i> (L. 1758)	South	Gillnet
Snoek <i>Thyrsites atun</i> (Euphrasen 1791)	South	Gillnet
Speckled smooth-hound <i>Mustelus mento</i> Cope 1877	South	Gillnet
†Piked dogfish <i>Squalus acanthias</i> L. 1758	South	Longline
†Yellownose skate <i>Zearaja chilensis</i> (Guichenot 1848)	South/Austral South	Longline

† Cartilaginous fish as target resource.

RESULTS

A total of 106 cartilaginous species occur in Chilean waters (58 sharks, 30 skates, 13 rays and five chimaeras), represented in 58 genera (37 shark, nine skate, nine ray and three chimaera genera) and 29 families (16 shark, six skate, four ray and three chimaera families). This represents an increase in the reported biodiversity of cartilaginous fishes in Chile with 14 species added to the known ichthyofauna, these are brown lanternshark *Etomopterus unicolor* (Engelhardt 1912), pocket shark *Mollisquama parini* Dolganov 1984, frog shark *Somniosus longus* (Tanaka 1912), smalltooth sand tiger shark *Odontaspis ferox* (Risso 1810), longfin mako *Isurus paucus* Guitart 1966, crocodile shark *Pseudocarcharias kamoharai* (Matsubara 1936), silky shark *Carcharhinus falciformis* (Müller & Henle 1839), scalloped hammerhead *Sphyrna lewini* (Griffith & Smith 1834), Chilean guitarfish *Tarsistes philippii* Jordan 1919, joined-fins skate *Bathyraja couesseauae* Díaz de Astarloa & Mabragaña 2004, dark-belly skate *Bathyraja meridionalis* Stehmann 1987, cuphead skate *Bathyraja scaphiops* (Norman 1937), spinetail mobula *Mobula japanica* (Müller & Henle 1841) and Eastern Pacific black ghostshark *Hydrolagus melanophasma* James, Ebert, Long & Didier 2009. While this total of 106 species is indicative of overall diversity, it is not a good index of ‘functional’ biodiversity as many species identifications are based on anecdotal or single verified observations, and as such, information about their distributions is poor or absent.

A total of 6,450 specimens of sharks, rays, skates and chimaeras were examined from 138 landing and 286 on-board surveys, which confirmed the presence of 40 cartilaginous fish species. Bibliographic records provide a further 53 species that meet the confirmed species criterion resulting in 93 confirmed species, of which 30 species are relatively rarely encountered. The situation for the other 13 species reported to occur in Chilean waters is less clear. The species reported in Chilean waters and their zonal distributions are summarized in Table 14.

Species that have been reported to occur in Chile based on their probable distribution include some for which there are no actual records in the area, e.g. sharpnose sevengill shark *Heptranchias perlo* (Bonnaterre 1788), whale shark *Rhincodon typus* Smith 1828 (Compagno, 1984), pygmy shark *Euprotomicrus bispinatus* (Quoy & Gaimard 1824) (Seigel, 1978; Compagno, 1984; Ebert *et al.*, 2013), spotted houndshark *Triakis maculata* Kner & Steindachner 1867 (Compagno, 1984; Ebert *et al.*, 2013), diamond stingray *Dasyatis dipterura* (Jordan & Gilbert 1880), Chilean devil ray *Mobula tarapacana* (Philippi 1892), smoothtail mobula *Mobula thurstoni* (Lloyd 1908) (Chirichigno, 1974; Pequeño, 1989; Ebert *et al.*, 2013), sparsetrooth dogfish *Scymnodalatias oligodon* Kukuev & Konovalenko 1988, *S. longus* (Pequeño, 1989; Ebert *et al.*, 2013), *C. falciformis* (Grove & Lavenberg, 1997) and the Pacific spookfish *Rhinochimaera pacifica*

(Mitsukuri 1895) (Inada & Garrick, 1979; Pequeño, 1989). In addition, Eaton's skate *Bathyraja eatonii* (Günther 1876) and McCain's skate *Bathyraja maccaini* Springer 1971 are Antarctic species that have been reported in Chile due to their presence in the Chilean Antarctic Territory (Pequeño, 1989).

Non-resident migrant species, single-specimen descriptions, documented anecdotal observations and incidental observations in remote locations collectively result in the group of 'confirmed' species, but of rare occurrence. This group includes those species for which there is taxonomic uncertainty and single-specimen reports (or descriptions) of species from Nazca and Sala y Gómez submarine ridges, *e.g.* shorttail lanternshark *Etmopterus brachyurus* Smith & Radcliffe 1912, smalleye lantern shark *Etmopterus litvinovi* Parin & Kotlyar 1990, blackbelly lanternshark *Etmopterus lucifer* Jordan & Snyder 1902, smooth lanternshark *Etmopterus pusillus* (Lowe 1839), dense-scale lantern shark *Etmopterus pycnolepis* Kotlyar 1990, Hawaiian lanternshark *Etmopterus villosum* Gilbert 1905, *E. unicolor*, *M. parini*, *O. ferox*, longnose spurdog *Squalus blainville* (Risso 1827), pointy-nosed blue chimaera *Hydrolagus trolli* Didier & Séret 2002, smalldisk torpedo *Torpedo microdiscus* Parin & Kotlyar 1985 and semipelagic torpedo *Torpedo semipelagica* Parin & Kotlyar 1985; or around the southern archipelago and Tierra del Fuego, *e.g.* southern thorny skate *Amblyraja doellojuradoi* (Pozzi 1935), Antarctic starry skate *Amblyraja georgiana* (Norman 1938), *B. scaphiops*, *B. couesseauae* and *B. meridionalis*. Rare species are those without capture records after 1990, and may include species of low natural abundance, such as the frilled shark *Chlamydoselachus anguineus* Garman 1884 (Morillas, 1977), broadnose skate *Bathyraja brachyurops* (Fowler 1910), slimtail skate *Bathyraja longicauda* (de Buen 1959), smallnose fanskate *Sympterygia bonapartii* Müller & Henle 1841 and Peruvian eagle ray *Myliobatis peruviana* Garman 1913 (Lamilla *et al.*, 2010). Particularly, interesting cases are Chilean round stingray *Urobatis marmoratus* (Philippi 1892) and *T. philippii*, two species with no known holotype (Pequeño, 1989), and Chilean round ray *Urotrygon chilensis* (Günther 1872), a relatively abundant coastal ray of the central-east Pacific Ocean with a distribution from Mexico to Peru, that was described from Chile (no location data, unique holotype) by Günther (1872), but has not been observed in the region since that time. In the case of the white shark *Carcharodon carcharias* (L. 1758), the last records of this species relate to a series of attacks on humans north of Valparaíso (Egaña & McCosker, 1984) and the capture of a large female *C. carcharias* at Iquique that was reported with photographs in local newspapers in December 1984. Additionally, swellshark *Cephaloscyllium ventriosum* (Garman 1880), humpback smooth-hound *Mustelus whitneyi* Chirichigno 1973 and *M. japanica* have been confirmed to occur in coastal waters of north and central Chile. A paucity of recent observations may relate to a low natural abundance of each of

these species in the region, or to natural oceanographic abnormalities that occasionally result in a southward latitudinal displacement of warm tropical water masses. Such oceanographic phenomena may facilitate a periodical invasion of Peruvian and Chilean coastal waters by more northerly species (Schaaf-Da Silva & Ebert, 2008; Bustamante *et al.*, 2012a).

Species with the most restricted distributions (present in a single zone only) were located in north (10 spp.), Oceanic Islands (18 spp.), austral south (nine spp.), central (two spp.) and south (one sp.) zones. Six species are widely distributed, with records from all mainland localities (north to austral south). The majority of the species span two or three zones, with 12 species in the north-south region, 13 species in the north-central region, four species in the central-south, six in the central-austral south region and 11 species in the south-austral south region. Finally, the brown catshark *Apristurus brunneus* (Gilbert 1892) was the only species that occurs at Oceanic Islands and along the mainland coast (in the central and south zones) (Table 14).

Table 14 Cartilaginous fishes reported to Chile, indicating the date of last record and its distribution zone along the country.

Species	Last record	Distribution
Hexanchiformes: Chlamydoselachidae		
<i>Chlamydoselachus anguineus</i> Garman 1884†	Morillas (1977)	N
Hexanchiformes: Hexanchidae		
<i>Hexanchus griseus</i> (Bonnaterre 1788)	Quiroz <i>et al.</i> (2008)	N, C, S
<i>Heptranchias perlo</i> (Bonnaterre 1788)‡	Pequeño (1989)	N
<i>Notorynchus cepedianus</i> (Péron 1807)	Acuña <i>et al.</i> (2005)	C, S
Squaliformes: Echinorhinidae		
<i>Echinorhinus cookei</i> Pietschmann 1928	Long <i>et al.</i> (2011)	N, C
Squaliformes: Etmopteridae		
<i>Aculeola nigra</i> de Buen 1959	Gatica & Acuña (2011)	N, C
<i>Centroscyllium granulatum</i> Günther 1887	Valenzuela <i>et al.</i> (2008)	C, S, AS
<i>Centroscyllium nigrum</i> Garman 1899	Gatica & Acuña (2011)	N, C, S
<i>Etmopterus brachyurus</i> Smith & Radcliffe 1912†	Oñate & Pequeño (2005)	OI
<i>Etmopterus granulosus</i> (Günther 1880)	Present study	S, AS
<i>Etmopterus litvinovi</i> Parin & Kotlyar 1990†	Parin <i>et al.</i> (1997)	OI
<i>Etmopterus lucifer</i> Jordan & Snyder 1902†	Oñate & Pequeño (2005)	OI
<i>Etmopterus pusillus</i> (Lowe 1839)†	Oñate & Pequeño (2005)	OI
<i>Etmopterus pycnolepis</i> Kotlyar 1990†	Parin <i>et al.</i> (1997)	OI

Table 14 Continued

Species	Last record	Distribution
<i>Etomopterus unicolor</i> (Engelhardt 1912) †	Reyes & Hüne (2006)	S
<i>Etomopterus villosus</i> Gilbert 1905†	Pequeño (1989)	OI
Squaliformes: Dalatiidae		
<i>Isistius brasiliensis</i> (Quoy & Gaimard 1824)	Sielfeld & Kawaguchi (2004)	OI
<i>Euprotomicrus bispinatus</i> (Quoy & Gaimard 1824)‡	Pequeño (1989)	OI
<i>Mollisquama parini</i> Dolganov 1984†	Pequeño (1989)	OI
Squaliformes: Somniosidae		
<i>Somniosus antarcticus</i> Whitley 1939	Reyes & Torres-Florez (2009)	AS
<i>Somniosus longus</i> (Tanaka 1912) ‡	Parin <i>et al.</i> (1997)	OI
<i>Centroscymnus crepidater</i> (Barbosa du Bocage & de Brito Capello 1864)*	Menares & Sepúlveda (2005)	C, S
<i>Centroscymnus macracanthus</i> Regan 1906*	Present study	S, AS
<i>Centroscymnus owstonii</i> Garman 1906	Acuña <i>et al.</i> (2005)	N, C
<i>Zameus squamulosus</i> (Günther 1877)	Present study	S, AS
<i>Scymnodalatias oligodon</i> Kukuev & Konovalenko 1988‡	Pequeño (1989)	OI
Squaliformes: Centrophoridae		
<i>Deania calcea</i> (Lowe 1839)	Valenzuela <i>et al.</i> (2008)	N, C, S, AS
Squaliformes: Squalidae		
<i>Squalus acanthias</i> L. 1758	Valenzuela <i>et al.</i> (2008)	S, AS
<i>Squalus blainville</i> (Risso 1827)†	Andrade & Pequeño (2008)	OI

Table 14 Continued

Species	Last record	Distribution
<i>Squalus</i> cf. <i>mitsukurii</i> Jordan & Snyder 1903	White & Iglésias (2011)	OI
Squatiniformes: Squatinidae		
<i>Squatina armata</i> (Philippi 1887)	Stelbrink <i>et al.</i> (2010)	N, C
Orectolobiformes: Rhincodontidae		
<i>Rhincodon typus</i> Smith 1828‡	Pequeño (1989)	OI
Lamniformes: Alopiidae		
<i>Alopias superciliosus</i> Lowe 1841	Hernández <i>et al.</i> (2008)	N
<i>Alopias vulpinus</i> (Bonnaterre 1788)	Hernández <i>et al.</i> (2008)	N
Lamniformes: Cetorhinidae		
<i>Cetorhinus maximus</i> (Gunnerus 1765)	Hernández <i>et al.</i> (2010)	C, S
Lamniformes: Lamnidae		
<i>Carcharodon carcharias</i> (L. 1758)†	Egaña & McCosker (1984)	N, C
<i>Isurus oxyrinchus</i> Rafinesque 1810	Bustamante & Bennett (2013)	N, C
<i>Isurus paucus</i> Guitart 1966	Bustamante <i>et al.</i> (2009)	N, C
<i>Lamna nasus</i> (Bonnaterre 1788)	Hernández <i>et al.</i> (2008)	N, C, S, AS
Lamniformes: Pseudocarchariidae		
<i>Pseudocarcharias kamoharai</i> (Matsubara 1936)	Meléndez <i>et al.</i> (2006)	N, C
Lamniformes: Odontaspidae		
<i>Odontaspis ferox</i> (Risso 1810)†	Long <i>et al.</i> (2014)	OI

Table 14 Continued

Species	Last record	Distribution
Carcharhiniformes: Scyliorhinidae		
<i>Apristurus brunneus</i> (Gilbert 1892)	Andrade & Pequeño (2008)	C, S, OI
<i>Apristurus nasutus</i> de Buen 1959	Andrade & Pequeño (2008)	N, C, S
<i>Cephaloscyllium ventriosum</i> (Garman 1880)†	Schaaf-Da Silva & Ebert (2008)	C
<i>Bythaelurus canescens</i> (Günther 1878)	Lopez <i>et al.</i> (2013)	N, C, S, AS
<i>Cephalurus cephalus</i> (Gilbert 1892)	Gatica & Acuña (2007)	N
<i>Schroederichthys bivius</i> (Müller & Henle 1838)	Valenzuela <i>et al.</i> (2008)	S, AS
<i>Schroederichthys chilensis</i> (Guichenot 1848)	Hernández <i>et al.</i> (2005)	N, C, S
Carcharhiniformes: Triakidae		
<i>Galeorhinus galeus</i> (L. 1758)	Hernández <i>et al.</i> (2008)	N, C
<i>Mustelus mento</i> Cope 1877	Quiroz <i>et al.</i> (2008)	N, C, S
<i>Mustelus whitneyi</i> Chirichigno 1973†	Angel & Ojeda (2001)	N
<i>Triakis maculata</i> Kner & Steindachner 1867‡	Castro & Baeza (1986)	N
Carcharhiniformes: Carcharhinidae		
<i>Carcharhinus falciformis</i> (Müller & Henle 1839)‡	Grove & Lavenberg (1997)	OI
<i>Carcharhinus galapagensis</i> (Snodgrass & Heller 1905)	Pequeño & Sáez (2003)	OI
<i>Carcharhinus obscurus</i> (Lesueur 1818)	Hernández <i>et al.</i> (2008)	OI
<i>Prionace glauca</i> (L. 1758)	Bustamante & Bennett (2013)	N, C

Table 14 Continued

Species	Last record	Distribution
Carcharhiniformes: Sphyrnidae		
<i>Sphyrna lewini</i> (Griffith & Smith 1834)	Hernández <i>et al.</i> (2008)	N
<i>Sphyrna zygaena</i> (L. 1758)	Hernández <i>et al.</i> (2008)	N
Rajiformes: Rhinobatidae		
<i>Rhinobatos planiceps</i> Garman 1880	Present study	N
<i>Tarsistes philippii</i> Jordan 1919†	Pequeño (1989)	OI
Rajiformes: Arhynchobatidae		
<i>Bathyraja albomaculata</i> (Norman 1937)	Present study	C, S, AS
<i>Bathyraja brachyurops</i> (Fowler 1910)†	Sielfeld & Vargas (1999)	S, AS
<i>Bathyraja cousseauae</i> Díaz de Astarloa & Mabragaña 2004†	Reyes & Torres-Florez (2008)	AS
<i>Bathyraja eatonii</i> (Günther 1876)‡	Pequeño (1989)	AS
<i>Bathyraja griseocauda</i> (Norman 1937)	Sáez & Lamilla (2004)	S, AS
<i>Bathyraja longicauda</i> (de Buen 1959)†	Pequeño (1989)	S, AS
<i>Bathyraja maccaini</i> Springer 1971‡	Pequeño (1989)	AS
<i>Bathyraja macloviana</i> (Norman 1937)	Reyes & Torres-Florez (2009)	AS
<i>Bathyraja magellanica</i> (Philippi 1902)	Present study	S, AS
<i>Bathyraja meridionalis</i> Stehmann 1987†	Reyes & Torres-Florez (2009)	AS
<i>Bathyraja multispinis</i> (Norman 1937)	Present study	N, C, S, AS
<i>Bathyraja peruana</i> McEachran & Miyake 1984	Present study	N, C, S

Table 14 Continued

Species	Last record	Distribution
<i>Bathyraja scaphiops</i> (Norman 1937)†	Sielfeld & Vargas (1999)	AS
<i>Bathyraja schroederi</i> (Krefft 1968)	Present study	S, AS
<i>Psammobatis normani</i> McEachran 1983	Sielfeld & Vargas (1999)	AS
<i>Psammobatis rudis</i> Günther 1870	Present study	C, S, AS
<i>Psammobatis scobina</i> (Philippi 1857)	Concha <i>et al.</i> (2009)	N, C, S, AS
<i>Sympterygia bonapartii</i> Müller & Henle 1841†	Pequeño (1997)	AS
<i>Sympterygia brevicaudata</i> (Cope 1877)	Acuña <i>et al.</i> (2005)	N, C, S
<i>Sympterygia lima</i> (Poeppig 1835)	Concha <i>et al.</i> (2013)	N, C, S
Rajiformes: Rajidae		
<i>Gurgesiella furvescens</i> de Buen 1959	Acuña <i>et al.</i> (2005)	N, C
<i>Amblyraja doellojuradoi</i> (Pozzi 1935)†	Pequeño (1997)	AS
<i>Amblyraja frerichsi</i> (Krefft 1968)	Bustamante <i>et al.</i> (2012d)	C, S, AS
<i>Amblyraja georgiana</i> (Norman 1938)†	Pequeño (1997)	AS
<i>Zearaja chilensis</i> (Guichenot 1848)	Bustamante <i>et al.</i> (2012c)	C, S, AS
<i>Dipturus trachyderma</i> (Krefft & Stehmann 1975)	Concha <i>et al.</i> (2012)	C, S, AS
<i>Rajella nigerrima</i> (de Buen 1960)	Present study	C, S, AS
<i>Rajella sadowskii</i> (Krefft & Stehmann 1974)	Present study	S, AS
Torpediniformes: Narcinidae		
<i>Discopyge tschudii</i> Heckel 1846	Present study	C, S

Table 14 Continued

Species	Last record	Distribution
Torpediniformes: Torpedinidae		
<i>Torpedo microdiscus</i> Parin & Kotlyar 1985†	Pequeño (1997)	OI
<i>Torpedo semipelagica</i> Parin & Kotlyar 1985†	Pequeño (1997)	OI
<i>Torpedo tremens</i> de Buen 1959	Andrade & Pequeño (2008)	N, C, S
Myliobatiformes: Dasyatidae		
<i>Pteroplatytrygon violacea</i> (Bonaparte 1832)	Acuña <i>et al.</i> (2002)	N, C
<i>Dasyatis dipterura</i> (Jordan & Gilbert 1880)‡	Pequeño (1989)	N
Myliobatiformes: Urotrygonidae		
<i>Urobatis marmoratus</i> (Philippi 1892)†	Pequeño (1989)	C
<i>Urotrygon chilensis</i> (Günther 1872)†	Pequeño (1989)	N
Myliobatiformes: Myliobatidae		
<i>Myliobatis chilensis</i> Philippi 1892	Present study	N, C, S
<i>Myliobatis peruviana</i> Garman 1913†	Acuña <i>et al.</i> (1998)	N
<i>Mobula japanica</i> (Müller & Henle 1841)†	Bustamante <i>et al.</i> (2012a)	N
<i>Mobula tarapacana</i> (Philippi 1892)‡	Pequeño (1989)	N
<i>Mobula thurstoni</i> (Lloyd 1908)‡	Pequeño (1989)	N
Chimaeriformes: Callorhinchidae		
<i>Callorhinchus callorynchus</i> (L. 1758)	Quiroz <i>et al.</i> (2008)	N, C, S

Table 14 Continued

Species	Last record	Distribution
Chimaeriformes: Chimaeridae		
<i>Hydrolagus macrophthalmus</i> de Buen 1959	Andrade & Pequeño (2008)	N, C
<i>Hydrolagus melanophasma</i> James, Ebert, Long & Didier 2009	Bustamante <i>et al.</i> (2012b)	N, C, S
<i>Hydrolagus trolli</i> Didier & Séret 2002†	Bustamante <i>et al.</i> (2012b)	OI
Chimaeriformes: Rhinochimaeridae		
<i>Rhinochimaera pacifica</i> (Mitsukuri 1895)‡	Pequeño (1989)	N

N, north; C, central; S, south; AS, austral south; OI, oceanic islands.

† Confirmed, but rarely collected species.

‡ Doubtful record for the species.

* Compagno (2005) and Ebert *et al.* (2013) place *Centroscelachus crepidater* and *Proscymnodon macracanthus* these species in different genera.

DISCUSSION

The reported and confirmed biodiversity of cartilaginous fishes in Chilean waters as updated here is based on specific knowledge gathered over 50 years of research (Pequeño, 1989, 1997; Pequeño & Lamilla, 1993, 1995, 1997; Lamilla & Bustamante, 2005). The scientific study of cartilaginous fishes in Chile started, however, in the late 18th Century with Molina (1782), Guichenot (1848), Philippi (1887, 1896, 1901), Pérez-Canto (1886), Delfin (1901), Quijada (1913) and Schneider (1943) providing descriptive studies of coastal and pelagic fishes. Ecological insights into cartilaginous fishes began with Mann (1954), who defined ichthyo-geographical zones for coastal fishes off the Chilean continental shelf. Later, Pequeño (1989, 1997) published a checklist of extant cartilaginous species reported for Chilean national waters, including Antarctic waters. The biodiversity of cartilaginous fishes is here increased to 106 by the addition of 10 species to the most recent review (96 species; Lamilla & Bustamante, 2005). This significant increase to the records of the national biodiversity reflects an increase in marine research since the implementation of the National Plan of Action to promote conservation and management of sharks and their relatives (Lamilla *et al.*, 2010).

Chile has a relatively impoverished cartilaginous fish fauna when compared to the global species inventory (Table 15). In absolute terms, Chile appears to have a cartilaginous fish fauna that is less diverse than neighbouring countries, as only 8% of world holocephalan and elasmobranch species are found in national waters. Chile's cartilaginous fish fauna is composed mainly of deep-water skates (30.1%, order Rajiformes) and sharks (24.7%, order Squaliformes), small coastal benthic sharks (16.1%, order Carcharhiniformes) and large oceanic, highly migratory sharks (9.7%, order Lamniformes) and rays (6.5%, order Myliobatiformes).

The species richness of cartilaginous fishes in Chile (106 species) is relatively conservative given the length of the coastline, compared to warm-temperate countries in South America (Menni & Lucifora, 2007; Domingo *et al.*, 2008; CPPS, 2009): Peru (123 species), Ecuador (93 species), Colombia (176 species from off the Pacific coast), Argentina (105 species) and Uruguay (100 species). Considering species richness in the region (Fig. 16), the relative proportions of sharks, rays and chimaeras are similar in Chile, Peru, Argentina and Uruguay despite their differing species compositions and geography. The cartilaginous fauna of Chile comprises c. 12% more sharks than batoids (skates and rays), compared to 14.6 and 27.2% in Peru and Ecuador, respectively. In comparison, Argentina and Uruguay have a lower proportion of sharks, 6.7 and 6.0%, respectively. The proportion of chimaeras is greatest in Chile (4.7%) and Peru (4.1%) compared to <2% in

Ecuador, Argentina and Uruguay. Chimaeras have not been reported from the Pacific coast of Colombia.

A latitudinal gradient in species richness is only observed if the 93 confirmed species are considered. Species richness of elasmobranchs in the south-east Pacific Ocean increases towards lower latitudes similar to other marine fishes (Rohde, 1992); however, holocephalans display an inverse pattern, increasing in diversity towards higher latitudes. Climate appears to have a direct influence on marine fish distributions with species richness generally declining with latitude (Hiddink & Hofstede, 2008), but research into the reasons for variation in local and regional species richness is required to understand the current distribution of cartilaginous fishes in South America.

Table 15 Number of cartilaginous fishes in the world by taxonomic order and species reported (and confirmed; in parentheses) to occur in Chile (modified after Eschmeyer & Fong, 2011 and Ebert *et al.*, 2013)

Order	World	Chile
Hexanchiformes	6	4 (3)
Heterodontiformes	9	0 (0)
Orectolobiformes	44	1 (0)
Lamniformes	15	9 (9)
Carcharhiniformes	280	17 (15)
Squaliformes	127	26 (23)
Pristiophoriformes	7	0 (0)
Squatiniformes	22	1 (1)
Pristiformes	7	0 (0)
Torpediniformes	67	4 (4)
Rajiformes	353	30 (28)
Myliobatiformes	220	9 (6)
Chimaeriformes	50	5 (4)

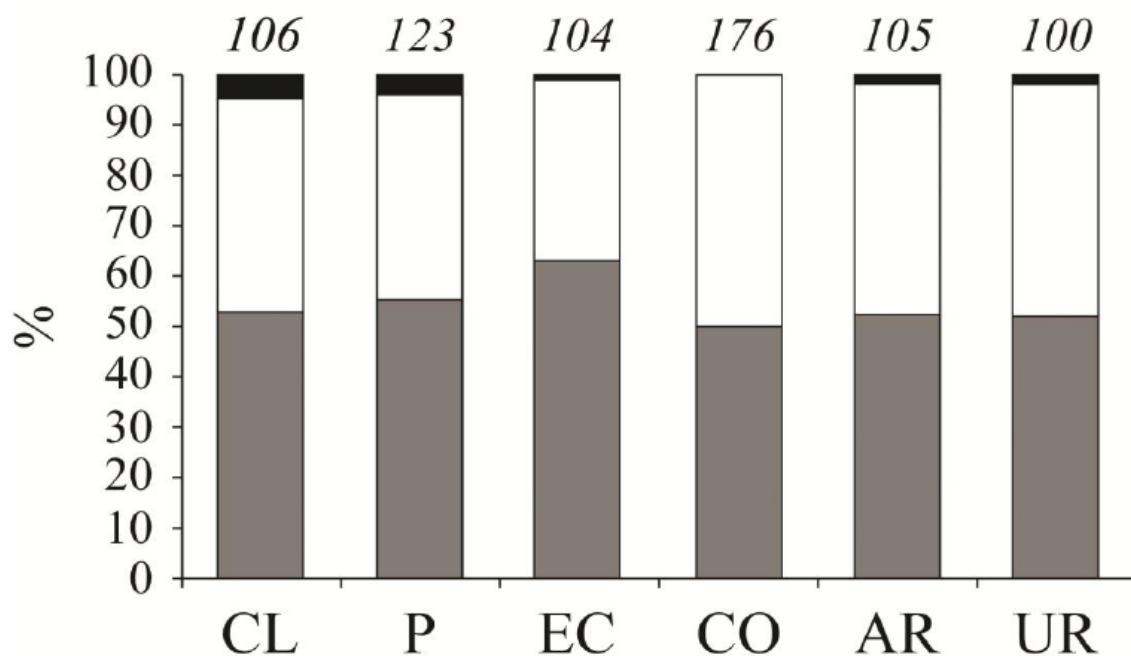


Figure 16 Per cent composition of the three major cartilaginous fish groups, sharks (grey), rays (white) and chimaeras (black), for six South American countries. Italics numbers represent species richness of confirmed species. CL, Chile; P, Peru; EC, Ecuador; CO, Pacific coast of Colombia; AR, Argentina; UR, Uruguay.

Chile's marine fish fauna is considered to generally 'belong' to either the Peruvian or the Magellan provinces (Fig. 15A) (Camus, 2001; Seeliger & Kjerfve, 2001). Warm-temperate waters species are shared in the north with Peru, and cold-temperate water species with Argentina in the south (Lucas *et al.*, 2005), with an intermediate area of mixed fauna located between the central and south zones (Camus, 2001). Species richness of marine fishes reported for the Peruvian and Magellan provinces (represented in this study by the north and austral south zones, respectively) is relatively low compared to the intermediate area; as has been documented by Seeliger & Kjerfve (2001). The transition zone between the Peruvian province and the intermediate area, corresponding to the central zone in this study, has a higher diversity (16.5% of confirmed species) than the Peruvian province (11.0%). Similarly, diversity of the transition zone between the Magellan province and the intermediate area, south zone in this study is greater (13.2%) compared to the austral south (9.9%). The cartilaginous ichthyofauna of Chile may be characterized as being temperate water species, as the highest biodiversity (53.8%) is observed within the central and south zones.

The inclusion of some species previously reported by Pequeño (1989), such as *M. parini* or *T. philippii*, is made despite the observation that the species have been not reported since the original descriptions provided by Dolganov (1984) and Jordan (1919), respectively. Three species of *Etmopterus* (*E. brachyurus*, *E. lucifer* and *E. unicolor*) have been reported from around the Chilean oceanic islands (Oñate & Pequeño, 2005; Reyes & Hüne, 2006), and are included as ‘rare occurrence’ species. Given that *E. brachyurus*, *E. lucifer* and *E. unicolor* are noted for having a restricted distribution in the north-west Pacific Ocean, these ‘rare occurrence’ species could be the result of misidentification of currently undescribed species in the Chilean oceanic Island region (Ebert *et al.*, 2011; Straube *et al.*, 2011). Species such as *I. paucus* and *P. kamoharai* are incorporated as new records, and are by-catch in the pelagic longline fishery targeting swordfish and tunas (Meléndez *et al.*, 2006; Bustamante *et al.*, 2009). Unconfirmed species are present in all zones and generally reflect low human population density and limited commercial fishing activity in coastal regions such as the Oceanic Islands and austral south zones, which limit accessibility and specimen collection. In contrast, unconfirmed species records in the north zone are more likely the result of the variability in oceanic conditions related to the El Niño Southern Oscillation, which affects the distribution range of tropical and sub-tropical species (Sielfeld *et al.*, 2010), and is reflected by anecdotal records of single specimens of tropical origin. The nomenclature of some species has been updated from previous reviews; *Somniosus antarcticus* Whitley 1939 replaces previous records of *Somniosus pacificus* Bigelow & Schroeder 1944 in the south hemisphere (Yano *et al.*, 2004); *S. oligodon* replaces records of *Scymnodalatias sherwoodi* (Archey 1921) in the Nazca and Sala y Gómez submarine ridges (Ebert *et al.*, 2013); specimens of *Squalus mitsukurii* reported from Robinson Crusoe and Santa Clara islands by Pequeño (1989) and Arana (2000) may represent more than one species (White & Iglésias, 2011), and therefore the notation *S. cf. mitsukurii* is adopted here.

Chile has one of the largest maritime territories in the world (Cubillos, 2005), and despite a relatively short commercial fishing history of <50 years, it is among the top five fishing countries in the world, measured in terms of landings and exports (Albarrán, 2005). Chile is the second largest producer of fishmeal (Sepúlveda *et al.*, 2005) and has the second largest farmed fish output in the world (Bustos, 2005). In terms of fishing, cartilaginous fishes are of relatively low commercial interest in Chile and are among the least researched species in national waters, in which effort is oriented towards small pelagic fishes (sardines, anchovies and mackerels) and the salmonid harvest (Cubillos, 2005). Despite the increased research effort that usually accompanies fisheries exploitation, the basic biology and taxonomy of cartilaginous fishes in Chile is still poorly known. Elasmobranchs and holocephalans are commonly caught as target and by-catch in several trawl,

coastal gillnets and longline fisheries along the Chilean coast, but capture records (by-catch and discard) are rarely reported, with the exception of target species (Lamilla *et al.*, 2010).

While target species are identified in the official landings records, there are only a few cartilaginous fishes landed as target species: shortfin mako *Isurus oxyrinchus* Rafinesque 1810, elephantfish *Callorhinichus callorynchus* (L. 1758) and yellownose skate *Zearaja chilensis* (Guichenot 1848). At least 14 other species are landed as by-catch and are reported in a generic category that lacks taxonomic validity such as ‘shark’ or ‘skate.’ Use and misuse of common names also occurs; for example, in official landings, records of all hound sharks are considered to be the speckled smooth-hound *Mustelus mento* Cope 1877, despite the fact that four other hound shark species are landed under this category. With the exception of *Z. chilensis*, the same situation is observed when skates are landed and recorded generically as ‘skate’ (Lamilla, 2005; Lamilla *et al.*, 2010). Similarly, in the pelagic longline fishery both, shortfin and longfin mako sharks (*I. oxyrinchus* and *I. paucus*) respectively, are combined under a single ‘mako shark’ landing category (Bustamante *et al.*, 2009). These are examples of a very significant problem that limits interpretation and understanding of the elasmobranch catch due to inadequate recording of landings (Pequeño & Lamilla, 1997).

REFERENCES

- Acuña, E., Moraga, J. & Uribe, E. (1998) La zona de Coquimbo: un sistema nerítico de urgencia de alta productividad. *Revista de la Comisión Permanente del Pacífico Sur* 1989, 145–157.
- Acuña, E., Villarroel, J.C. & Grau, R. (2002) Fauna íctica asociada a la pesquería del pez espada (*Xiphias gladius* Linnaeus). *Gayana* 66, 263–267.
- Acuña, E., Villarroel, J.C., Cortés, A. & Andrade, M. (2005) Fauna acompañante en pesquerías de arrastre de crustáceos de Chile: implicancias y desafíos desde la perspectiva de la biodiversidad. In *Biodiversidad Marina: Valoración, Usos y Perspectivas* (Figueroa, E., ed), pp. 395–425. Editorial Universitaria: Santiago de Chile.
- Albarrán, D. (2005) Marco Regulatorio de la Actividad Pesquera en Chile. In *Biodiversidad Marina: Valoración, Usos y Perspectivas* (Figueroa, E., ed), pp. 15–20. Editorial Universitaria: Santiago de Chile.

- Andrade, I. & Pequeño, G. (2008) Mesobathic chondrichthyes of the Juan Fernández seamounts: are they different from those of the central Chilean continental slope? *Revista de Biología Tropical* 56, 181–190.
- Angel, A. & Ojeda, P. (2001) Structure and trophic organization of subtidal fish assemblages on the northern Chilean coast: the effect of habitat complexity. *Marine Ecology Progress Series* 217, 81–91.
- Arana, P.M. (2000) Experiencias de pesca con red de enmalle en las islas Robinson Crusoe y Santa Clara, Chile. *Investigaciones Marinas* 28, 231–237.
- Bustamante, C. & Bennett, M.B. (2013) Insights into the reproductive biology and fisheries of two commercially exploited species, shortfin mako (*Isurus oxyrinchus*) and blue shark (*Prionace glauca*), in the south-east Pacific Ocean. *Fisheries Research* 143, 174–183.
- Bustamante, C., Concha, F., Balbontín, F. & Lamilla, J. (2009) Southernmost record of *Isurus paucus* Guitart Manday, 1966 (Elasmobranchii: Lamnidae) in the southeast Pacific Ocean. *Revista de Biología Marina y Oceanografía* 44, 523–526.
- Bustamante, C., Couturier, L. & Bennett, M.B. (2012a) First record of *Mobula japonica* (Rajiformes, Myliobatidae) from the southeastern Pacific Ocean. *Marine Biodiversity Records* 5, e48.
- Bustamante, C., Flores, H., Concha-Pérez, Y., Vargas-Caro, C., Lamilla, J. & Bennett, M.B. (2012b) First record of *Hydrolagus melanophasma* James, Ebert, Long & Didier, 2009 (Chondrichthyes, Chimaeriformes, Holocephali) from the southeastern Pacific Ocean. *Latin American Journal of Aquatic Research* 40, 236–242.
- Bustamante, C., Vargas-Caro, C., Oddone, M.C., Concha, F., Flores, H., Lamilla, J. & Bennett, M.B. (2012c) Reproductive biology of *Zearaja chilensis* (Chondrichthyes: Rajidae) in the south-east Pacific Ocean. *Journal of Fish Biology* 80, 1213–1226.
- Bustamante, C., Lamilla, J., Concha, F., Ebert, D.A. & Bennett, M.B. (2012d) Morphological characters of the thickbody skate *Amblyraja frerichsi* (Krefft 1968) (Rajiformes: Rajidae), with notes on its biology. *PLoS One* 7, e39963.
- Bustos, E. (2005) Avances en la Investigación para la Acuicultura en el Sur de Chile. In *Biodiversidad Marina: Valoración, Usos y Perspectivas* (Figueroa, E., ed), pp. 353–364. Editorial Universitaria: Santiago de Chile.
- Camus, P. (2001) Marine biogeography of continental Chile. *Revista Chilena de Historia Natural* 74, 587–617.

- Castro, R. & Baeza, H. (1986) *Lernaeopoda tenuis* n.sp. and *Pseudolernaeopoda caudocapta* n.g., n.sp. (Copepoda, Lernaeopodidae) parasitic on *Triakis maculata* (Kner and Steindachner) from the Chilean coast, South Pacific. *Systematic Parasitology* 8, 227–233.
- Chirichigno, N. (1974) *Clave para Identificar los Peces Marinos del Perú*. Instituto del Mar del Perú: Callao.
- Compagno, L.J.V. (1984) FAO species catalogue, Sharks of the world, An annotated and illustrated catalogue of the shark species known to date. Part 1. Hexanchiformes to Lamniformes. *FAO Fishery Synopsis* 125, 1–250.
- Compagno, L.J.V. (1999). An overview of chondrichthyan systematics and biodiversity in southern Africa. *Transactions of the Royal Society of South Africa* 54, 75–120.
- Compagno L.J.V. (2005) Checklist of living chondrichthyes. In *Reproductive biology and phylogeny of Chondrichthyes: Sharks, Batoids, and Chimaeras* (Hamlett, W.C., ed.), pp. 501–548. Science Publishers, Inc: Enfield, New Hampshire.
- Concha, F., Hernández, S. & Oddone, M.C. (2009) Egg capsules of the raspthorn sandskate, *Psammobatis scobina* (Philippi, 1857) (Rajiformes, Rajidae). *Revista de Biología Marina y Oceanografía* 44, 253–256.
- Concha, F., Oddone, M.C., Bustamante, C. & Morales, N. (2012) Egg capsules of the yellownose skate *Zearaja chilensis* (Guichenot 1848) and the roughskin skate *Dipturus trachyderma* (Krefft and Stehmann 1974) (Rajiformes: Rajidae) from the south-eastern Pacific Ocean. *Ichthyological Research* 59, 323–327.
- Concha, F., Morales, N. & Larraguibel, J. (2013) Egg capsules of the Filetail fanskate *Sympterygia lima* (Poeppig 1835) (Rajiformes, Arhynchobatidae) from the southeastern Pacific Ocean, with observations on captive egg-laying. *Ichthyological Research* 60, 203–208.
- CPPS, (2009) *Plan de Acción Regional (PAR-CPPS) para la conservación de tiburones, rayas y quimeras en el Pacífico Sudeste*. Comisión Permanente del Pacífico Sur: Guayaquil.
- Cubillos, L. (2005) Diagnóstico, Aspectos Críticos y Propuesta de Sustentabilidad para las Pesquerías Nacionales. In *Biodiversidad Marina: Valoración, Usos y Perspectivas* (Figueroa, E., ed), pp. 27–46. Editorial Universitaria: Santiago de Chile.
- Delfin, F.T. (1901) Catálogo de los peces de Chile. *Revista Chilena de Historia Natural* 3, 21–25.
- Dolganov, V.N. (1984) A new shark from the family Squalidae caught on the Naska submarine ridge. *Zoologicheskii Zhurnal* 63, 1589–1591.

- Domingo, A., Forselledo, R., Miller, P. & Passadore, C. (2008) *Plan de Acción Nacional para la conservación de condrictios en las pesquerías uruguayas*. DINARA: Montevideo.
- Ebert, D.A., Compagno, L.J.V. & De Vries, M.J. (2011) A new lanternshark (Squaliformes: Etmopteridae: *Etmopterus*) from Southern Africa. *Copeia* 2011, 379–384.
- Ebert, D.A., Fowler, S. & Compagno, L.V.J. (2013) *Sharks of the World*. Wild Nature Press: Plymouth.
- Egaña, A.C. & McCosker, J.E. (1984) Attacks on divers by white sharks in Chile. *California Fish and Game* 70, 173–179.
- Eschmeyer, W.N. & Fong, J.D. (2011) Animal biodiversity, Pisces: An outline of higher-level classification and survey of taxonomic richness. *Zootaxa* 3148, 26–38.
- Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R. & Lotze, H.K. (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters* 13, 1055–1071.
- Gatica, C. & Acuña, E. (2007) Biología reproductiva de los tiburones de profundidad *Aculeola nigra* De Buen 1959, *Centroscyllium nigrum* Garman 1899, *Cephalurus* sp. y *Haleelurus canescens* (Günther 1878) en la zona norte y centro de Chile. In *XXVII Congreso Ciencias del Mar* (Anon., ed), pp. 56. Universidad Arturo Prat: Iquique.
- Gatica, C. & Acuña, E. (2011) Reproductive biology of deep-sea sharks *Aculeola nigra* De Buen, 1959, and *Centroscyllium nigrum* Garman, 1899 (Chondrichthyes: Etmopteridae), from Central Northern Chile. *Gayana* 75, 1–16.
- Grove, J.S. & Lavenberg, R.E. (1997) *Fishes of the Galápagos Islands*. Stanford University Press: Stanford, CA.
- Guichenot, A. (1848) Fauna Chilena, Peces. In *Historia física y política de Chile*, vol. II (Gay, C., ed), pp. 137–370. Museo de Historia Natural de Chile: Santiago.
- Günther, A. (1872) Report on several collections of fishes recently obtained for the British Museum. *Proceedings of the Zoological Society of London* 3, 652–675.
- Hernández, S., Lamilla, J., Dupré, E. & Stotz, W. (2005) Desarrollo embrionario de la pintarroja común *Schroederichthys chilensis* (Guichenot, 1848) (Chondrichthyes: Scyliorhinidae). *Gayana* 69, 191–197.
- Hernández, S., Haye, P.A. & Shivji, M.S. (2008) Characterization of the pelagic shark-fin trade in north-central Chile by genetic identification and trader surveys. *Journal of Fish Biology* 73, 2293–2304.

- Hernández, S., Vögler, R., Bustamante, C. & Lamilla, J. (2010) Review of the occurrence and distribution of the basking shark (*Cetorhinus maximus*) in Chilean waters. *Marine Biodiversity Records* 3, e67.
- Hiddink, J.G. & Hofstede, R.T. (2008) Climate induced increases in species richness of marine fishes. *Global Change Biology* 14, 453–460.
- Inada, T. & Garrick, J.A.F. (1979) *Rhinochimaera pacifica*, a long snouted chimaera (Rhinochimaeridae), in New Zealand waters. *Japanese Journal of Ichthyology* 24, 235–243.
- Jordan, D.S. (1919) New genera of fishes. *Proceedings of the Academy of Natural Sciences of Philadelphia* 70, 341–344.
- Lamilla, J. (2005) Bycatch: tiburones en peligro. *Oceana* 11, 1–16.
- Lamilla, J. & Bustamante, C. (2005) Guía para el reconocimiento de tiburones, rayas y quimeras de Chile. *Oceana* 18, 1–80.
- Lamilla, J., Bustamante, C., Roa, R., Acuña, E., Concha, F., Meléndez, R., López, S., Aedo, G., Flores, H. & Vargas-Caro, C. (2010) *Estimación del descarte de condrictios en pesquerías artesanales*, Informe Final FIP 2008-60. Valdivia: Universidad Austral de Chile. Available at <http://www.fip.cl/Proyectos.aspx> (last accessed 25 March 2014).
- Long, D.J., Mccosker, J.E., Blum, S. & Klapfer, A. (2011) Tropical Eastern Pacific Records of the Prickly Shark, *Echinorhinus cookei* (Chondrichthyes: Echinorhinidae). *Pacific Science* 65, 433–440.
- Long, D.J., Sala, E., Ballesteros, E., Caselle, J.E., Friedlander, A.M., Klapfer, A., Blum, S. & Constable, H. B. (2014). Summary of South American records of the smalltooth sand tiger shark *Odontaspis ferox* (Chondrichthyes: Odontaspidae), with the first record from Chilean waters. *Marine Biodiversity Records* 7, e67.
- Lopez, S., Zapata-Hernández, G., Bustamante, C., Sellanes, J. & Meléndez, R. (2013) Trophic ecology of the dusky catshark *Bythaelurus canescens* (Chondrychthyes: Scyliorhinidae) in the southeast Pacific Ocean. *Journal of Applied Ichthyology* 29, 751–756.
- Lucas, A.J., Guerrero, R.A., Mianzán, H.W., Acha, E.M. & Lasta, C.A. (2005) Coastal oceanographic regimes of the Northern Argentine Continental Shelf (34°–43°S). *Estuarine, Coastal and Shelf Science* 65, 405–420.
- Magurran, A. E. (2003) *Measuring Biological Diversity*. Wiley-Blackwell: Oxford.

- Mann, G. (1954) *La vida de los peces en aguas chilenas*. Instituto de Investigaciones Veterinarias y Universidad de Chile: Santiago.
- Mejía-Falla, P.A., Navia, A.F., Mejía-Ladino, L.M., Acero, A. & Rubio, E.A. (2007) Tiburones y rayas de Colombia (Pisces: Elasmobranchii): Lista actualizada, revisada y comentada. *Boletín de Investigaciones Marinas y Costeras* 36, 1–31.
- Meléndez, R., López, S. & Yáñez, E. (2006) Nuevos antecedentes de *Pseudocarcharias kamoharai* (Matsubara, 1936) (Chondrichthyes: Lamniformes: Pseudocarchariidae), frente al norte de Chile. *Investigaciones Marinas* 34, 223–226.
- Menares, B. & Sepúlveda, J.T. (2005) Grupos recurrentes de peces y crustáceos demersales en la zona centro-sur de Chile. *Investigaciones Marinas* 33, 91–100.
- Menni, R. & Lucifora, L.O. (2007) *Condichtios de la Argentina y Uruguay: lista de trabajo*. Serie Técnica y Didáctica-ProBiota, Universidad Nacional de La Plata: Argentina.
- Molina, J.I. (1782) *Saggio sulla storia naturale del Chili*. Stamperia di S Tomase D'Aquino: Bologna, Italia.
- Morillas, J.A. (1977) Primer registro de *Chlamydoselachus anguineus* Garman frente a la costa de Chile. *Noticiario Mensual del Museo Nacional de Historia Natural* XXI 250, 9–10.
- Novacek, M. (2001) *The Biodiversity Crisis: Losing What Counts*. The New Press: New York
- Oñate, J. & Pequeño, G. (2005) *Etmopterus brachyurus* Smith and Radcliffe, 1912 (Chondrichthyes, Dalatiidae): primer registro en aguas del Pacífico oriental. *Revista de Biología Marina y Oceanografía* 40, 67–70.
- Parin, N.V., Mironov, A.N. & Nesis, K.N. (1997) Biology of the Nazca and Sala y Gomez submarine ridges, an outpost of the Indo-West Pacific fauna in the Eastern Pacific Ocean: composition and distribution of the fauna, its communities and history. *Advances in Marine Biology* 32, 145–242.
- Pequeño, G. (1989) Peces de Chile. Lista sistemática revisada y comentada. *Revista de Biología Marina y Oceanografía* 24, 1–132.
- Pequeño, G. (1997) Peces de Chile. Lista sistemática revisada y comentada: addendum. *Revista de Biología Marina y Oceanografía* 32, 77–94.
- Pequeño, G. & Lamilla, J. (1993) Batoideos comunes a las costas de Chile y Argentina-Uruguay (Pises: Chondrichthyes). *Revista de Biología Marina y Oceanografía* 28, 203–217.

- Pequeño, G. & Lamilla, J. (1995) Preliminary reports on the fishes collected by the B.I.C. "Victor Hensen" in the Magellanic Channels, Chile. *Berichte zur Polarforschung* 190, 68–106.
- Pequeño, G. & Lamilla, J. (1997) Las pesquerías de condrictios en Chile: primer análisis. *Biología Pesquera* 26, 13–24.
- Pequeño, G. & Sáez, S. (2003) The shark *Carcharhinus galapagensis* from Salas y Gómez Island, Chile (Chondrichthyes: Carcharhinidae). *Revista de Biología Tropical* 51, 795–796.
- Pérez-Canto, C. (1886) Estudio sobre algunos escualos de la costa de Chile. *Anales de la Universidad de Chile* 69, 1–12.
- Philippi, R.A. (1887) Sobre los tiburones y algunos otros peces de Chile. *Anales de la Universidad de Chile* 71, 535–537.
- Philippi, R.A. (1896) Peces nuevos de Chile. *Anales de la Universidad de Chile* 93, 375–890.
- Philippi, R.A. (1901) Descripción de cinco nuevas especies del orden Plagióstomos. *Anales de la Universidad de Chile* 109, 303–315.
- Quijada, B. (1913) *Catálogo ilustrado y descriptivo de los vertebrados vivientes del Museo Nacional No. 3: Peces chilenos y extranjeros*. Editorial Universitaria: Santiago de Chile.
- Quiroz, J.C., Wiff, R., Gatica, C. & Leal, E. (2008) Composición de especies, tasas de captura y estructura de tamaño de peces capturados en la pesquería espinelera artesanal de rayas en la zona sur-austral de Chile. *Latin American Journal of Aquatic Research* 36, 15–24.
- Reyes, P.R. & Hüne, M. (2006) Primer registro del tiburón *Etmopterus unicolor* (Engelhardt, 1912) frente a Valdivia, Chile (Chondrichthyes: Dalatiidae). *Investigaciones Marinas* 34, 137–142.
- Reyes, P.R. & Torres-Florez, J.P. (2008) Presencia de *Bathyraja couesseua* (Batoidea; Rajiformes) en el Cabo de Hornos e islas Diego Ramírez, Chile. *Latin American Journal of Aquatic Research* 36, 309–314.
- Reyes, P.R. & Torres-Florez, J.P. (2009) Diversity, distribution, richness and abundance of deep-sea Chondrichthyans along south Patagonian Archipelago, Cape Horn, Diego Ramirez Islands and the northern area of the Drake passage. *Revista de Biología Marina y Oceanografía* 44, 243–251.
- Rohde, K. (1992) Latitudinal Gradients in Species Diversity: The Search for the Primary Cause. *Oikos* 65, 514–527.
- Rozzi, R., Armesto, J.J., Goffinet B., Buck, W., Massardo, F., Silander, J., Arroyo, M.T.K., Russell, S., Anderson, C.B., Cavieres, L.A. & Callicott, J.B. (2008) Changing lenses to assess

biodiversity: patterns of species richness in sub-Antarctic plants and implications for global conservation. *Frontiers in Ecology and the Environment* 6, 131–137.

Sáez, S. & Lamilla, J. (2004). Sexual homodonty in *Bathyraja griseoocauda* (Norman 1937) from the Southern Eastern Pacific (Chile) (Chondrichthyes, Rajidae: Arhynchobatinae). *Journal of Applied Ichthyology* 20, 189–193.

Sahney, S., Benton, M.J. & Ferry, M.J. (2010) Links between global taxonomic diversity, ecological diversity and the expansion of vertebrates on land. *Biological Letters* 6, 544–547.

Schaaf-Da Silva, J.A. & Ebert, D.A. (2008) A re-description of the eastern Pacific swellshark, *Cephaloscyllium ventriosum* (Garman 1880) (Chondrichthyes: Carcharhiniformes: Scyliorhinidae), with comments on the status of *C. uter* (Jordan & Gilbert 1896). *Zootaxa* 1872, 59–68.

Schneider, C.O. (1943) Catálogo de los peces marinos del litoral de Concepción y Arauco. *Boletín de la Sociedad de Biología de Concepción* 12, 75–126.

Seeliger, U. & Kjerfve, B. (2001) *Ecological Studies: Coastal Marine Ecosystems of Latin America*, vol. 144. Springer-Verlag: Berlin.

Seigel, J.A. (1978) Revision of the dalatiid shark genus *Squaliolus*: anatomy, systematics, ecology. *Copeia* 1978, 602–614.

Sepúlveda, A., Cubillos, L. & Arcos, D. (2005) Pesquerías Pelágicas Chilenas: Una Síntesis sobre la Incertidumbre Biológica. In *Biodiversidad Marina: Valoración, Usos y Perspectivas* (Figueroa, E., ed), pp. 91–108. Editorial Universitaria: Santiago de Chile.

Sielfeld, W. & Kawaguchi, A. (2004) Mesopelagic fishes captured during CIMAR 6-Oceanic Islands Cruise. *Ciencia y Tecnología del Mar* 27, 87–97.

Sielfeld, W., & Vargas, M. (1999) Review of marine fish zoogeography of Chilean Patagonia (42°–57° S). *Scientia Marina* 63, 451–463.

Sielfeld, W., Laudien, J., Vargas, M. & Villegas, M. (2010) El Niño induced changes of the coastal fish fauna off northern Chile and implications for ichthyogeography. *Revista de Biología Marina y Oceanografía* 45, 705–722.

Stelbrink, B., Von Rintelen, T., Cliffm G. & Kriwet, J. (2010) Molecular systematics and global phylogeography of angel sharks (genus Squatina). *Molecular Phylogenetics and Evolution* 54, 395–404.

- Stevens, J.D., Bonfil, R., Dulvy, N.K. & Walker, P.A. (2000) The effects of fishing on shark, rays, and chimaeras (Chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* 57, 476–494.
- Straube, N., Kriwet, J. & Schliewen, U.K. (2011) Cryptic diversity and species assignment of large lantern sharks of the *Etmopterus spinax* clade from the Southern Hemisphere (Squaliformes, Etmopteridae). *Zoologica Scripta* 40, 61–75.
- Valenzuela, A., Bustamante, C. & Lamilla, J. (2008) Morphological characteristics of five bycatch sharks caught by southern Chilean demersal longline fisheries. *Scientia Marina* 72, 231–237.
- Wetherbee, B.M. & Cortés, E. (2004) Food consumption and feeding habits. In *Biology of Sharks and Their Relatives* (Carrier, J. C., Musick, J. A. & Heithaus, M. R., eds), pp. 223–244. CRC press: Boca Raton, FL.
- White, W.T. & Iglésias, S.P. (2011) *Squalus formosus*, a new species of spurdog shark (Squaliformes: Squalidae), from the western North Pacific Ocean. *Journal of Fish Biology* 79, 954–68.
- Whittaker, R.H. (1972) Evolution and measurement of species diversity. *Taxon* 21, 213–251.
- Yano, K., Stevens, J.D. & Compagno, L.J.V. (2002) A review of the systematics of the sleeper shark genus *Somniosus* with redescriptions of *Somniosus (Somniosus) antarcticus* and *Somniosus (Rhinoscymnus) longus* (Squaliformes: Somniosidae). *Ichthyological Research* 51, 360–373.

3.2. Biogeographic patterns in the cartilaginous fauna (Pisces: Elasmobranchii and Holocephali) in the southeast Pacific Ocean

Originally published in PeerJ (ISSN: 2167-8359)

Copyright © Carlos Bustamante, 2014

Published online: 21 March 2014

License Number: open-access article

Abstract

The abundance and species richness of the cartilaginous fish community of the continental shelf and slope off central Chile is described, based on fishery-independent trawl tows made in 2006 and 2007. A total of 194,705 specimens comprising 20 species (9 sharks, 10 skates, 1 chimaera) were caught at depths of 100 – 500 m along a 1,000 km transect between 29.5° S and 39° S. Sample site locations were grouped to represent eight geographical zones within this latitudinal range. Species richness fluctuated from 1 to 6 species per zone. There was no significant latitudinal trend for sharks, but skates showed an increased species richness with latitude. Standardised catch per unit effort (CPUE) increased with increasing depth for sharks, but not for skates, but the observed trend for increasing CPUE with latitude was not significant for either sharks or skates. A change in community composition occurred along the depth gradient with the skates, *Psammobatis rudis*, *Zearaja chilensis* and *Dipturus trachyderma* dominating communities between 100 and 300 m, but small-sized, deep-water dogfishes, such as *Centroscyllium* spp. dominated the catch between 300 and 500 m. Cluster and ordination analysis identified one widespread assemblage, grouping 58% of sites, and three shallow-water assemblages. Assemblages with low diversity (coldspots) coincided with highly productive fishing grounds for demersal crustaceans and bony fishes. The community distribution suggested that the differences between assemblages may be due to compensatory changes in mesopredator species abundance, as a consequence of continuous and unselective species removal. Distribution patterns and the quantitative assessment of sharks, skates and chimaeras presented here complement extant biogeographic knowledge and further the understanding of deep-water ecosystem dynamics in relation to fishing activity in the south-east Pacific Ocean.

INTRODUCTION

Cartilaginous fishes play an important role as top predators and have complex distribution patterns (Wetherbee & Cortés, 2004), affecting the structure and function of marine communities through interactions with other trophic links in food webs to which they belong (Ferretti *et al.*, 2010). Spatial distribution patterns of marine fishes in the south-east Pacific Ocean are poorly understood, and most studies of demersal communities have focused on the ecology of continental shelf fauna at depths of between 20 and 150 m (Brattström & Johanssen, 1983; Ojeda, 1983; Carrasco, 1997; Ojeda *et al.*, 2000; Camus, 2001; Sellanes, 2007). Descriptions of geographical patterns of marine fishes have been restricted to littoral species (Mann, 1954; Pequeño *et al.*, 1990), and based on regional inventories (Ojeda *et al.*, 2000). A general lack of quantification of species abundance limits our understanding of the functional biodiversity of the continental shelf of Chile (Pequeño, 1989; Bustamante *et al.*, 2014).

Chile has a cartilaginous fish fauna that is relatively rich when compared with warm-temperate countries in South America (Bustamante *et al.*, 2014), but poor in the global context despite having one of the largest maritime territories in the world (Cubillos, 2005). Species checklists and biological observations constitute the first approaches in the study of the cartilaginous fish fauna in the Chilean marine ecosystem and there are a number of studies that have reported on elasmobranch species around the central and southern continental shelf, from both fishery-dependent and -independent surveys (Meléndez & Meneses, 1989; Pequeño, 1989; Pequeño *et al.*, 1990; Pequeño & Lamilla, 1993). In northern Chile, bycatch analysis of the crustacean trawl fishery has contributed to knowledge of the continental slope ecosystem through the description of biological diversity, composition and structure of the demersal fish fauna over a wide depth range (Sielfeld & Vargas, 1999; Acuña *et al.*, 2005; Menares & Sepúlveda, 2005). While fishery-dependent studies offer a description of diversity and species assemblages of cartilaginous fishes, using catch per unit effort (CPUE) as a proxy for abundance (Acuña *et al.*, 2005), they generally lack the ability to adequately identify or provide quantitative information on species richness, abundance hotspots and conspecific assemblages that are required for a better understanding of marine ecosystem interrelationships (Kyne & Simpfendorfer, 2007).

The aim of the present study is to analyse abundance and species richness of cartilaginous fishes of the continental shelf and slope in Chile to identify patterns in the geographical and bathymetric distribution of sharks, skates and chimaeras in the south-east Pacific Ocean to complement existing biogeographic models, and improve the understanding of deep-water ecosystem dynamics in the context of fishing activities.

MATERIAL AND METHODS

Data were collected through direct observation of total catch on fishery-independent surveys made along the Chilean continental slope and shelf as part of a broader project to assess the biological and oceanographical characteristics of the Chilean seafloor (Melo *et al.*, 2007). Surveys were carried out on-board two fishing vessels, “Crusoe I” and “Lonquimay”, equipped as oceanographic research platforms. Fishing gear comprised a bottom trawl constructed from 3 mm diameter polyamide nylon with 50 mm stretch-measured diamond-mesh in the tunnel and cod-end. The trawl had a 24 m headrope, a 28 m footrope, and a stretched circumference of 34 m with an average net opening during tows of 11 m. Tows lasted 18 – 53 min at a speed of 3.7 km h⁻¹ which resulted in a swept area of 12.2 – 35.9 km². Geometric construction of fishing gear and tow speed were used to calculate CPUE which was standardised as individuals per hour and square kilometre swept (ind km⁻² h⁻¹). For each species, CPUE data were calculated separately and log-transformed (Log (CPUE+1)) in order to assess the departure of original data from normality. Geographic coordinates and depth of each trawl were recorded for each tow.

A total of 128 tows were made in 32 sites grouped in eight regions, numbered from north to south as zones 1 to 8, that span approximately 1,000 km between the latitudes 29.5° S and 39° S (Fig. 17). Survey data were collected from sites in four depth strata (labelled as A: 100 – 199 m, B: 200 – 299 m, C: 300 – 399 m and D: 400 – 499 m) with four pseudoreplica tows in each site (16 tows per zone with 4 tows per site). Zones 1, 2, 4 and 5 were sampled in July/August 2006, zones 6, 7 and 8 in November/December 2006, and zone 3 was sampled twice, in July 2006 and again in March 2007. Each site was recorded and coded with the zone (1 to 8), depth strata (A to D) and pseudoreplica tow (numbered 1 to 4), i.e., tow coded as “1.A.2” represents the second tow made in zone 1, between 100 – 199 m depth.

This study was carried out in accordance with the “standards for the use of animals in research” approved by the Animal Care and Ethics Committee of the Universidad Austral de Chile (UACH/FIP 2005-61). Capture of fishes during this study was permitted through Fisheries Undersecretariat Research Permit Number 1959-06, 2931-06 and 181-07 issued by Ministry of Economy, Development and Tourism.

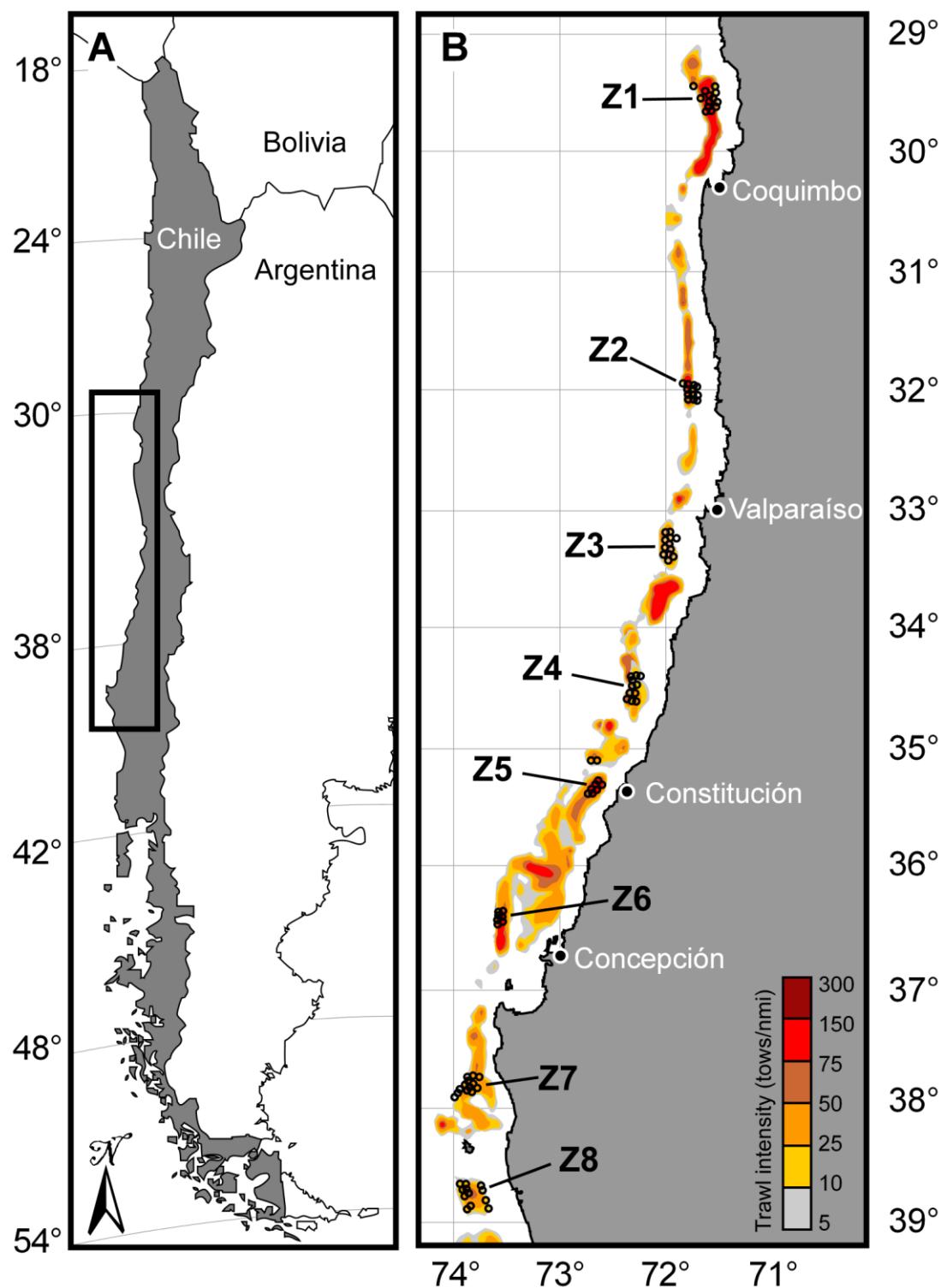


Figure 17 Map of (A) Chile showing location of study area (inset box) and (B) location of zones (Z1 to Z8) and sampling sites (circles). Commercial trawl intensity is indicated in (B), in terms of tows per nautical mile (nmi). Modified after Melo et al., (2007).

Community definition

All cartilaginous fishes captured during surveys were counted and identified to species. A number of individuals caught (~1%) were landed frozen to validate on-board identification using diagnostic features described in literature (Compagno, 1984a; Compagno, 1984b; Lamilla & Sáez, 2003; Lamilla & Bustamante, 2005; Ebert *et al.*, 2013). Species diversity was calculated from the number of species at each tow; and compared using the Shannon diversity index (H according to Spellerberg & Fedor, 2003) by depth and zone.

Species richness (S) was calculated per depth stratum in each zone, and is defined as the number of species within a specific number of individuals sampled (Kempton, 1979). Relative frequency of occurrence (F_O) was determined for each species to explore the variability of species' occurrence along bathymetric and latitudinal gradients; and is expressed as a percentage of occurrence of a species in relation to the total number of tows within sites and zones. Three categories of F_O were determined according to Solervicens (1973): Regular species, where $F_O = >50\%$; Accessory species, where $F_O = 25 - 49\%$ and; Incidental species, where $F_O = 10 - 24\%$. Latitudinal and bathymetric gradients of species diversity of the major taxonomic groups (sharks and skates) were compared using analysis of covariance (ANCOVA) with significance accepted at $P < 0.05$.

Community structure

Faunal assemblages and geographic patterns of cartilaginous fishes were determined through a global similarity matrix. Species composition and abundance in each tow were considered for the entire study area with CPUE values fourth-root transformed to balance outliers (rare and abundant species). Sampling sites were sorted by an agglomerative hierarchical cluster and through non-dimensional metric scaling (nMDS) considering the global similarity matrix (Clarke, 1993; Clarke & Warwick, 1994). Log-transformed CPUE values were used for hierarchical agglomerative clustering with group-averaging linking, based on the Bray–Curtis similarity measure to delineate groupings with a distinct community structure. A one-way ANOSIM was used to establish possible differences between sampling site groups. Additionally, a SIMPER analysis was used to determine the contribution of each species to the average Bray-Curtis dissimilarity between groups. All indices and statistical procedures were made using software PRIMER v.6.0 (Plymouth Marine Lab, Plymouth, UK).

RESULTS

From 32 sites sampled, the total catch was 194,705 cartilaginous fishes from the 76 tows that contained specimens, of which 2,725 individuals were landed and examined. In 52 tows (40.6% of the total) there was no catch of cartilaginous fishes and were thus excluded from the remaining analysis. A total of 20 species (nine sharks, ten skates and one chimaera) was confirmed (Table 16). Note, that for the purpose of the current study the term ‘skate’ includes *Torpedo tremens*. Bathymetrically, the shallowest depth stratum (100 – 199 m) and latitudinally, the northernmost zone (zone 1) yielded the lowest percentage occurrence of cartilaginous fishes caught in 3.13% and 37.5% of tows respectively (Table 17). The greatest number of species caught per family was five, in the family Arhynchobatidae, followed by the families Rajidae (four species), Etmopteridae and Scyliorhinidae (both three species). The Hexanchidae, Somniosidae, Centrophoridae, Torpedinidae and Chimaeridae were each represented by a single species (Table 16).

Community definition

Species richness fluctuated between one and six species per site with no significant differences between sharks and skates in slopes of the regression (ANCOVA; $F = 0.826$; $df = 1, 117$; $P = 0.365$; Fig. 18), but there were significant differences in the intercepts (ANCOVA; $F = 24.972$; $df = 1, 117$; $P > 0.001$). There was no significant relationship between species richness and latitude for sharks, but species richness for skates increased with increasing latitude (Fig. 18A, C). Chimaeras were absent in the catch from zones 6 and 8, but occurred in the other six zones (Fig. 18E). Species richness increased significantly with depth for sharks, but not for skates (Fig. 18B, D). The slopes and intercepts of the regressions were significantly different (ANCOVA, $F = 17.06$; $df = 1, 117$; $P > 0.001$ and $F = 13.954$; $df = 1, 117$; $P > 0.001$, respectively). Chimaeras were restricted to 430 – 480 m within the deepest depth stratum, and were observed off most of the central coast of Chile, between approximately 29.5° and 37.5° S (Fig 18E, F).

The CPUE per site ranged widely, from 5.5 – 2,785 ind $\text{km}^{-2} \text{ h}^{-1}$ among individual sites and 728 – 7,942 ind $\text{km}^{-2} \text{ h}^{-1}$ among zones (Table 18). Log-transformed CPUE increased with latitude for both sharks and skates, although the slopes of the regressions were not significantly different (Fig. 19A, C). Based on latitude, the ANCOVA did not reveal significant differences in slope ($F = 0.412$; $df = 1, 117$; $P = 0.523$), but did in elevation between sharks and skates ($F = 43.942$; $df = 1, 117$; $P > 0.001$). There was a significant effect of depth on the CPUE for sharks, but not for skates (Fig 19B, D), and there was a significant difference between the slopes and elevations of the

regressions (ANCOVA; $F = 19.59$; $df = 1, 117$; $P > 0.001$; $F = 31.12$; $df = 1, 117$; $P > 0.001$, respectively). For chimeras, the CPUE was generally low across the species' latitudinal range (Fig. 19E).

Diversity index (H) was not influenced by latitude for sharks, but increased significantly for skates (Fig. 20; ANCOVA; $F = 5.056$; $df = 1, 117$; $P = 0.263$) and the intercepts were significantly different (ANCOVA; $F = 15.92$; $df = 1, 117$; $P > 0.0001$). Values of H for sharks averaged approximately 0.6 across the eight zones, but showed high variability among sites in each zone (Fig. 20A). For skates, there were zero-values for H in all zones, particularly zone 1, but values of up to approximately 1.1 also occurred at sites in the central and southern zones (Fig. 20C). Significant differences were observed in the slopes and intercepts of the regression between sharks and skates based on depth (ANCOVA; $F = 15.35$; $df = 1, 117$; $P > 0.001$ and $F = 8.40$; $df = 1, 117$; $P > 0.001$). Diversity index for sharks was markedly higher in waters over about 325 m deep, and was almost absent in shallowed depth strata (Fig. 20B). Skate diversity varied considerably within most depth strata and, overall, showed no significant trend with depth (Fig. 20D).

Three incidental species (*Bathyraja multispinis* *Dipturus trachyderma*, *Torpedo tremens*) and two regular species (*Psammobatis rufus*, *Zearaja chilensis*), represent the community at 200 – 299 m depth. *Hexanchus griseous* and *T. tremens* are regular species, along with six accessory species in the 300 – 399 m depth stratum. *Hexanchus griseus* was restricted to this stratum, whereas *T. tremens* was also captured at shallower depths. *Centroscymnus macracanthus*, *Apristurus nasutus*, *Bathyraja peruviana*, *Bathyraja albomaculata*, *Rajella sadowskii* and *Hydrolagus macrophthalmus* were only found in the deepest stratum (400 – 499 m), whereas there were nine other regular species that were also represented in shallower strata (Table 20).

A taxonomic change in community composition occurred along the depth gradient. Three skates, *Psammobatis rufus*, *Zearaja chilensis* and *Dipturus trachyderma* dominated communities between 100 and 300 m accounting for >80% of total cartilaginous fish CPUE, but as depth increased there was a major shift in community, as small-sized, deep-water dogfishes, such as *Centroscyllium* spp. came to dominate the catch (Fig. 20, Table 19). Other contributors to this species-complex change were relative reductions in *Bythaelurus canescens* and small-sized skates (i.e., *Psammobatis rufus* and *Gurgesiella furvescens*) (Table 19, 20).

Table 16 Depth and latitudinal range of cartilaginous fishes caught during surveys.

Order	Family	Species	Depth range (m)	Latitudinal range ($^{\circ}$ S)
Hexanchiformes	Hexanchidae	<i>Hexanchus griseus</i> (Bonnaterre 1788)	358–376	35–35.1
Squaliformes	Etmopteridae	<i>Aculeola nigra</i> de Buen 1959	262–492	29.4–36.5
Squaliformes	Somniosidae	<i>Centroscymnus macracanthus</i> Regan 1906	455	33.3
Squaliformes	Etmopteridae	<i>Centroscyllium granulatum</i> Günther 1887	262–482	33.2–38.9
Squaliformes	Etmopteridae	<i>Centroscyllium nigrum</i> Garman 1899	335–455	32–38.8
Squaliformes	Centrophoridae	<i>Deania calcea</i> (Lowe 1839)	362–492	29.5–38.9
Carcharhiniformes	Scyliorhinidae	<i>Apristurus brunneus</i> (Gilbert 1892)	443–461	34.5–36.5
Carcharhiniformes	Scyliorhinidae	<i>Apristurus nasutus</i> de Buen 1959	338–482	29.5–38.9
Carcharhiniformes	Scyliorhinidae	<i>Bythaelurus canescens</i> (Günther 1878)	237–492	29.4–38.9
Rajiformes	Arhynchobatidae	<i>Bathyraja albomaculata</i> (Norman 1937)	356–436	37.8–38.7
Rajiformes	Arhynchobatidae	<i>Bathyraja brachyurops</i> (Fowler 1910)	482	38.9
Rajiformes	Arhynchobatidae	<i>Bathyraja multispinis</i> (Norman 1937)	445	36.4
Rajiformes	Arhynchobatidae	<i>Bathyraja peruana</i> McEachran & Miyake 1984	243–492	29.6–38.9
Rajiformes	Arhynchobatidae	<i>Psammobatis rufis</i> Günther 1870	240–475	32–38.8
Rajiformes	Rajidae	<i>Gurgesiella furvescens</i> de Buen 1959	362–484	29.4–32
Rajiformes	Rajidae	<i>Zearaja chilensis</i> (Guichenot 1848)	159–476	33.3–38.7
Rajiformes	Rajidae	<i>Dipturus trachyderma</i> (Krefft & Stehmann 1975)	234–482	32–38.9
Rajiformes	Rajidae	<i>Rajella sadowskii</i> (Krefft & Stehmann 1974)	475	33.4
Rajiformes	Torpedinidae	<i>Torpedo tremens</i> de Buen 1959	149–376	34.5–38.9
Chimaeriformes	Chimaeridae	<i>Hydrolagus macrophthalmus</i> de Buen 1959	430–483	29.6–37.8

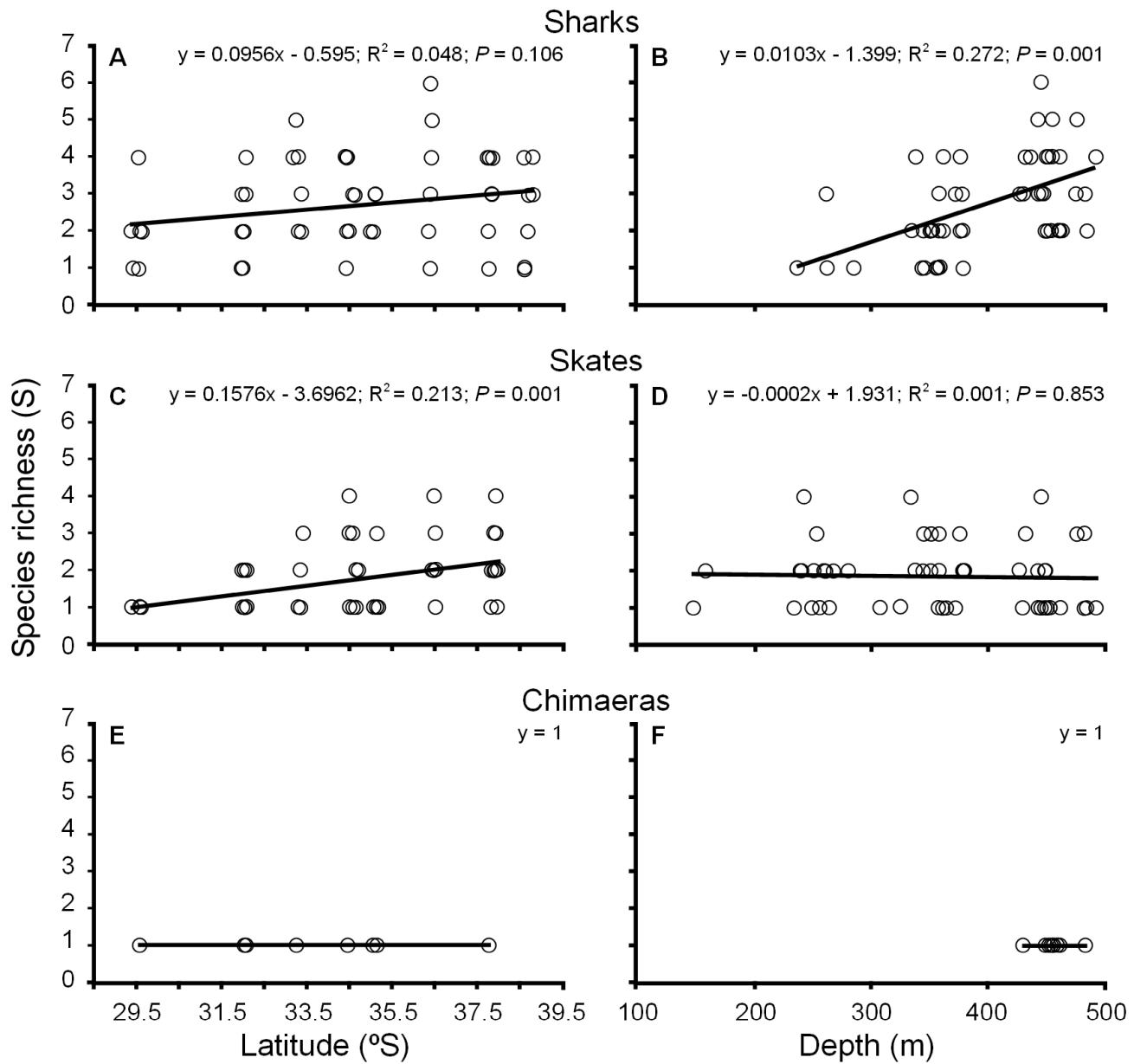


Figure 18 Latitudinal and bathymetric changes of species richness of sharks (A–B), skates (C–D) and chimaeras (E–F) across the study area. Fitted least-square regression model (solid line) and statistical significance are indicated in each case.

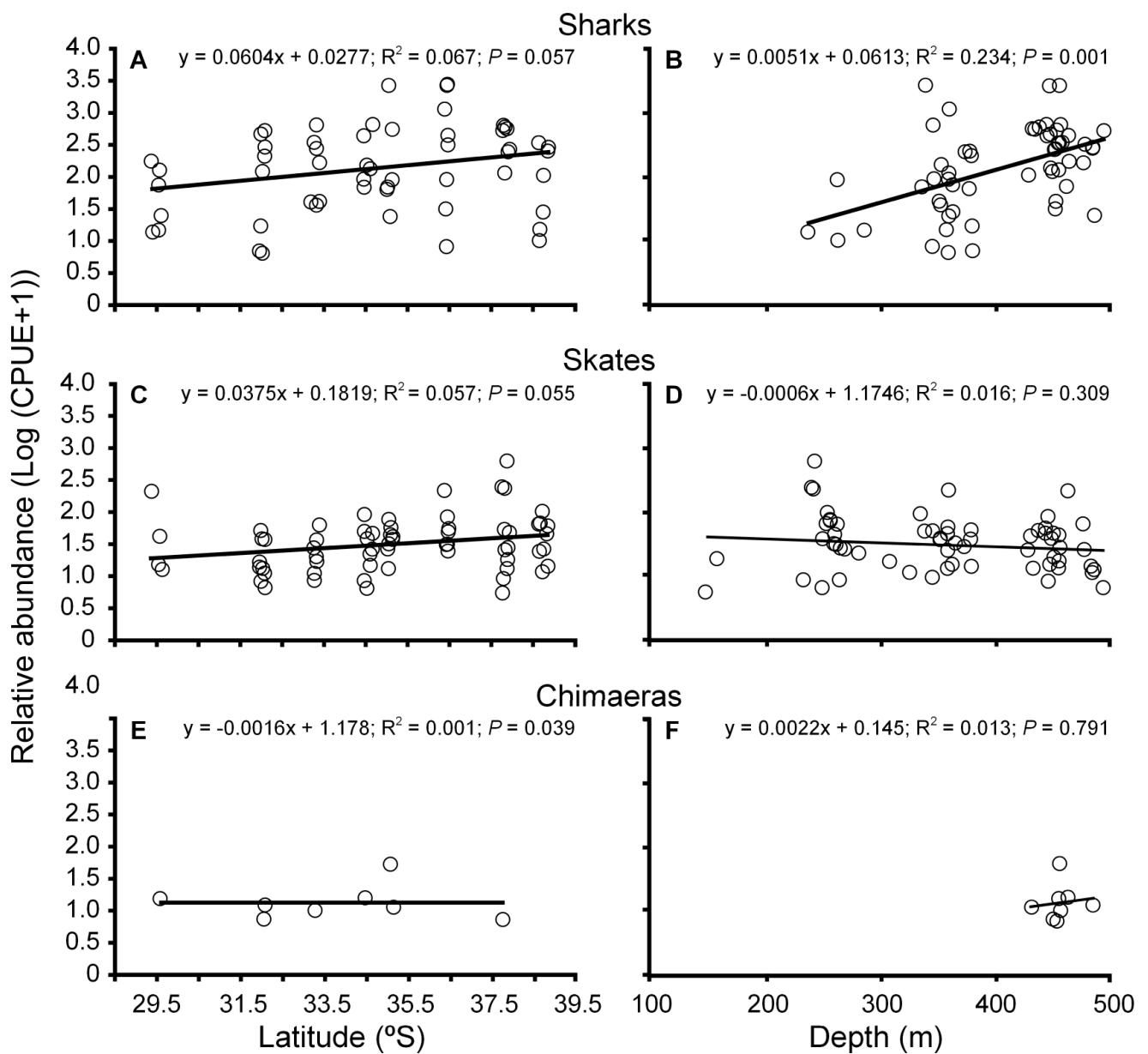


Figure 19 Latitudinal and bathymetric changes of relative abundance (Log (CPUE+1)) of sharks (A–B), skates (C–D) and chimaeras (E–F) across the study area. Fitted least-square regression model (solid line) and statistical significance are indicated in each case.

Table 17 Percentage of tows with cartilaginous fishes in the catch, species richness (S) and total number (N) of cartilaginous fishes caught in each zone and depth stratum.

Zone	Catch (%)	S	N
1	37.5	7	2,921
2	56.25	10	14,871
3	56.25	11	12,199
4	62.5	11	15,058
5	68.75	10	23,224
6	56.25	12	60,651
7	75	12	47,862
8	62.5	12	17,919

Depth stratum (m)	Catch (%)	S	N
100–200	3.13	2	203
200–300	65.63	8	18,907
300–400	78.13	14	58,597
400–500	90.63	18	116,998

Table 18 Abundance, as total CPUE (ind km⁻²h⁻¹) of cartilaginous fishes caught during surveys in each zone (geographic location of zones is indicated in Fig. 17).

Species	Zone							
	1	2	3	4	5	6	7	8
<i>H. griseus</i>	--	--	--	--	54.7	--	--	--
<i>A. nigra</i>	130	249.4	208	390	10	11	--	--
<i>C. macracanthus</i>	--	--	9.2	--	--	--	--	--
<i>C. granulatum</i>	--	770.6	109.9	259.8	64.7	4,611	1,730	577.6
<i>C. nigrum</i>	--	257.5	752.6	363.8	2,845.1	1,639.8	435.7	5.2
<i>D. calcea</i>	15	54.7	68.5	37.8	41.5	28.4	122.1	85.1
<i>A. brunneus</i>	15	--	--	--	--	15.5	326.3	206.7
<i>A. nasutus</i>	--	--	--	30.6	--	59.2	--	--
<i>B. canescens</i>	272.7	312.5	403.8	476.5	483.2	1084.4	361.4	160.5
<i>B. albomaculata</i>	--	--	--	--	--	--	14.5	5
<i>B. brachyurops</i>	--	--	--	--	--	--	--	4.7
<i>B. multispinis</i>	--	--	--	--	--	8.4	--	--
<i>B. multispinis</i>	42.4	52	65.7	121.8	21.5	50.2	29	92
<i>P. rutilus</i>	--	32.7	71.0	38.5	192.2	77.1	154.2	14.9
<i>G. furvescens</i>	239.5	55.5	--	--	--	--	--	--
<i>Z. chilensis</i>	--	--	9.2	--	--	21	984.1	5
<i>D. trachyderma</i>	--	55.8	--	127.8	159.3	336.2	100.6	395.3
<i>R. sadowskii</i>	--	--	38.2	--	--	--	--	--
<i>T. tremens</i>	--	--	--	18.7	--	--	10.1	4.4
<i>H. macrophthalmus</i>	14.2	17.6	9.2	15.2	63.9	--	5.9	--
Total	728.8	1,858.3	1,745.3	1,880.5	3,936.1	7,942.2	4,273.9	1,556.4

Table 19 Frequency of occurrence of cartilaginous fishes caught during surveys in each zone (geographic location of zones is indicated in Fig. 16).

Species	Zone							
	1	2	3	4	5	6	7	8
<i>H. griseus</i>	--	--	--	--	100	--	--	--
<i>A. nigra</i>	7.2	27.6	20.1	43.2	0.8	1.2	--	--
<i>C. macracanthus</i>	--	--	100	--	--	--	--	--
<i>C. granulatum</i>	--	8.7	1.1	2.9	0.5	49.6	27.2	10
<i>C. nigrum</i>	--	4.6	11.8	6.5	37.7	28.2	10.9	0.1
<i>D. calcea</i>	1.4	10.5	11.5	7.3	5.9	5.9	32.8	25.2
<i>A. brunneus</i>	0.9	--	--	--	--	1.9	57.3	39.9
<i>A. nasutus</i>	--	--	--	35.2	--	64.8	--	--
<i>B. canescens</i>	4	9.1	10.3	13.9	10.4	30.3	14.7	7.2
<i>B. albomaculata</i>	--	--	--	--	--	--	72.6	27.4
<i>B. brachyurops</i>	--	--	--	--	--	--	--	100
<i>B. multispinis</i>	--	--	--	--	--	100	--	--
<i>B. peruana</i>	4.3	10.4	11.5	24.5	3.2	9.6	8.1	28.4
<i>P. rutilus</i>	--	5.6	10.6	6.6	24.2	12.5	36.7	3.9
<i>G. furvescens</i>	68.4	31.6	--	--	--	--	--	--
<i>Z. chilensis</i>	--	--	0.6	--	--	1.4	97.5	0.5
<i>D. trachyderma</i>	--	94.5	--	10.4	9.5	26.1	12.6	36.9
<i>R. sadowskii</i>	--	--	100	--	--	--	--	--
<i>T. tremens</i>	--	--	--	18.7	--	--	35.6	17
<i>H. macrophthalmus</i>	6.9	17	7.7	14.8	45.6	--	8	--

Table 20 Abundance, as total CPUE (ind km⁻²h⁻¹) and frequency of occurrence (F_O) of cartilaginous fishes caught in each depth stratum†.

Species	CPUE				F _O			
	Depth stratum				Depth stratum			
	A	B	C	D	A	B	C	D
<i>H. griseus</i>	--	--	54.7	--	--	--	100	--
<i>A. nigra</i>	--	4.1	45.8	948.1	--	0.4	4.6	95
<i>C. macracanthus</i>	--	--	--	9.2	--	--	--	100
<i>C. granulatum</i>	--	85.4	3,258.8	4,779.3	--	1.1	40.1	58.8
<i>C. nigrum</i>	--	--	1,541.1	4,758.6	--	--	24.5	75.5
<i>D. calcea</i>	--	--	220.9	232.3	--	--	48.7	51.3
<i>A. brunneus</i>	--	--	23.2	540.2	--	--	4.1	95.9
<i>A. nasutus</i>	--	--	--	89.8	--	--	--	100
<i>B. canescens</i>	--	18.7	1,121.4	2,415.4	--	0.5	31.6	67.9
<i>B. albomaculata</i>	--	--	9.4	10.0	--	--	48.4	51.6
<i>B. brachyurops</i>	--	--	--	4.7	--	--	--	100
<i>B. multispinis</i>	--	--	--	8.4	--	--	--	100
<i>B. peruana</i>	--	61.1	214.2	199.3	--	12.9	45.1	42
<i>P. rufus</i>	--	430.1	122.4	28.1	--	74.1	21.1	4.8
<i>G. furvescens</i>	--	--	38.4	254.3	--	--	13.1	86.9
<i>Z. chilensis</i>	13.7	951.1	39.9	14.5	1.3	93.3	3.9	1.4
<i>D. trachyderma</i>	--	375.4	431.2	278.5	--	34.6	39.7	25.7
<i>R. sadowskii</i>	--	--	--	38.2	--	--	--	100
<i>T. tremens</i>	5.3	6.5	21.4	--	16.1	19.6	64.3	--
<i>H. macrophthalmus</i>	--	--	--	126.0	--	--	--	100
Total	19.0	1,932.4	7,142.8	14,734.9				

†Depth strata are A: 100–199 m; B: 200–299 m; C: 300–399; D: 400–499.

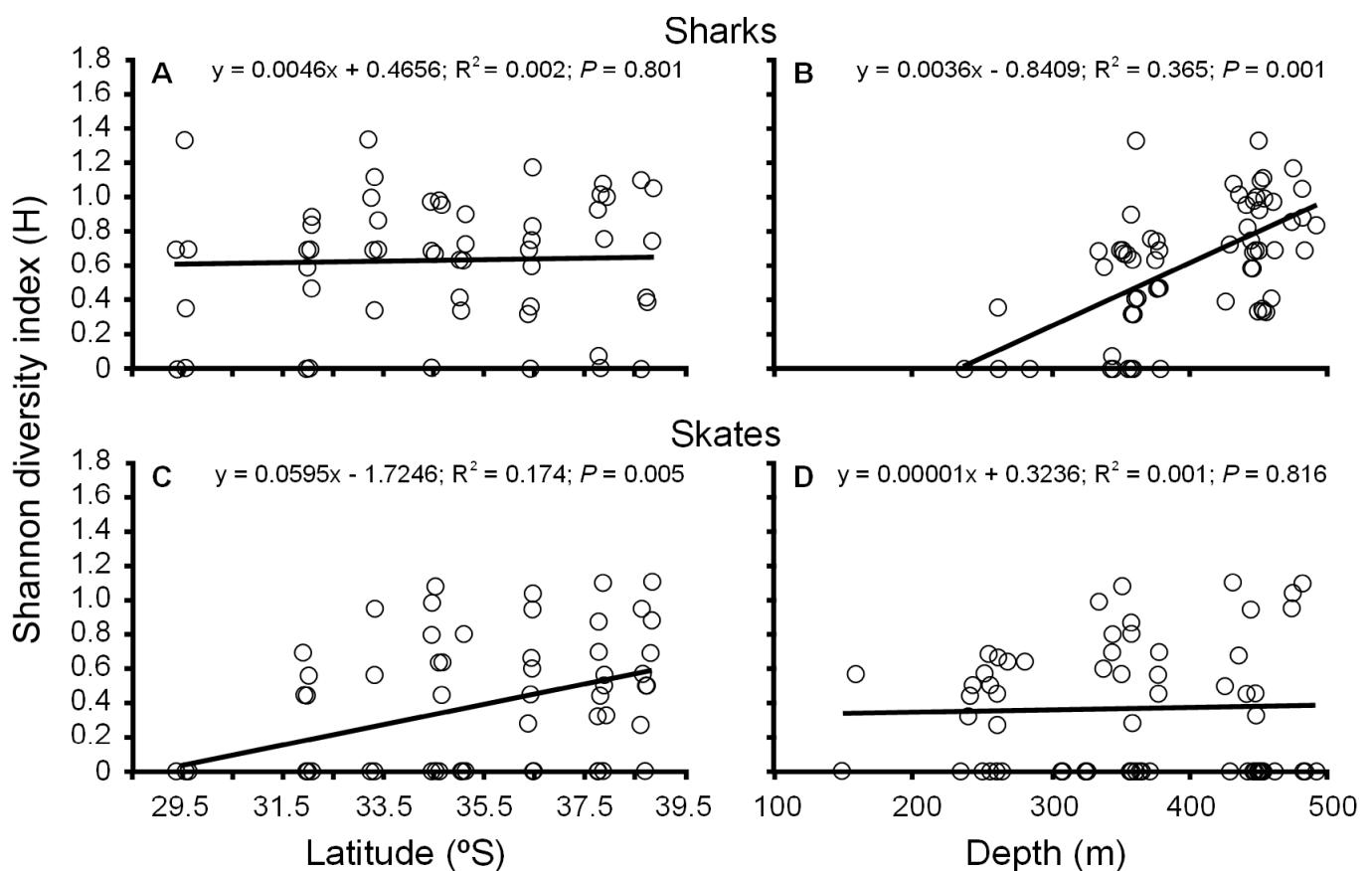


Figure 20 Latitudinal and bathymetric changes of Shannon diversity index (H) of sharks (A–B) and skates (C–D) across the study area. Fitted least-square regression model (solid line) and statistical significance are indicated in each case.

Community structure

Agglomerative hierarchical cluster analysis (Fig. 21) revealed four major fish assemblages (I – IV) at similarity level of 40%, and one outlier. The ANOSIM showed that the four assemblages were significantly separated from each other ($n = 76$, R Global = 0.68; $P > 0.01$), with the outlier characterised by presence of one single species (*Bathyraja peruviana*) with the lowest total CPUE (8.6 ind $\text{km}^{-2} \text{ h}^{-1}$). Geographically, assemblage I grouped 11 sites located north of Coquimbo to Valparaíso (zones 1 – 3, Fig. 17) and between depths of 237 to 379 m, with an average of CPUE of 56.3 ind $\text{km}^{-2} \text{ h}^{-1}$ for 10 species (5 sharks and 5 skates). This community was dominated by *Centroscyllium nigrum* that comprised 34.3% of the CPUE, *Bythaelurus canescens* (22.2% CPUE) and *Psammobatis rufus* (11.5% CPUE) (Table 21). Assemblage II included the largest number of sites (45), taxa (20) and specimens (average CPUE = 475 ind $\text{km}^{-2} \text{ h}^{-1}$). Sites in this assemblage were scattered over the entire study area and occupied a depth range of 335 – 492 m. Prominent

species in this assemblage were *C. granulatum* (37.6% CPUE), *C. nigrum* (28.5% CPUE), and *B. canescens* (15.9% CPUE) (Table 21). Assemblage III comprised 10 relatively shallow sites (149 – 262 m) in the most southerly zone offshore from Concepción, the second largest port in Chile. The skates *Z. chilensis* and *D. trachyderma* dominated this assemblage of 6 species with 83.3% of the assemblage CPUE (158 ind $\text{km}^{-2} \text{ h}^{-1}$; Table 5). Assemblage IV grouped 10 relatively shallow sites (243 – 281 m) located south of Valparaíso in zones 4, 5 and 6. This assemblage had the lowest diversity (5 species) and abundance (39.9 ind $\text{km}^{-2} \text{ h}^{-1}$). Two species, *Psammobatis rufus* and *C. granulatum*, were the most abundant species accounting for 63.4% and 20.4% of CPUE respectively (Table 21).

Ordination analysis (nMDS) produced similar results to cluster analysis with four assemblages (Fig. 22). The outlier observed (zone 3, site B, tow 1) was a tow off Valparaíso apparently separated from other tows due to the presence of a single species (*Bathyraja peruviana*) with low abundance (8.5 ind $\text{km}^{-2} \text{ h}^{-1}$). SIMPER analysis showed low average within-assemblage similarity of 29.9 – 38.6% for all assemblages. Two main consolidating species, *P. rufus* and *D. trachyderma* were identified within each assemblage, and accounted for 100% within-assemblage similarity in assemblage III; 59.4% in assemblage IV and >6% in assemblages I and II, respectively. Unlike within-assemblage similarity, the between-assemblage dissimilarity levels in all four assemblages were high, ranging from 92.7 to 96.7%. *Psammobatis rufus*, *Bythaelurus canescens*, *Centroscyllium nigrum* and *Dipturus trachyderma*, accounted for 80.7% of total (84.2%) dissimilarity between assemblages I and III. Nine species together contributed 92.9% towards total (96.7%) dissimilarity between assemblages I and II. Eight species were responsible for 91.9% (95.1%) and 90.5% (94.3%) of total dissimilarity in both, assemblages II and III and assemblages II and IV respectively. Finally, seven species contributed 92% towards total (93.4%) dissimilarity between assemblages II and III; while between assemblages III and IV, *Zearaja chilensis*, *Dipturus trachyderma*, *Psammobatis rufus* and *Centroscyllium granulatum* accounted for 91.9% of total (92.7%) dissimilarity.

Table 21 Average abundance (ind km⁻²h⁻¹) and percentage of contribution per species in each assemblage (*n* indicates the number of sites included per assemblage).

Species/Assemblage	I (<i>n</i> = 11)		II (<i>n</i> = 45)		III (<i>n</i> = 9)		IV (<i>n</i> = 10)	
	Avg.	%	Avg.	%	Avg.	%	Avg.	%
<i>H. griseus</i>	--	--	1.2	0.3	--	--	--	--
<i>A. nigra</i>	4.1	7.2	21.1	4.4	--	--	0.4	1.0
<i>C. macracanthus</i>	--	--	0.2	0.0	--	--	--	--
<i>C. granulatum</i>	--	--	178.5	37.6	1.1	0.7	8.1	20.4
<i>C. nigrum</i>	19.3	34.3	135.3	28.5	--	--	--	--
<i>D. calcea</i>	1.4	2.4	9.7	2.0	--	--	--	--
<i>A. brunneus</i>	1.4	2.4	12.2	2.6	--	--	--	--
<i>A. nasutus</i>	--	--	2.0	0.4	--	--	--	--
<i>B. canescens</i>	12.5	22.2	75.9	16.0	--	--	--	--
<i>B. albomaculata</i>	--	--	0.4	0.1	--	--	--	--
<i>B. brachyurops</i>	--	--	0.1	0.0	--	--	--	--
<i>B. multispinis</i>	--	--	0.2	0.0	--	--	--	--
<i>B. peruana</i>	2.5	4.5	8.9	1.9	4.1	2.6	--	--
<i>P. rufus</i>	6.5	11.5	2.0	0.4	18.3	11.6	25.3	63.4
<i>G. furvescens</i>	2.8	4.9	5.9	1.2	--	--	--	--
<i>Z. chilensis</i>	0.8	1.5	1.2	0.3	106.2	67.4	--	--
<i>D. trachyderma</i>	5.1	9.0	16.3	3.4	26.8	17.0	5.7	14.2
<i>R. sadowskii</i>	--	--	0.8	0.2	--	--	--	--
<i>T. tremens</i>	--	--	0.5	0.1	1.1	0.7	--	--
<i>H. macrophthalmus</i>	--	--	2.8	0.6	--	--	--	--

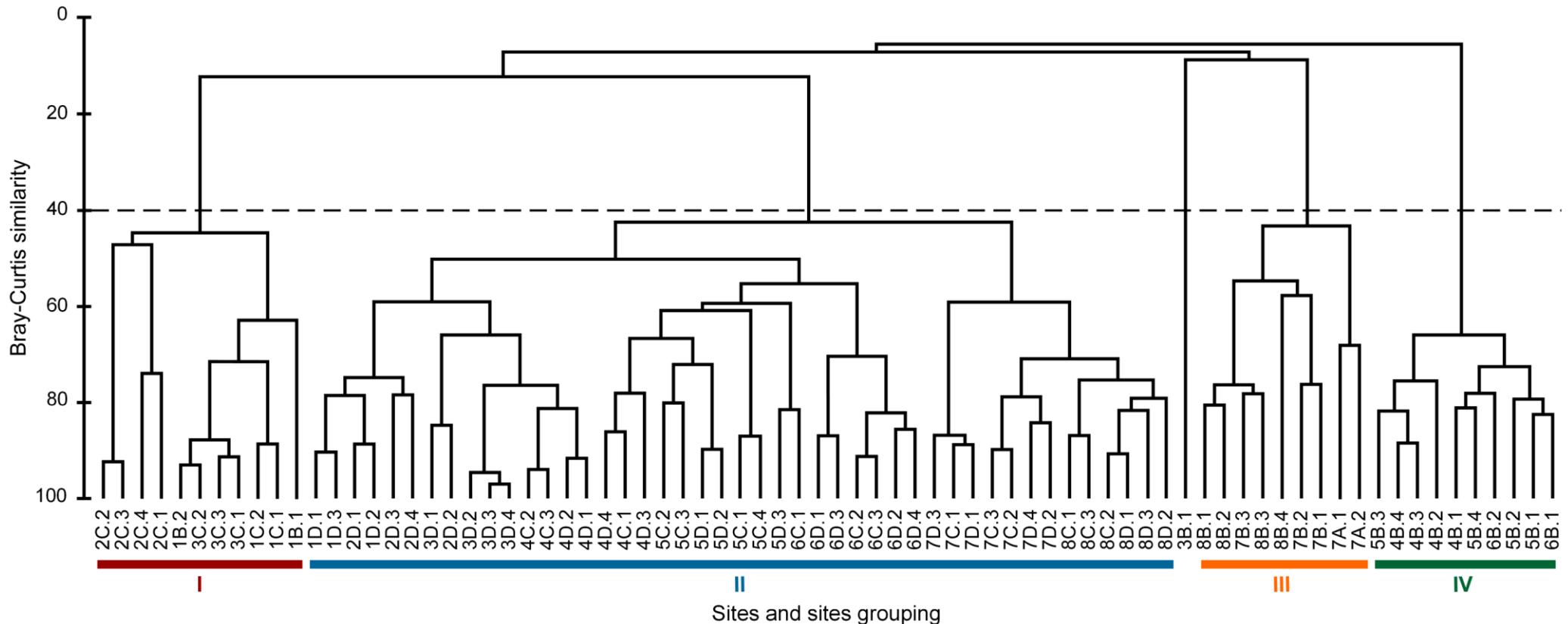


Figure 21 Agglomerative hierarchical cluster indicating the clustering of the four assemblages. Site grouping is colour coded and indicates 40% similarity. Sites are coded following zone (1 to 8), depth strata (A to D) and pseudoreplica (1 to 4).

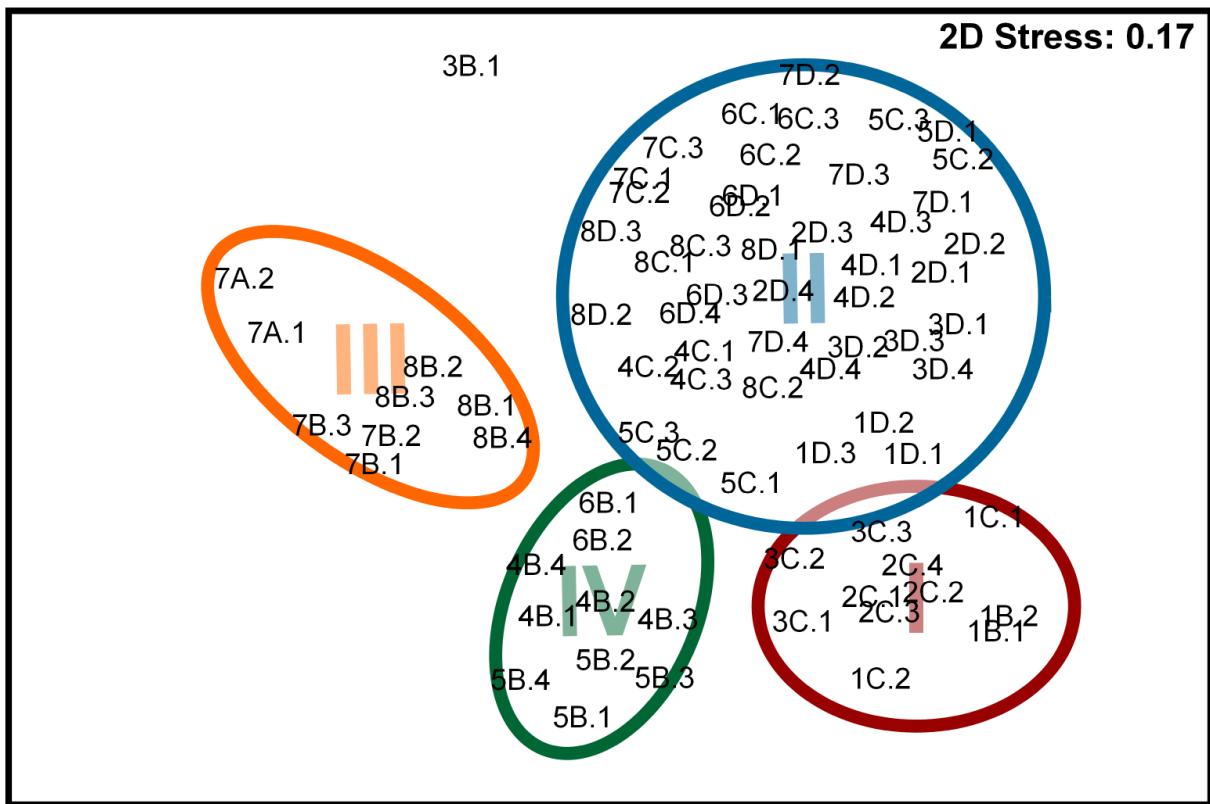


Figure 22 Ordination in two-dimensions using non-dimensional metric scaling indicating the clustering of the four assemblages. Sites grouping is colour coded and indicate 40% similarity. Colour and sites codes follows Fig. 21.

DISCUSSION

Trawling has long been used to explore waters off the central-north and central-south coasts of Chile in order to identify regions where benthic crustaceans and teleost fishes of commercial interest occur in high abundance (Sielfeld & Vargas, 1996; Menares & Sepulveda, 2005). Currently, trawl-fishing effort is centred, but not restricted, to squat lobsters (*Cervimunida johni* and *Pleuroncodes monodon*), deep-water shrimps (*Heretocarpus reedi*), hakes (*Merluccius gayi* and *M. australis*) and Chilean horse mackerel (*Trachurus murphyi*). The abundance of these target species is estimated through regular trawl surveys to allow the fishing effort to be adjusted to achieve ‘maximum sustainable yield’. A useful by-product of such surveys has been the production of species checklists that have enriched knowledge of Chile’s national marine biodiversity (Pequeño, 2000; Acuña *et al.*, 2005). These extensive fishery-dependent and independent surveys, that include cartilaginous fishes in the catch, are conducted annually in central Chilean waters (c. 21.5 – 38.5°

S). For example, between 1994 and 2004, exploratory surveys for demersal crustaceans comprised 6,143 trawl hauls made at depths of 100 – 500 m (Acuña *et al.*, 2005). Although 13 shark, 8 skate and 1 chimaera species were caught, published data are limited to a simple indication of the latitudinal range for each species (Acuña *et al.*, 2005). The absence of quantitative data on the species' abundance, particularly in respect of fishing effort, location (latitude) and depth provides a challenge for management, whether for exploitation or for conservation. It is also of relevance to note that these fishery-dependent and independent surveys report on the diversity of animals from areas that are subject to continuous and often intense fishing activity which is implicated in the decline in species richness (Wolff & Aroca, 1995).

There has also been a number of fishing-independent studies, such as Ojeda (1983), that reported the presence of 2 shark and 3 skate species from 118 hauls made at depths of over 500 m on a trawl survey in austral Chile (52° S – 57° S). Further north, 133 hauls made between 31° S – $41^{\circ}28'$ S at depths of 50 – 550 m produced 7 shark, 5 skate and 1 chimaera species (Menares & Sepúlveda, 2005). In central Chile, Meléndez & Meneses (1989) reported 11 shark species from 173 hauls in exploration surveys using bottom trawl nets between 18° S – $38^{\circ}30'$ S and at depths of 500 – 1260 m. In the most northerly survey, between 18° S and 21° S, the same gear type used over a wider depth range (30 – 1050 m) resulted in 4 shark, 4 skate and 1 chimaera species from 21 hauls (Sielfeld & Vargas, 1996). Each of these studies, however, also lacked quantification of the catch and are therefore of limited value, beyond providing information on the presence (or apparent absence) of species within a geographic region.

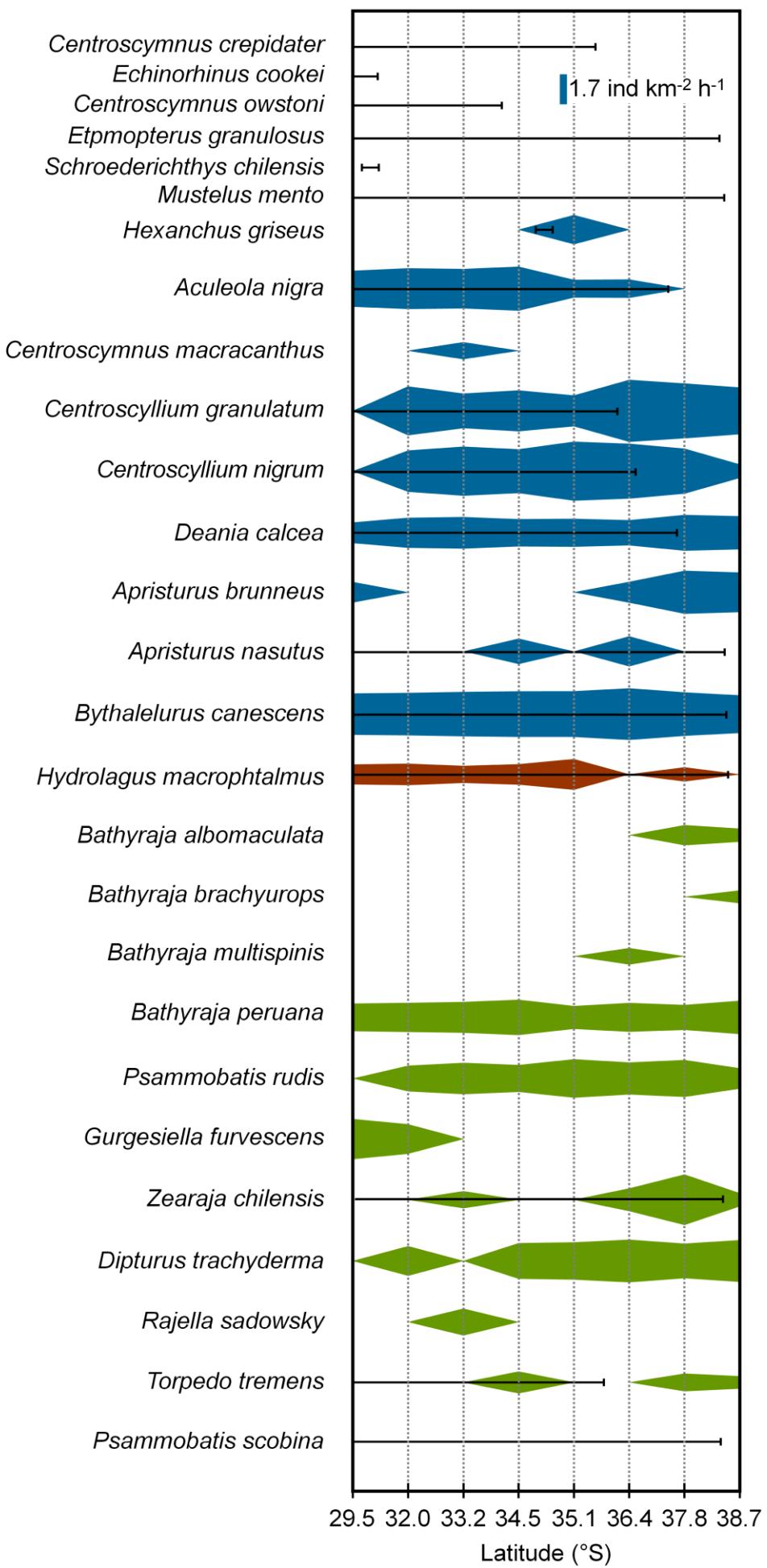
Community definition

The species richness observed in the current study (20 species), is higher than those found in surveys conducted previously in the region (Ojeda, 1983; Meléndez & Meneses, 1989; Sielfeld & Vargas, 1996; Ojeda *et al.*, 2000; Acuña & Villarroel, 2002; Acuña *et al.*, 2005; Menares & Sepulveda, 2005). Variation in the reported species richness of cartilaginous fishes within the region among years may reflect the different gear types used, different effort, different depths sampled, and species misidentifications (Pequeño & Lamilla, 1993; Lamilla *et al.*, 2010). While the species richness reported here is similar to that reported by Acuña *et al.* (2005), the cartilaginous fish community appears to differ between the two studies. Direct comparisons are somewhat speculative as while our study provides quantification of the fauna in terms of CPUE and F_0 while the results of Acuña *et al.* (2005) are limited to whether a species was present, in unreported abundance. Nevertheless, a couple of thematic differences are apparent with small, shallow-water

skates (i.e., *Psammobatis scobina*, *Sympterygia lima*, *S. brevicaudata* and *Discopyge tschudii*) absent in our study, while deep-sea skates of the genera *Bathyraja* and *Rajella* were not caught in the earlier study (Fig. 23). These results suggest that, in comparison to our study, (a) shallower waters may have been sampled, and (b) the fishing effort in deeper waters was more limited in the study reported by Acuña *et al.* (2005). Taken together, these two studies indicate that at least 30 cartilaginous fishes inhabit (or did inhabit) the continental shelf and slope off central Chile; although some species showed pronounced latitudinal variation in distribution (e.g. *Aculeola nigra*, *Centroscyllium nigrum*, *Gurgesiella furvescens*) while in some others, the latitudinal extension is not reported (i.e., *Bathyraja peruviana*, *Sympterygia brevicaudata*, *S. lima*, *Discopyge tschudii*).

Species abundance was highly variable between zones with the lowest abundance in the north (zone 1). The abundance in the central and the most southern zones (2, 3, 4 and 8) was about double this value, in zones 5 and 7 it was four times as large and in zone 6 it was an order of magnitude greater. Interestingly, five species (e.g., *Hexanchus griseus*, *Centroscymnus macracanthus*, *Bathyraja brachyurops*, *B. multispinis* and *Rajella sadowskii*) were caught, mostly in low numbers, only within a single zone and within a single depth stratum. The pattern of occurrence suggests that the species are naturally uncommon or, more likely, that the trawl regime only sampled the upper end of their natural range (Fig. 19). In contrast, two species (e.g., *Apristurus nasutus* and *Hydrolagus macrophthalmus*) showed a marked preference for a particular depth stratum but occurred in more than one zone. Others species showed an obvious latitudinal variation in abundance, for example, *Aculeola nigra* was common in the north (zones 1 – 4), rare in central zones (5 – 6) and absent in the southern zones (7 – 8); whereas, *Psammobatis rufis* and *Dipturus trachiderma* showed the opposite trend. Both *Centroscyllium* species (*C. granulatum* and *C. nigrum*) have a high abundance in central Chile and are less common in both north and south, and appear to become extremely abundant with increasing depth. Between 300 and 500 m, the diversity further doubled and the abundance of most species increased. With the exception of two species (*Zearaja chilensis* and *Torpedo tremens*), all cartilaginous fishes were caught at depths below 200 m and most increase their abundance with depth. This relative absence of cartilaginous fishes in shallow waters (100 – 199 m) was both unexpected and difficult to explain, and needs to be addressed in future studies.

Figure 23 (next page) Latitudinal distribution and abundance (Log (CPUE+1)) of cartilaginous fishes present in the continental shelf and slope of Chile. Black lines represent species range reported by Acuña *et al.* (2005).



Community structure

Species richness of cartilaginous fishes in the south-east Pacific has been described as increasing towards lower latitudes following the same geographic pattern of other marine fishes (Meléndez & Meneses, 1989; Pequeño *et al.*, 1990; Rohde, 1992; Pequeño & Lamilla, 1993; Camus, 2001); however, these observations are based on species inventories without reference to latitudinal or bathymetric ranges which obviously can have a marked influence on species distributions. Also, elasmobranch diversity in the Atlantic and Pacific oceans have been described to decrease with depth, especially below 1,000 m depth (Pakhomov *et al.*, 2006; Priede *et al.*, 2006). Our results provided evidence of an overall increase in species richness with increasing latitude and depth down to 500 m, in contrast to a decrease in diversity with increasing latitude demonstrated by littoral fishes (Ojeda *et al.*, 2000), but similar to diversity gradients of benthic invertebrates and in the Northern Hemisphere described by Rex *et al.* (2000). In our study, the latitudinal and bathymetric stability of assemblage II (Fig. 21), is consistent with a “transition intermediate area” as described by Camus (2001), and suggests that differences between assemblages were due to compensatory changes in mesopredator abundance (Navia *et al.*, 2011). There is a correlation between the location of assemblages I, III and IV and intensive trawl fishing areas (Wolff & Aroca, 1995; Escribano *et al.*, 2003; Acuña *et al.*, 2005). Continuous and unselective removal of certain species by commercial fisheries may explain in part the variation of species abundance among assemblages.

At the community level, the main assemblage (II) was distributed across the entire surveyed area comprising 58% of sites; and showed a high average dissimilarity to assemblages I, III and IV (96.7, 95.1 and 94.3% respectively). Differences were mainly due to the importance of small-sized sharks (*Bythaelurus canescens*, *Centroscyllium granulatum* and *C. nigrum*), although diversity of small-sized skates also contributed to overall dissimilarity. In our study assemblages I, III and IV represented ‘coldspots’ of diversity, similar to those found along the outer shelf in south-west Atlantic cartilaginous fish community (Lucifora *et al.* 2011). While those coldspots were simply defined as areas of low diversity, in the current study coldspots coincide with traditional fishing grounds. Commercial fisheries in Chile, in particular trawl-based activities, are likely to have a direct effect on cartilaginous fish community structure and distribution as has been previously documented for other marine fishes in central Chile (Arancibia & Neira, 2005).

Different levels of fishing pressure can generate multiple effects on the function of species and their interactions (Navia *et al.*, 2011). High species richness and abundance represented in assemblage II, is consistent with a more stable community as high biodiversity has been linked to the stability of trophic networks through the complex interactions that arise among its components

(Navia *et al.*, 2011). In contrast, when there is an external disturbance, in this case differential exposure to fishing pressure, the result may be a complete reorganisation of the community (Bascompte *et al.*, 2005).

Considering the overall species composition without counting rare species (defined in relation to low species abundance), such as *Echinorhinus cookei* and *Centroscymnus owstonii*, the absence of mid- to large-sized sharks is evident in our study (Fig. 19), however fishing gear selectivity and species catchability may influence the frequency of occurrence observed. Ferretti *et al.* (2010) described the ecological restructuring of demersal elasmobranch communities in fishing areas worldwide. Diversity and abundance of elasmobranchs erodes quickly as fisheries remove, unselectively, both small and large species despite the lower catchability of the latter. As large sharks disappear from the catch as fisheries develop, the community tends to become dominated by mesopredators. In the current study these mesopredators are predominantly small-sized sharks, which are more fecund and more resilient to fishing pressures than other elasmobranchs. Examples of similar community restructuring have been documented for trawl fishing areas in the Atlantic (Ellis *et al.*, 2005), Gulf of Mexico (Shepherd & Myers, 2005), the Mediterranean Sea (Ferretti *et al.*, 2008) and Australian waters (Graham *et al.*, 2001); although its extension to similar trawl fisheries elsewhere has not been properly evaluated due to a lack of temporal and seasonal catch-composition data for elasmobranch species.

Limitations and future directions

Previous research has identified two distinct biogeographic provinces based on multiple taxa along the Chilean coast, the Peruvian province in the north (4° – 30° S) and the Magellanic province in the south (42° – 56° S) (Camus, 2001). There is also an “intermediate area” between these two provinces that has been described as a rich, mixed-origin species’ transition zone for teleost fishes (Pequeño, 2000; Ojeda *et al.*, 2000). Considering the limitations of geographic scale, the single main biogeographic province (assemblage II) that was identified between 29.5° S and 38.5° S only showed limited evidence of species more usually associated with the Peruvian and Magellanic provinces.

Fishery-independent surveys allowed us to explore an extensive area, including traditional commercial trawling zones and non-traditional fishing zones with similar effort. It should be mentioned that the methodology used was designed to sample demersal and bottom-dwelling species, and therefore the cartilaginous fish community’ definitions used here effectively excludes species that occur in mid- to surface waters and likely underestimates species richness (Pakhomov

et al., 2006). Potential limitations of our analysis include differential vulnerability to fishing gear, which could be species-specific or relate to swimming performance or the size of individuals. The original experimental design attempted to cover all zones during the same season but some were sampled in separated cruises during summer and winter due logistical issues. Oceanographic variability may influence species distribution and potential seasonal changes of abundance and species richness need to be addressed in future research, especially at shallower depths (100 to 200 m). Also, the sampling effort was not evenly distributed throughout the whole of the latitudinal range with sites clustered within each zone; as such it is unlikely that all habitat types were sampled. This may be important as rocky substrates and other irregular habitats such as coral reefs and seamounts have been described as high diversity areas (hotspots), especially for cartilaginous fishes (Henry *et al.*, 2013).

The clusters of sample sites also resulted in a relatively low resolution ‘picture’, and precluded a fine scale description of species’ distributions and abundance, and how these might be influenced by local conditions (e.g., habitat type).

Our results provide a quantitative description of species richness and abundance of the cartilaginous fish community on the outer continental shelf and slope of Chile to complement and extend knowledge of biological and ecological interactions of this demersal ecosystem. More than 90% of elasmobranch species worldwide inhabit demersal ecosystems on continental shelves and slopes (Compagno, 1990), which makes them vulnerable to trawl fishing (Shepherd & Myers, 2005) and we are just beginning to understand the potential ecological consequences of removal and declines of cartilaginous fishes. The information presented here is of immediate value in the assessment of the conservation status of species and the threats to their populations posed by demersal trawling. This study is also of particular value for future assessment of how natural or anthropogenic activities may impact the various species by providing quantitative baseline information against which change can be assessed.

REFERENCES

- Acuña, E. & Villarroel, J.C. (2002) Bycatch of sharks and rays in the deep sea crustacean fishery off the Chilean coast. *Shark News* 14, 16–18. Available at <http://www.flmnh.ufl.edu/fish/organizations/ssg/sharknews/sn14/shark14news15.htm> (accessed 25 February 2014).
- Acuña, E., Villarroel, J.C., Cortés, A. & Andrade, M. (2005) Fauna acompañante en pesquerías de arrastre de crustáceos de Chile: implicancias y desafíos desde la perspectiva de la biodiversidad.

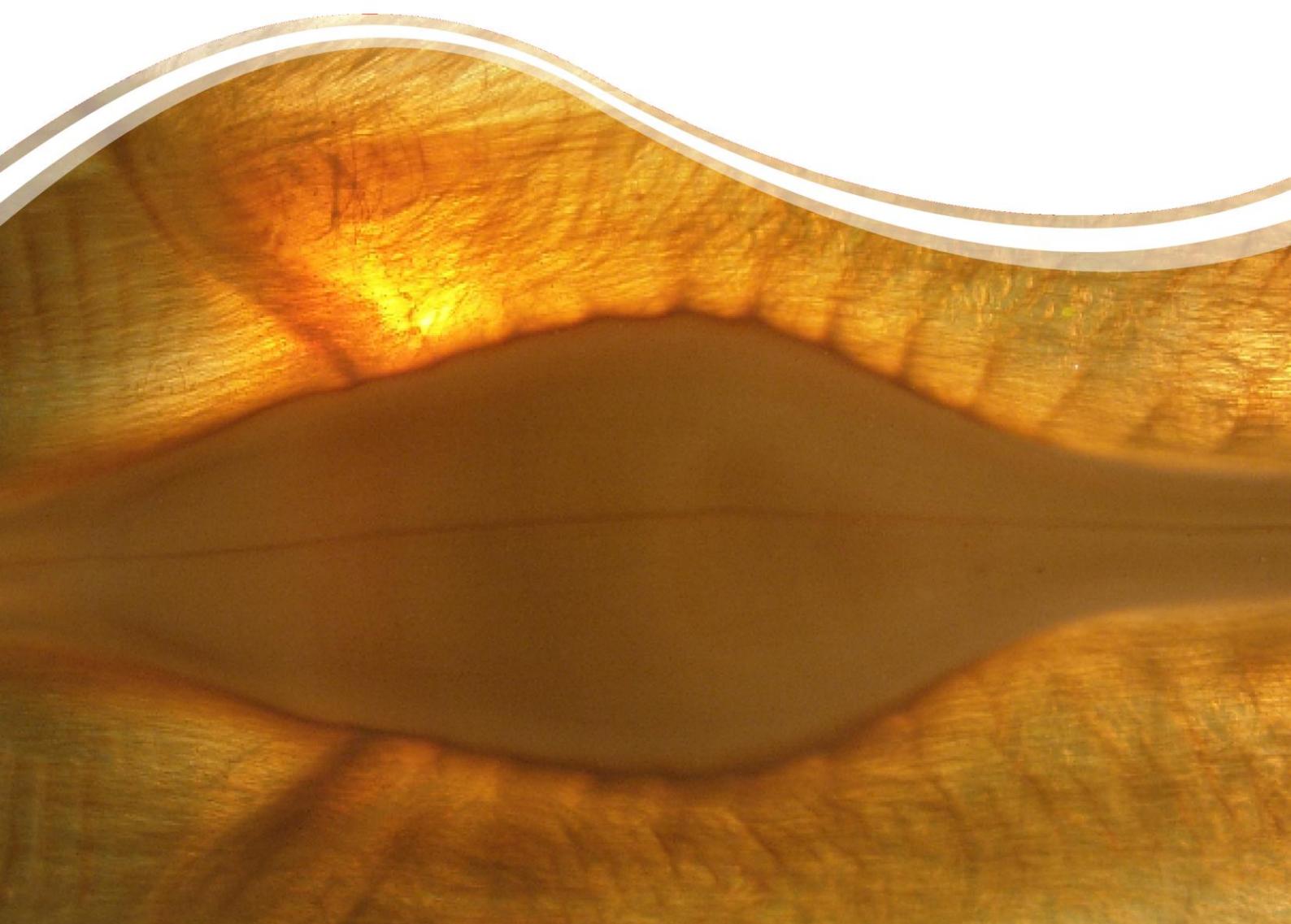
- In *Biodiversidad Marina: Valoración, Usos y Perspectivas* (Figueroa, E., ed), pp. 395–425. Editorial Universitaria: Santiago de Chile.
- Arancibia, H. & Neira, S. (2005) Long-term changes in the mean trophic level of Central Chile fishery landings. *Scientia Marina* 69, 295–300.
- Bascompte, J., Melián, C.J. & Sala, E. (2005) Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences of the United States of America* 102, 5443–5447.
- Brattström, H. & Johanssen, A. (1983) Ecological and regional zoogeography of the marine benthic fauna of Chile. *Sarsia* 68, 289–339.
- Bustamante, C., Vargas-Caro, C. & Bennett, M.B. (2014) Not all fish are equal: Which species best represent the functional diversity of a nation's cartilaginous fishes? Using Chile as a case study. *Journal of Fish Biology* In Press (01/04/2014).
- Camus, P.A. (2001) Marine biogeography of continental Chile. *Revista Chilena de Historia Natural* 74, 587–617.
- Carrasco, F.D. (1997) Sublittoral macrobenthic fauna off Punta Coloso, Antofagasta, northern Chile: high persistence of the polychaete assemblage. *Bulletin of Marine Science* 60, 443–459.
- Clarke, K.R. (1993) Non-parametric multivariate analyses of changes in community structure. *Australian Journal of Ecology* 18, 117–143.
- Clarke, K.R. & Warwick, R.M. (1994) *Change in marine communities: an approach to statistical analysis and interpretation*. Plymouth Marine Laboratory: Plymouth, UK
- Compagno, L.J.V. (1984a) FAO species catalogue, Sharks of the world, An annotated and illustrated catalogue of the shark species known to date. Vol. 4, Part 1. Hexanchiformes to Lamniformes. *FAO Fishery Synopsis* 125, 1–250.
- Compagno, L.J.V. (1984b) FAO species catalogue, Sharks of the world, An annotated and illustrated catalogue of the shark species known to date. Vol. 4, Part 2. *FAO Fishery Synopsis* 125, 251–655.
- Compagno, L.J.V. (1990) Alternative life-history styles of cartilaginous fishes in time and space. *Environmental Biology of Fishes* 28, 33–75.
- Cubillos, L. (2005) Diagnóstico, Aspectos Críticos y Propuesta de Sustentabilidad para las Pesquerías Nacionales. In *Biodiversidad marina: valoración, usos y perspectivas* (Figueroa, E., ed.), pp. 27–46. Editorial Universitaria: Santiago de Chile.

- Ebert, D.A., Fowler, S. & Compagno, L.V.J. (2013). *Sharks of the World*. Wild Nature Press: Plymouth.
- Ellis, J.R., Cruz-Martinez, A., Rackham, B. & Rogers, S.I. (2005) The distribution of chondrichthyan fishes around the British Isles and implications for conservation. *Journal of Northwest Atlantic Fishery Science* 35, 195–213.
- Escribano, R., Fernandez, M. & Aranis, A. (2003) Physical-chemical processes and patterns of diversity of the Chilean eastern boundary pelagic and benthic marine ecosystems: An overview. *Gayana* 67, 190–205.
- Ferretti, F., Myers, R.A., Serena, F., Lotze, H.K. (2008) Loss of large predatory sharks from the Mediterranean Sea. *Conservation Biology* 22, 952–64.
- Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R. & Lotze, H.K. (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters* 13, 1055–1071.
- Graham, K.J., Andrew, N.L. & Hodgson, K. (2001) Changes in relative abundance of sharks and rays on Australian south east fishery trawl grounds after twenty years of fishing. *Marine & Freshwater Research* 52, 549–61.
- Henry, L.A., Navas, J.M., Hennige, S.J., Wicks, L.C., Vad, J. & Roberts, J.M. (2013) Cold-water coral reef habitats benefit recreationally valuable sharks. *Biological Conservation* 161:67–70.
- Kempton, R.A. (1979) The Structure of Species Abundance and Measurement of Diversity. *Biometrics* 35, 307–321.
- Kyne, P.M. & Simpfendorfer, C.A. (2007) A collation and summarization of available data on deepwater Chondrichthyans: biodiversity, life history and fisheries. IUCN Shark Specialist Group Available at <http://www.flmnh.ufl.edu/fish/organizations/> ssg/deepchondreport.pdf (accessed 25 February 2014).
- Lamilla, J. & Sáez, S. (2003) Taxonomic key for the identification of Chilean rays and skates species (Chondrichthyes, Batoidei). *Investigaciones Marinas, Valparaíso* 31:3–16.
- Lamilla, J. & Bustamante, C. (2005) Guía para el reconocimiento de tiburones, rayas y quimeras de Chile. *Oceana* 18:1–80.
- Lamilla, J., Bustamante, C., Roa, R., Acuña, E., Concha, F., Meléndez, R., López, S., Aedo, G., Flores, H. & Vargas-Caro C. (2010) Estimación del descarte de condriictios en pesquerías artesanales. *Universidad Austral de Chile Informe técnico No. 2008-60, Valdivia*. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 February 2014).

- Lucifora, L.O., García, V.B., Menni, R.C. & Worm, B. (2011) Spatial patterns in the diversity of sharks, rays, and chimaeras (Chondrichthyes) in the Southwest Atlantic. *Biodiversity and Conservation* 21, 407–419.
- Mann, G. (1954) *La vida de los peces en aguas chilenas*. Instituto de Investigaciones Veterinarias y Universidad de Chile: Santiago.
- Meléndez, R. & Meneses, D. (1989) Tiburones del talud continental recolectados entre Arica (18°19'S) e Isla Mocha (38°30'S), Chile. *Investigaciones Marinas, Valparaíso* 17, 3–73.
- Melo, T., Silva, N., Muñoz, P., Díaz-Naveas, J., Sellanes, J., Bravo, A., Lamilla, J., Sepúlveda, J., Vögler, R., Guerrero, Y., Bustamante, C., Alarcón, M.A., Queirolo, D., Hurtado, F., Gaete, E., Rojas, P., Montenegro, I., Escobar, R. & Zamora, V. (2007) Caracterización del fondo marino entre la III y X Regiones (Informe Final FIP 2005-61). Valparaíso: Pontificia Universidad Católica de Valparaíso. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 February 2014).
- Menares, B. & Sepúlveda, J.T. (2005) Grupos recurrentes de peces y crustáceos demersales en la zona centro-sur de Chile. *Investigaciones Marinas, Valparaíso* 33, 91–100.
- Navia, A.F., Cortés, E., Jordán, F., Cruz-Escalona, V.H. & Mejía-Falla, P.A. (2011) Changes to Marine Trophic Networks Caused by Fishing. In *Diversity of Ecosystems* (Mahamane, A., ed.), pp. 418–452. InTech Press: Croatia.
- Ojeda, P. (1983) Distribución latitudinal y batimétrica de la ictiofauna demersal del extremo austral de Chile. *Revista Chilena de Historia Natural* 56, 61–70.
- Ojeda, F.P., Labra, F.A. & Muñoz, A.A. (2000) Biogeographic patterns of Chilean littoral fishes. *Revista Chilena de Historia Natural* 73, 625–641.
- Pakhomov, E.A., Bushula, T., Kaehler, S., Watkins, B.P. & Leslie, R.W. (2006). Structure and distribution of the slope fish community in the vicinity of the sub-Antarctic Prince Edward Archipelago. *Journal of Fish Biology* 68, 1834–1866.
- Pequeño, G. (1989) Peces de Chile. Lista sistemática revisada y comentada. *Revista de Biología Marina, Valparaíso* 24, 1–132.
- Pequeño, G. (2000) Delimitaciones y relaciones biogeográficas de los peces del Pacífico suroriental. *Estudios Oceanológicos* 19, 53–76.
- Pequeño, G. & Lamilla, J. (1993) Batoideos comunes a las costas de Chile y Argentina-Uruguay (Pisces: Chondrichthyes). *Revista de Biología Marina, Valparaíso* 28, 203–217.

- Pequeño, G., Rucabado, J. & Lloris, D. (1990) Tiburones comunes a las costas de Chile, California-Oregon y Namibia-Sud África. *Revista de Biología Marina, Valparaíso* 25, 65–80.
- Priede, I.G., Froese, R., Bailey, D.M., Bergstad, O.A., Collins, M.A., Dyb, J.A., Henriques, C., Jones, E.G. & King, K. (2006) The absence of sharks from abyssal regions of the world's oceans. *Proceedings of the Royal Society B* 273, 1435–1441.
- Rex, M.A., Stuart, C.T. & Coyne, G. (2000) Latitudinal gradients of species richness in the deep-sea benthos of the North Atlantic. *Proceedings of the National Academy of Sciences of the United States of America* 97, 4082–4085.
- Rohde, K. (1992) MINI- Latitudinal gradients in species diversity : the search for the primary cause. *Oikos* 65, 514–527.
- Sellanes, J., Quiroga, E., Neira, C. & Gutiérrez, D. (2007) Changes of macrobenthos composition under different ENSO conditions on the continental shelf off central Chile. *Continental Shelf Research* 27, 1002–1016.
- Shepherd, T.D. & Myers, R.A. (2005) Direct and indirect fishery effects on small coastal elasmobranchs in the northern Gulf of Mexico. *Ecology Letters* 8, 1095–1104.
- Sielfeld, W. & Vargas, M. (1999) Review of marine fish zoogeography of Chilean Patagonia (42°–57° S). *Scientia Marina* 63, 451–463.
- Spellerberg, I.F. & Fedor, P.J. (2003) A tribute to Claude Shannon (1916–2001) and a plea for more rigorous use of species richness, species diversity and the ‘Shannon–Wiener’ Index. *Global Ecology and Biogeography* 12, 177–179.
- Solervicens, J. (1973) Coleópteros del bosque de Quintero. *Anales del Museo de Historia Natural de Valparaíso* 6, 115–159.
- Wetherbee, B.M. & Cortés, E. (2004) Food consumption and feeding habits. In *Biology of Sharks and Their Relatives* (Carrier, J. C., Musick, J. A. & Heithaus, M. R., eds), pp. 223–244. CRC press: Boca Raton, FL.
- Wolff, M. & Aroca, T. (1995) Population dynamics and fishery of the Chilean squat lobster *Cervimunida johni* Porter (Decapoda, Galatheidae) off the coast of Coquimbo, Northern Chile. *Revista de Biología Marina, Valparaíso* 30, 57–60.

CHAPTER 4
LIFE HISTORY



4.1. Reproductive biology of *Zearaja chilensis* (Guichenot 1848) (Chondrichthyes: Rajidae) in the southeast Pacific Ocean

Originally published in Journal of Fish Biology (ISSN: 1095-8649)

Copyright © Carlos Bustamante 2012

Published online: 01 December 2011

License Number: 3303480469515

Abstract

The yellownose skate *Zearaja chilensis* is a batoid of high commercial value in Chile, where it is captured by an artisanal fishery comprising small vessels and an industrial trawl fleet that targets hake (*Merluccius gayi* and *M. australis*). Although size-at-maturity for this species has been determined from industrial landings, comparable information from the coastal, artisanal fishery stock remains unknown. Between 2000 and 2002, three artisanal landing sites were sampled in southern Chile, with data on population structure and reproductive development collected from 5477 skates. Total length (LT) ranged from 33 to 158 cm for females and 34 to 155 cm for males. No sexual dimorphism was evident in disc size (length or width) or in length-mass relationships. The smallest mature female was 95 cm LT and the size at which 50% were mature (LT_{50}) was 109 cm. Males matured between 80–90 cm LT with a LT_{50} of 88 cm. Although the largest skate captured by the artisanal fishery was 155 cm LT, 89% of landings comprised relatively small, immature skates. This situation may compromise the stock integrity if intrinsic vulnerability and probable long-life span of *Z. chilensis* are considered. Consequences for the survival of the species and possible signs of a fishery collapse must be reviewed by management authorities by consideration of both artisanal and industrial landings in Chile.

INTRODUCTION

Skates are cartilaginous benthic fishes that occupy the same spatial niche as demersal teleosts, such as flatfishes, hakes and eels (Walker & Hislop, 1998). However, unlike the majority of bony fishes, skates have intrinsic life history patterns that make them highly susceptible to commercial over-exploitation (Dulvy *et al.*, 2000; Dulvy & Reynolds, 2002; Frisk, 2010). Skates present unique challenges for fishery management (Stevens *et al.*, 2000) and conservation (Roberts & Hawkins, 1999; Dulvy & Reynolds, 2002) due to their low fecundity, late age at sexual maturity and relatively high longevity (Holden, 1977; Frisk *et al.*, 2001). Over the last decade, evaluation of the conservation status of skates and rays in several geographic areas has established that commercially exploited species could be seriously threatened (Dulvy & Reynolds, 2002) or even extirpated (Dulvy *et al.*, 2003) from a given fishing area. For example, large declines in populations and local extinctions of North Atlantic skates, such as the common skate *Dipturus batis* (Linnaeus 1758), the barndoor skate *D. laevis* (Mitchill 1818), the white skate *Rostroraja alba* (Lacepède 1803) and thornback ray *Raja clavata* Linnaeus 1758; have resulted from commercial fishing activities (Dulvy & Forrest, 2010). However, resilience to fishing pressure varies among skate species and while some populations have decreased dramatically (Brander, 1981; Iglesias *et al.*, 2009), others have not, and in some cases may even have increased because of reorganisation of ecological niches (Walker & Hislop, 1998; Dulvy *et al.*, 2000; Dulvy & Forrest, 2010). The vulnerability of batoid populations is mostly assessed through the examination of fisheries' catch trends (Dulvy *et al.*, 2000), but in many South American countries, including Argentina (Massa & Hozbor, 2003), Brazil (M. C. Oddone, *pers. obs.*) and Chile (Lamilla *et al.*, 2005) skates and rays have generally been recorded as a single unidentified category (e.g. "rays", including Rajoids and Myliobatiformes) in official fisheries records for several decades. However, from 2003 landings of the target species (*Zearaja chilensis*) and bycatch (a combination of six other skate species) in the Chilean skate fishery have been recorded separately.

The yellownose skate *Zearaja chilensis* (Guichenot 1848) is the most commercially valuable batoid that inhabits the continental slope of southern South America from Uruguay (south-western Atlantic) to central Chile (south-eastern Pacific) (Menni & López, 1984) and to the east of the Falkland Islands (Agnew *et al.*, 2000). The first recorded landings of *Z. chilensis* in Chile were made in the early 1970s (Bahamonde *et al.*, 1996). Since then, the catch effort for this species has gradually intensified especially in the small-scale coastal fleet located between Valdivia (40° S) and Aisén (45° S), which is considered an "artisanal fishery" by local management authorities (Licandeo *et al.*, 2006). In addition to this target fishery, *Z. chilensis* is caught as bycatch by two industrial

trawl fisheries: the southern hake *Merluccius australis* (Hutton, 1872) fishery that operates southwards of 41° 28.6' S (Quiroz *et al.*, 2009) and the common hake *M. gayi* (Guichenot, 1848) bottom trawl fishery that operates between 34° 28' S and 41° 28.6' S (Gálvez *et al.*, 1998). These artisanal and industrial fishing grounds do not overlap due to local management measures which restrict the target catch of *Z. chilensis* for industrial vessels to south of 41° 28.6' S and five nautical miles out into Chilean waters. According to official records, the annual national landing (from artisanal and industrial fleets) of *Z. chilensis* has increased from 1317 tonnes in 1990 to 3010 tonnes in 2007, with an average landing of 2663 tonnes for this period (SERNAP, 2007). After a biological closure was imposed on the artisanal fisheries in 2008, the annual landing by industrial fleets has averaged 1727 tonnes for 2008 and 2009 (SERNAP, 2009). Despite this closure, a fishing quota of 2307 tonnes and 642 tonnes has been granted to the artisanal fishery during 2009 and 2010 respectively.

Although size-at-maturity (Fuentealba *et al.*, 1990; Bahamonde *et al.*, 1996) and the life history of this species (Licandeo *et al.*, 2006; Quiroz *et al.*, 2009) have been determined previously, based on landings in southern bottom longline fishery grounds, there is a lack of information about the northern, coastal, artisanal fishery population. In order to provide additional information on the reproductive biology of *Z. chilensis*, sexual dimorphism was assessed and size-at-maturity was determined from the artisanal exploited stock. Further details of the sexual development of both males and females, as well as estimates of ovarian fecundity are also presented.

MATERIALS AND METHODS

Skate landings were sampled from three localities in south Chile: Queule (39.4° S), Corral (39.8° S) and Bahía Mansa (40.5° S) (Fig. 24); between September 2000 and December 2002. All specimens were caught by artisanal vessels of 6 to 15.5 m length using bottom set longlines of 300 to 400 hooks (M/K No. 7). Total length (*LT*), disc width (*WD*) and length (*LD*) were recorded for each specimen following Hubbs & Ishiyama (1968) and Last *et al.* (2008), along with sex and left clasper post-cloacal length (*L_C*). Measurements were made to the nearest centimetre (cm). Total body mass (*MT*) and liver mass (*ML*) were determined for all skates and recorded to the nearest gram. The hepatosomatic index (*HSI*) was calculated as: $HSI = (ML / MT^1) \times 100$. Ovary and oviducal gland mass and maximum ovarian follicle diameters were measured for female skates, while testes and epigonal organ mass were determined for males. All measurements are presented as the mean and standard deviation (s.d.).

The χ^2 (chi-square) Goodness-of-Fit (Sokal & Rohlf, 1987), was used to test whether the ratio of males to females varied significantly from a 1:1 ratio. Linear relationships between LT , partial lengths (LD and WD) and body mass were fitted separately for sex and tested for sexual dimorphism using an analysis of covariance (ANCOVA). Regressions were fitted to raw data, except for L_T and M_T , which were log-transformed. A t -test was used to evaluate differences between hepatosomatic index of mature and immature skates according to sex. Paired t -tests were performed to explore possible differences in left versus right ovary mass, oviducal gland mass and ovarian follicle size and number in females and differences between epigonal organ and testes mass in males. Ovary-oviducal gland mass and L_T relationship in females, and the relationship between LC and LT in males, were used to further assess the onset of maturity (Capapé & Quignard, 1974; Restrepo & Watson, 1991). One-way analysis of variance (ANOVA) was used to test for significant differences in mean maximum ovarian follicle diameter and HSI in available months (September to December).

Binomial maturity data (immature 0, mature 1) were determined by sex at 10 cm intervals. Size-at-maturity in both sexes were calculated by fitting the following logistic curve (by minimization of the least squares), to the relationship between the fraction of mature males or females as a function of LT , $Y = [1 + e^{-(a + bX)}]^{-1}$; where Y is the fraction of mature individuals in length class X , and a and b are the model coefficients. The ratio $a:b$ represents the size at which 50% of the skates were mature (Mollet *et al.*, 2000; Oddone *et al.*, 2005). Females were considered mature when vitellogenic (yellow) ovarian follicles and/or egg capsules were present (Chen *et al.*, 1997; Oddone *et al.*, 2005). Individual male skates with sperm in their seminal vesicles and calcified, rigid claspers were considered mature (Sosebee, 2005). All data analyses were performed using the freeware software PAST (Hammer *et al.*, 2001), with significance accepted at $P < 0.05$.

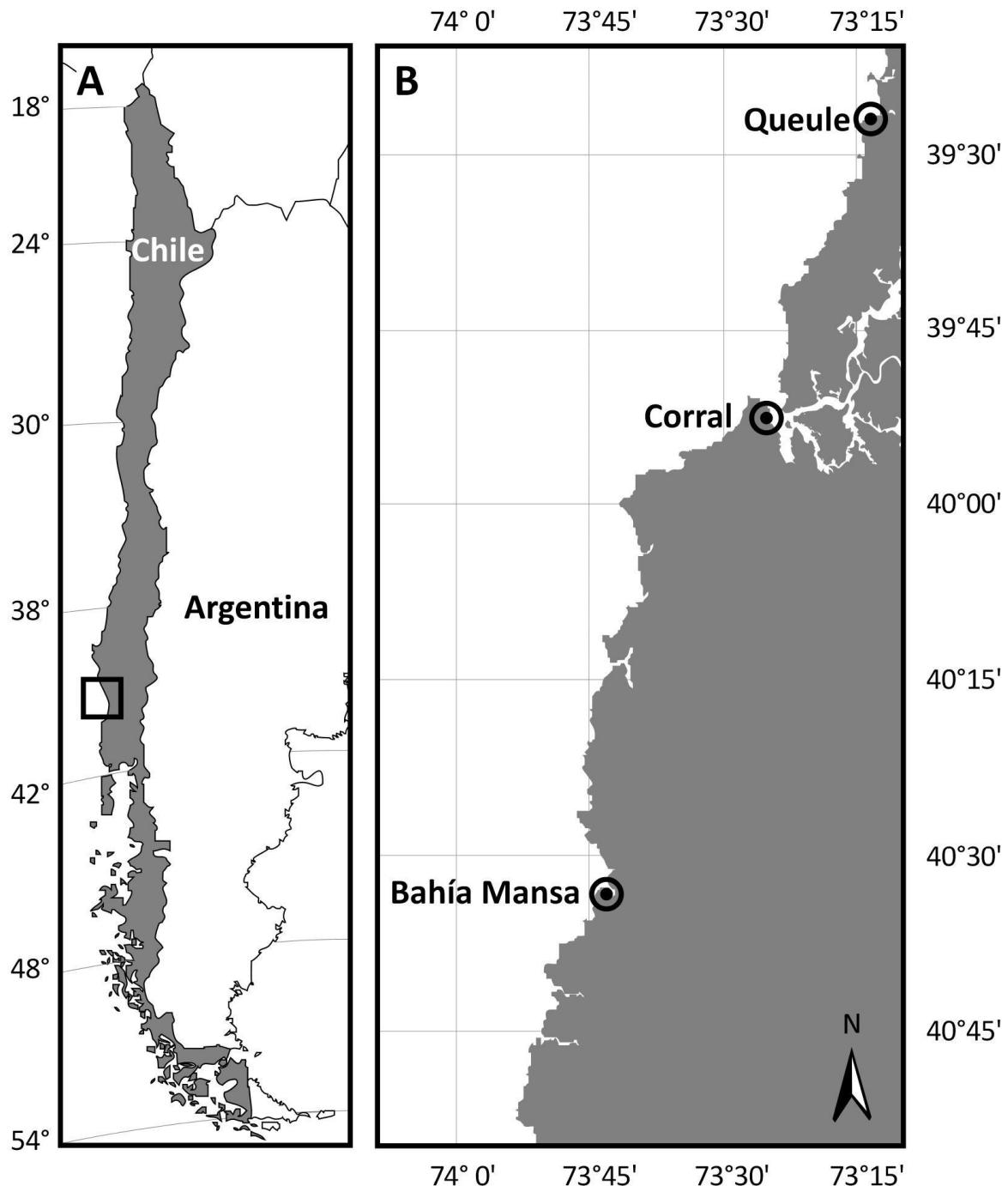


Figure 24 Map of Chile (A) showing location of study area (inset box), and three *Zearaja chilensis* landings sites (B), indicated by circles.

RESULTS

Catch composition

A total of 5477 specimens were examined (2356 females and 3121 males). The catch composition sex ratio of 1:0.75, had a significant bias towards males ($\chi^2 = 53.692$; d.f. = 1; $P > 0.001$). Body size of females caught ranged between 33 and 158 cm LT (75.4 ± 12.6 cm); males ranged between 34 and 155 cm LT (85.4 ± 7.2 cm) (Fig. 25). Length-mass relationship was influenced by sex ($MT = 1e-05 * LT^{2.9165}$ in females and $MT = 3e-05 * LT^{2.6614}$ in males), but no significant differences were observed between slopes (ANCOVA; $F = 0.293$; d.f. = 5202; $P = 0.588$) (Fig. 26a). Size-related sexual dimorphism was not obvious despite significant differences when comparing slopes between LT and LD (ANCOVA; $F = 12.14$; d.f. = 5254; $P < 0.001$; Fig. 26b) or WD (ANCOVA; $F = 4586$; d.f. = 4848; $P < 0.001$; Fig. 26c). The overall mass of skates caught was 24.6 tonnes with an average of $4530 \text{ g} \pm 3625 \text{ g}$ (mean \pm s.d.). Minimum and maximum skate mass was 800 g and 3800 g, respectively.

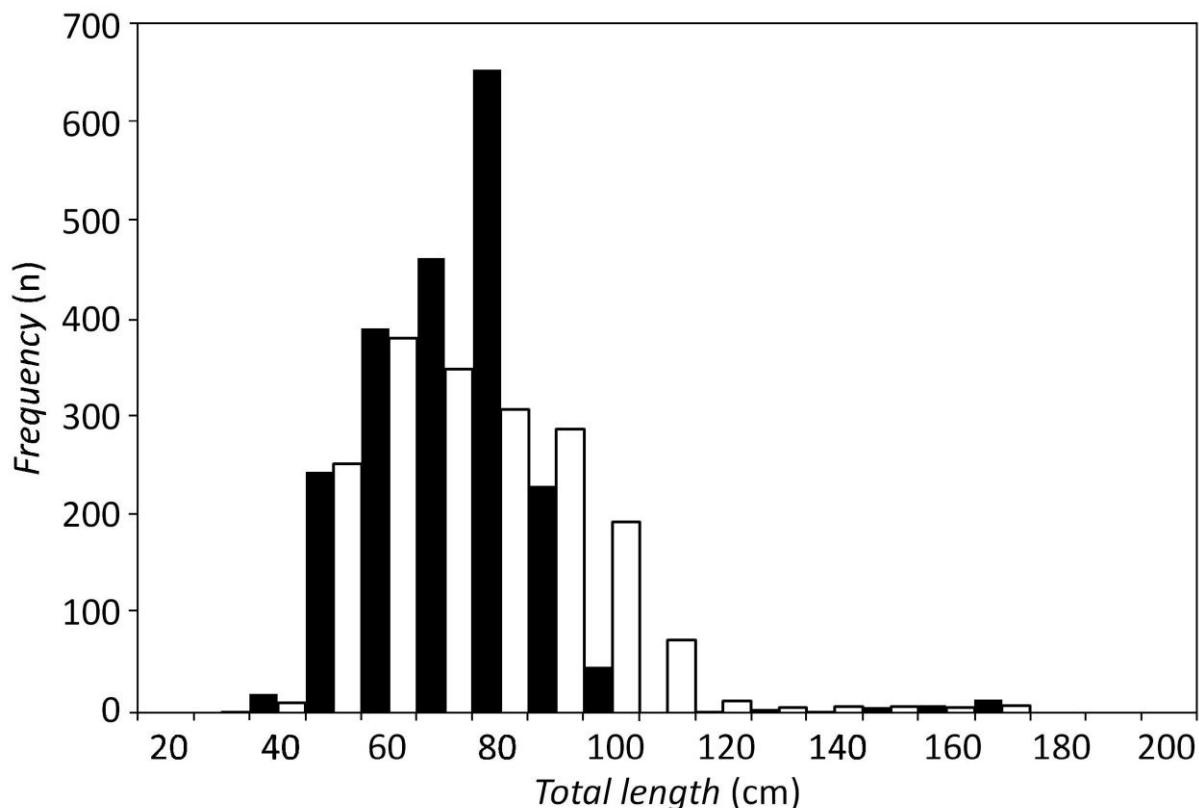


Figure 25 Length absolute frequency distribution of *Zearaja chilensis* (n=5,477). Black bars represent males (n=3,121) and white bars represent females (n=2,356).

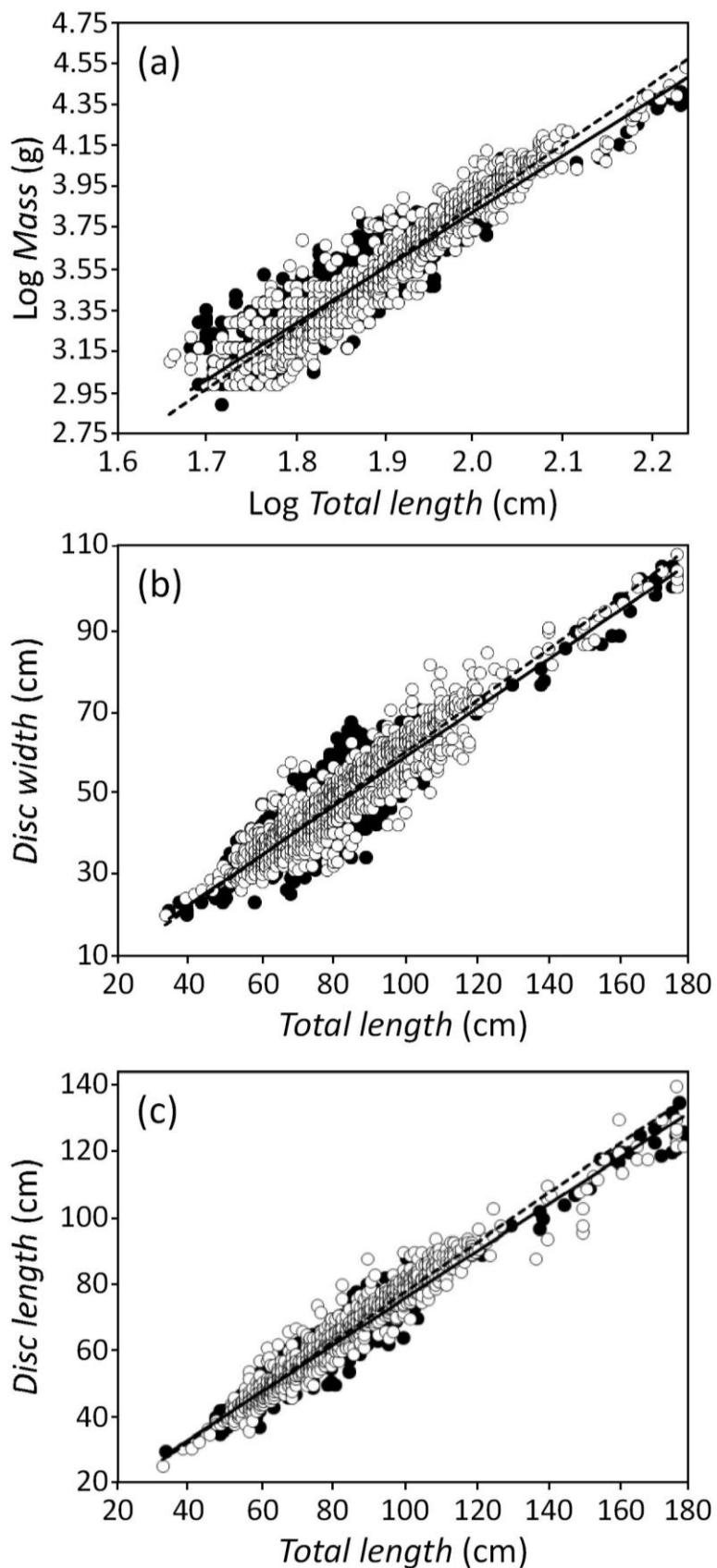


Figure 26 Relationships between total length and body mass (a), disc width (b) and disc length (c) of male (\bullet) and female (\circ) *Zearaja chilensis*. Circles represent observed values and linear models are presented for males (solid line) and females (dashed line).

Liver measurements

The mean *HSI* was 5.135 ± 1.443 for males, and 5.157 ± 1.254 for females, with no significant differences observed between months ($F_{4,244} = 10.17; P = 0.031$) for either sex (Fig. 27). Significant differences were observed between *HSI* of mature and immature males ($t = -3.524$; d.f. = 2802; $P < 0.001$) and between mature and immature females ($t = -3.939$; d.f. = 2064; $P < 0.001$); with relatively heavier livers present in mature specimens. There was no significant difference between overall mature male and female *HSI* ($t = 1.916$; d.f. = 4074; $P = 0.056$).

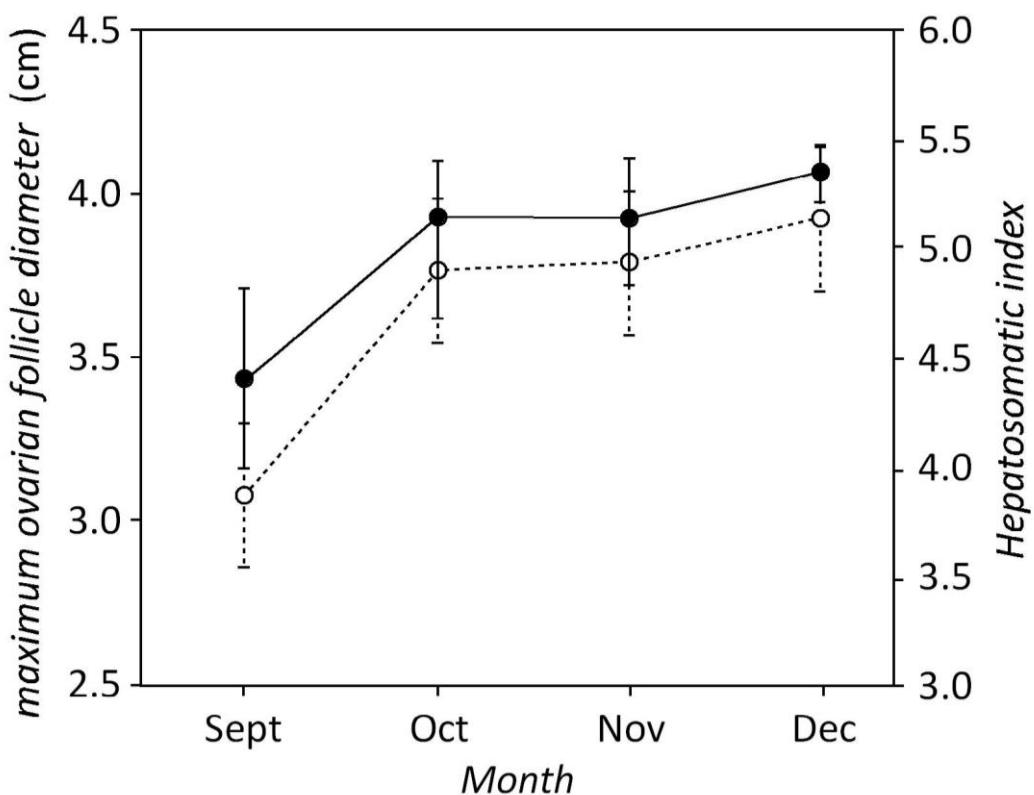


Figure 27 Monthly variation of maximum ovarian follicle diameter (●) and hepatosomatic index (○) of *Zearaja chilensis*. Circles indicate observed values along with standard deviation.

Female reproductive biology

Asymmetry of the reproductive tract was not observed in mature skates, with no significant differences between the mass of the left (127.08 ± 52.22 g) and right (130.57 ± 48.03 g) ovaries ($t = 0.588$; d.f. = 2084; $P = 0.319$). Similarly, there were no significant differences between left (43.57 ± 38.65 g) and right (44.44 ± 40.24 g) oviducal gland mass ($t = 0.187$; d.f. = 2132; $P = 0.968$). However, significant differences were detected in ovarian follicle counts between left (142.91 ± 48.73) and right (163.26 ± 62.39) ovaries ($t = 3.145$; d.f. = 2368; $P < 0.001$). Ovarian follicles were $0.3 - 4.1$ cm in diameter, and $0.04 - 19.21$ g in mass. No significant differences ($t = 1.730$; d.f. = 2110; $P = 0.086$) were observed between maximum diameters of ovarian follicles in left (3.38 ± 0.35 cm) and right (3.50 ± 0.43 cm) ovaries. The minimum size at first maturity occurred at about 95 cm *LT* based on ovary and oviducal gland mass (Fig. 28a, b). Substantial variations in ovarian follicle mass were observed for follicles of the same diameter as result of differences in yolk consistency (Fig. 28c). Mean maximum ovarian follicle diameter ranged from 3.45 ± 0.24 cm in September to 4.1 ± 0.43 cm in December, although no significant differences were observed between months (ANOVA; $F_{3,273} = 4.0$; $P = 0.132$) (Fig. 4a). The size at which 50% of the skates were mature (LT_{50}) was 109 cm *LT* (Fig. 28d), and mature females represented only 8% of the female skate catch at this size.

Male reproductive biology

Clasper length varied markedly between mature specimens with the smallest mature male recorded at 62 cm *LT* whereas some individuals were immature at about 95 cm *LT* (Fig. 29a). No significant differences were found between left (11.2 ± 5.6 g, range = $0.08 - 26.5$ g) and right (11.4 ± 4.8 g, range = $0.09 - 27.57$ g) testis mass ($t = 0.245$; d.f. = 2214; $P = 0.748$). No significant differences were found between left (38.8 ± 14.2 g, range = $2.39 - 82.44$ g) and right (38.7 ± 10.4 g, range = $1.83 - 81.28$ g) epigonal organ mass ($t = 0.075$; d.f. = 2214; $P = 0.874$). Based on the calculated LT_{50} of 88 cm *LT* for males (Fig. 29b), 13.6% of male skates in the catch were mature.

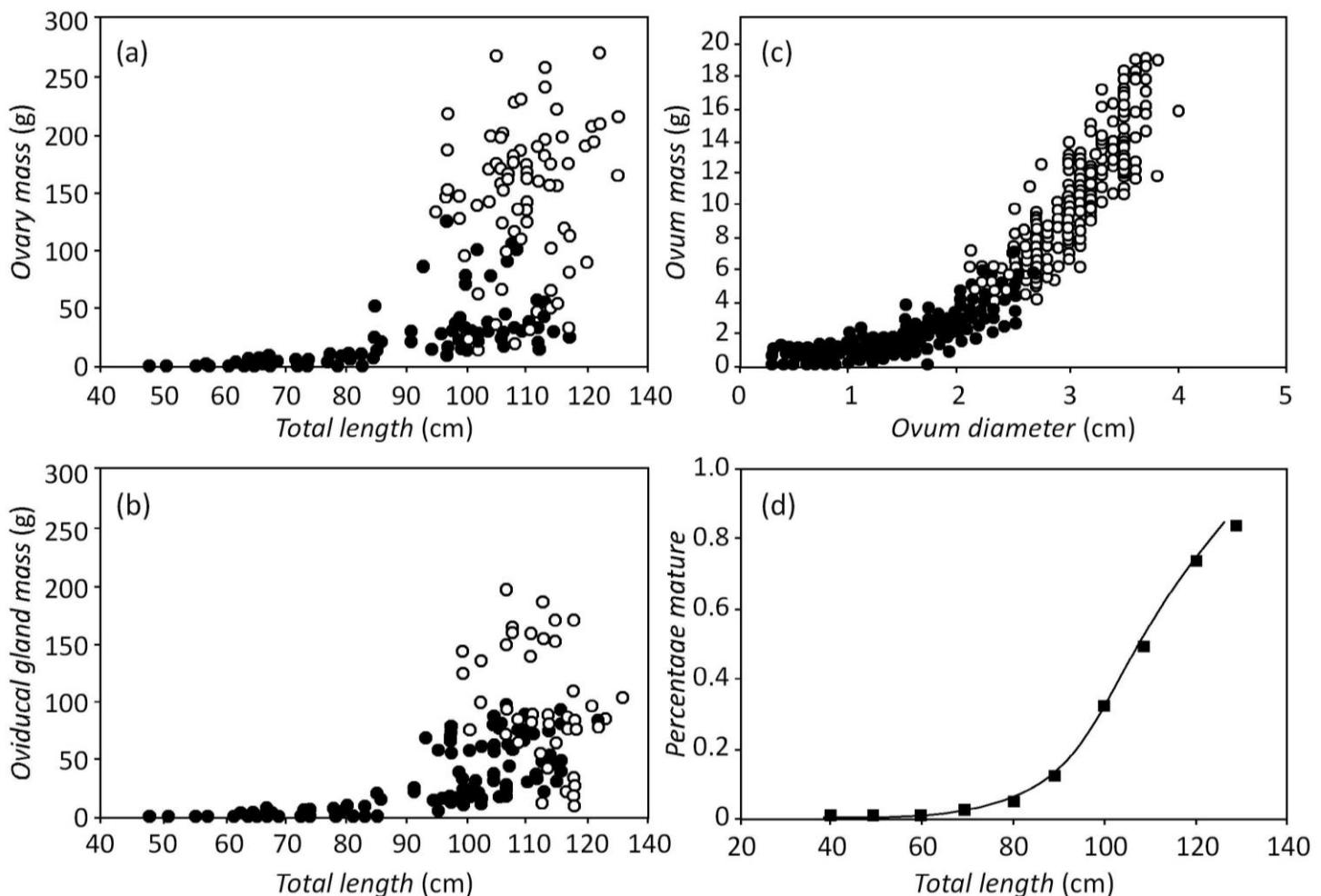


Figure 28 Relationships between total length and ovary mass (a) and oviducal gland mass (b); ovum diameter and ovum mass (c) and logistic model (line) fitted for the relationship between total length and percentage of mature (d) female *Zearaja chilensis*. Immature (●) and mature (○) specimens are represented by circles; squares indicate the observed percentage of mature individual in each size interval.

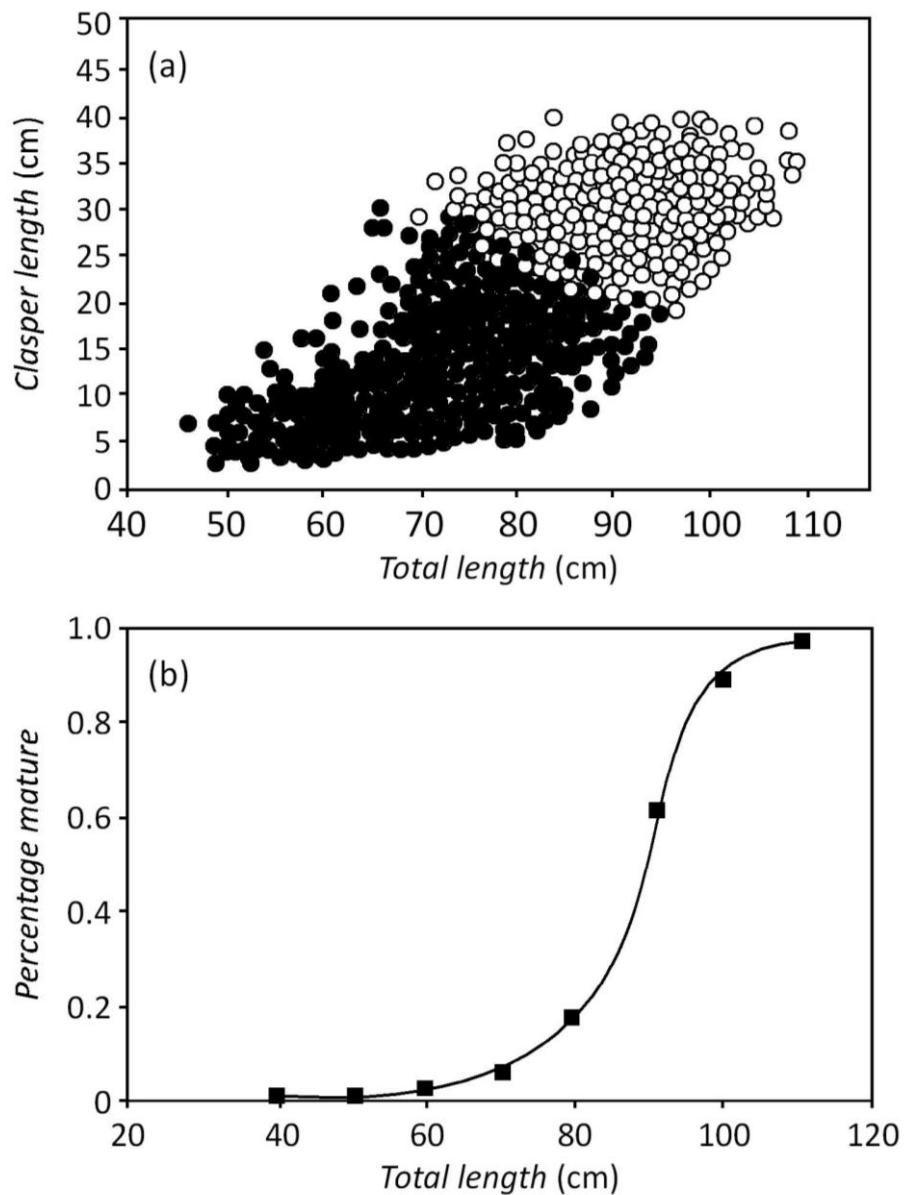


Figure 29 Relationships between total length and clasper length (a) and logistic model (line) fitted for the relationship between total length and percentage of mature (b) male of *Zearaja chilensis*. Immature (●) and mature (○) specimens are represented by circles; squares indicate the observed percentage of mature individual in each size interval.

DISCUSSION

The sex ratio in *Zearaja chilensis* was biased towards males, which suggests some sexual segregation in the study area although the reason for this is not known. Differences in sexual composition may be a consequence of behaviour, and many deep-sea skates are known to segregate by sex, size, and maturity (Ebert *et al.*, 2008).

In elasmobranch fishes, size is commonly regarded as a major secondary sexual characteristic, with females often larger and heavier than males (Cortés, 2000). This characteristic seems to be common in rajoid species (Lamilla *et al.*, 1984; Smith & Merriner, 1986; Martin & Cailliet, 1988), but while the size frequency distribution in the current study indicated that skates over 100 cm TL were predominantly female, in absolute terms it appeared that males and females attained similar maximum sizes. There may be a selective advantage for female *Z. chilensis* to grow to a larger size than males (Licandeo *et al.*, 2006) in order to accommodate relatively large ova (that mature at about 41 mm in diameter) and the associated reproductive tract. A large body size would in itself provide a large energy reserve to draw upon for egg production and may also influence the diet, by allowing larger and possibly different species of prey to be taken as seen in other skate species (Brickle *et al.*, 2003; Kyne *et al.*, 2008). However, in some species, such as the ovoviparous apron ray *Discopyge tschudii* Heckel, 1846, the length-mass relationship and body size (measured as disc width) indicates that males grow larger than females (García, 1984; Pequeño *et al.*, 1988). A similar situation has also been reported for *Bathyraja interrupta*, *B. minispinosa* and *B. parmifera* (Ebert, 2005), as well as for *Leucoraja wallacei*, *Raja straeleni*, *R. barnardi* and *R. leopardus* (Ebert *et al.*, 2008). Pequeño *et al.* (1988), argued that this could be an adaptation to activities such as mating or swimming behaviour in those species that undergo significant migrations. It is also common to find that size-at-maturity varies according to sex, with males commonly reaching maturation at smaller sizes than the females (Wetherbee, 1996; Ellis & Shackley, 1997; Girard & Du Buit, 1999). In *Z. chilensis*, males matured at about 80% of the size of maturity of females but Mabragaña *et al.* (2002), suggest that this dimorphism could be due to local ecological characteristics rather than to biological peculiarity.

The hepatosomatic index was significantly larger in mature skates compared to immature specimens in both sexes, which is presumably correlated with larger energy reserves in animals in which growth has slowed. Interestingly, while female elasmobranchs often have larger livers than males, due to requirements for egg and yolk development (Quiroz *et al.*, 2011), these differences are not reflected in our findings. Unlike mature males, the liver of mature females produces vitellogenin, the precursor protein molecule of vitellogenic material during the oocyte maturation.

But according *HSI*, there are not significant differences between both mature males and females despite that females needs to store great amounts of lipids in their livers during previtellogenesis and gestation phases. This is consistent to mature females of the Aleutian skate *Bathyraja aleutica* (Gilbert, 1896) reported by Ebert (2005). Mabragaña *et al.* (2002) and Oddone & Velasco (2006), described similar observations in the smallnose fanskate *Sypterygia bonapartii* Müller & Henle, 1841; and the eyespot skate *Atlantoraja cyclophora* (Regan 1903), respectively, from the southwest Atlantic.

While many elasmobranchs have a single functional ovary (Dodd *et al.* 1983; Hamlett & Koob, 1999; Musick & Ellis, 2005) ovarian symmetry, as observed in *Z. chilensis* is common in all skates (Oddone *et al.* 2007). The symmetry of paired structures extended to other part of the reproductive system, which is also consistent with previous studies on skates that have shown no difference between oocyte number and oviducal gland width (Mabragaña *et al.* 2002; Ebert 2005; Ebert *et al.* 2008). However, while male maturity occurred at about 88 cm *LT* the relationship between clasper length and *LT* during the maturation phase suggested that there was an unusually high degree of plasticity in the size at maturity compared to other skates (e.g. Ebert, 2005).

Despite relatively large geographical differences between sampling locations, the results from the present study provide similar estimates of sexual maturity to those made previously in the south-western Pacific (Licandeo *et al.*, 2006) and the south-western Atlantic Oceans (Oddone *et al.*, 2005; Paesch & Oddone, 2008); suggesting that size-at-maturity is a conservative trait in this species as compensatory dynamic over latitudinal gradients in the entire fishery and occurrences zones (Frisk, 2010).

Large size batoids appear to be longer-lived, slower growing, and have lower reproductive output among the elasmobranchs which makes them highly susceptible to over-exploitation (Dulvy *et al.*, 2000). Besides, fisheries may change abundance and distribution of skates as most of these fisheries are biased toward larger individuals (Jennings *et al.*, 1999; Frisk, 2010). Indeed, there is a negative correlation between skate body size and population trend (Walker & Hislop, 1998; Dulvy *et al.*, 2000) and *Z. chilensis* is no exception. According to Licandeo *et al.* (2006), the main targets of the skate fishery in Chile are immature skates. Our results indicate that 106 cm *LT* females (\approx 14 years old) and 86 cm *LT* males (\approx 11 years old) represent 85% of total catch and, if we consider that small skates ($<$ 35 cm *LT*) are discarded, there is evidence of a fishery highly biased towards mid-sized skates that may comprise the stock integrity.

Reproductive seasonality could not be determined given the scarcity of gravid females and the limited number of months sampled by this fishery. However, the monthly mean maximum

ovarian follicle diameter and *HSI* did not differ significantly across the four month study period which is consistent with the suggestion that deep-water skate species may not exhibit a defined reproductive or egg-laying season (Braccini & Chiaramonte, 2002; Mabragaña *et al.*, 2002; Ruocco *et al.*, 2006; Ebert *et al.*, 2008). It should be noted though, that the data in the current study would also be consistent with a defined reproductive season that coincided with the sampling period and further studies of this species across all months of the year are necessary to resolve the issue. Fishing records of *Z. chilensis* in the southern Falkland Islands demonstrated that an intense fishing operation culminated in a drastic stock collapse (Agnew, 2000). Our results indicate that 89% of the females captured were below size-at-maturity, which may pose a serious threat to their population.

The size structure of the *Z. chilensis* catch in the Valdivia fishing zone (39.4° S to 40.5° S) differs considerably when compared to the reported catch from fishing grounds to the south; around Chiloé Island (41.5° S to 43.5° S), Moraleda Channel (43.8° S to 45.9° S) and Castro-Magallanes Channel (51.0° S to 54.0° S) (Quiroz *et al.*, 2009). In the case of females, mature individuals comprised only 8–10% of the catch in the northern fishing grounds (Valdivia, Chiloé Island and Moraleda Channel), but closer to 50% in the most southerly fishing grounds (Fig. 30a). This pattern is repeated for males, with mature individuals comprising about 75% of the catch in the Castro-Magallanes Channel zone compared with about 14% in the Valdivia zone (Fig. 30b). Evidence of an increasing median length (length of 50% of the catch) with respect to latitude can be observed in both sexes even though the same fishing gear is used in all zones. The reason for these differences in catch size structure may be the result of fishing effort moving south as the southernmost fishing grounds have been developed relatively recently compared to the Valdivia zone (Quiroz *et al.*, 2011). If the southern fishery catch composition represents a relatively natural situation, then the catch size-structure in the northern fisheries suggests that they are at particular risk of collapse if the tonnage landed is maintained, as mature skate numbers appear to have been fished down. Growth rates and recruitment needs to be evaluated in each fishery zone for a better understanding of the population ecology and dynamics of *Z. chilensis* in south Chile. If the intrinsic vulnerability and long-life spans of *Z. chilensis* are considered, the implication for survival and the signs for an imminent fishery collapse need to be reviewed by management authorities before local extirpation occurs, which have been documented for other species of skates by Dulvy & Forrest (2010).

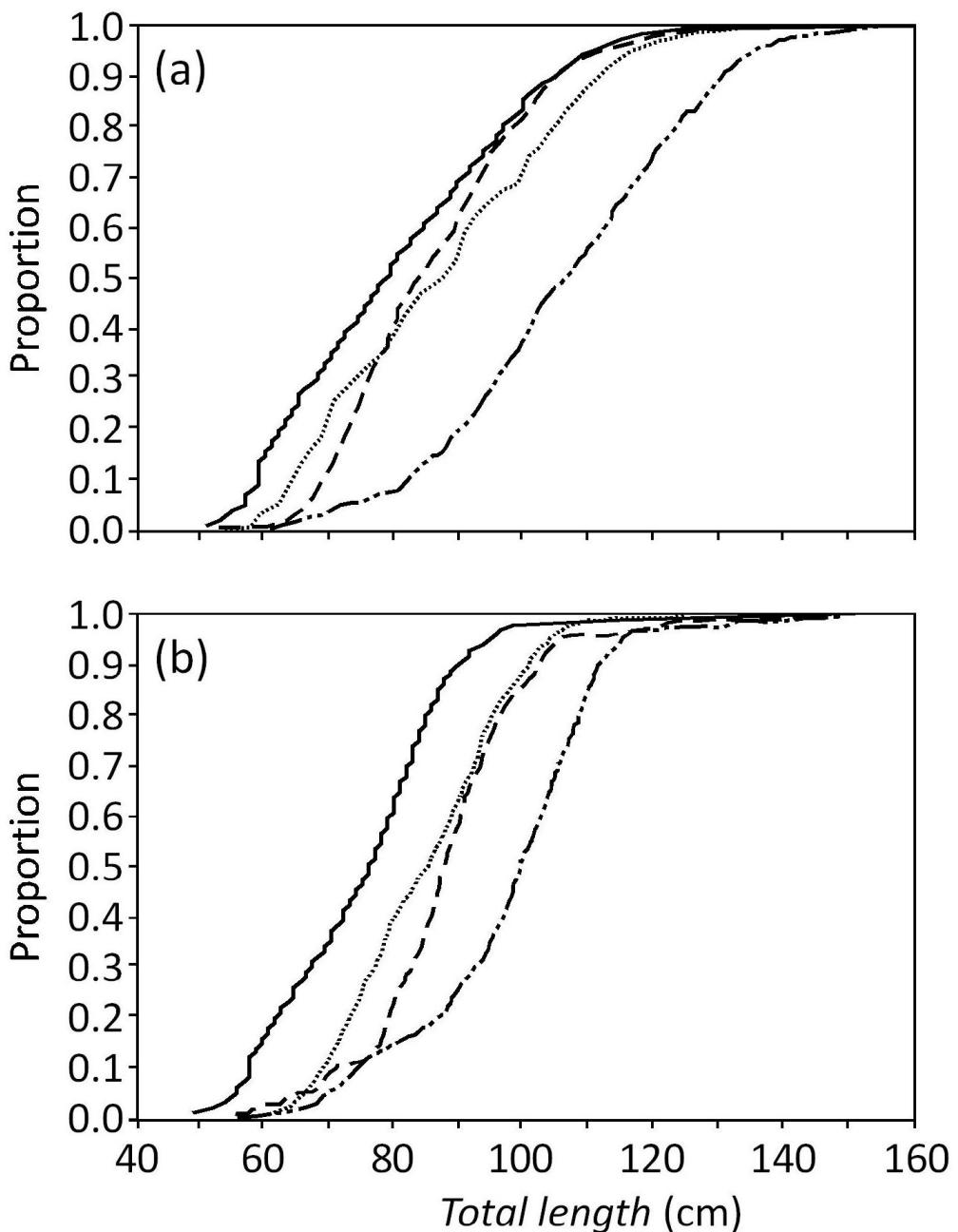


Figure 30 Accumulated size frequencies of *Zearaja chilensis* females (a) and males (b) by fishing grounds (Modified from Quiroz *et al.*, 2009). Valdivia, 39.4° S to 40.5° S (—); Chiloé Island, 41.5° S to 43.5° S (····); Moraleda Channel, 43.8° S to 45.9° S (— · —); and Castro-Magallanes Channel, 51.0° S to 54.0° S (— · ·).

REFERENCES

- Agnew, D.J., Nolan, C.P., Beddington, J.R. & Baranowski, R. (2000) Approaches to the assessment and management of multispecies skate and ray fisheries using the Falkland Islands fishery as an example. *Canadian Journal of Fisheries and Aquatic Sciences* 57, 429–440.
- Bahamonde, F., Ojeda. G., Leiva, B., Muñoz, L., Rojas, M., Donoso, M., Céspedes, R. & Gili, R. (1996) Pesca exploratoria de raya volantín en la zona sur-austral. *Instituto de Fomento Pesquero Informe técnico* No. 94–11. IFOP: Valparaíso, Chile.
- Braccini, J.M. & Chiaramonte, G.E. (2002) Reproductive biology of *Psammobatis extenta*. *Journal of Fish Biology* 61, 272–288.
- Brander, K. (1981) Disappearance of common Skate *Raia batis* from Irish Sea. *Nature* 290, 48–49.
- Brickle, P., Laptikhovsky, V., Pompert, J. & Bishop, A. (2003) Ontogenetic changes in the feeding habits and dietary overlap between three abundant rajid species on the Falkland Islands' shelf. *Journal of the Marine Biological Association of the United Kingdom* 83, 1119–1125.
- Capapé, C. & Quignard, J.P. (1974) Contribution à la biologie des Rajidae des côtes tunisiennes. 1. *Raja miraletus*, Linné, 1758: répartition géographique et bathymétrique, sexualité, reproduction, fécondité. *Archives de Institut Pasteur Tunis* 51, 39–60.
- Chen, C.T., Liu K.M. & Chang, Y.C. (1997) Reproductive biology of the bigeye thresher shark, *Alopias superciliosus* (Lowe, 1839) (Chondrichthyes: Alopiidae), in the northwester Pacific. *Ichthyological Research* 44, 227–235.
- Cortés, E. (2000) Life-history patterns and correlations in sharks. *Reviews in Fisheries Science* 8, 299–344.
- Dodd, J.M., Dodd, M.H.I. & Duggan, R.T. (1983) Control of reproduction in elasmobranch fishes. In *Control Process in Fish Physiology* (Rankin, J.C.; Pitcher, T.J., Duggan, R.T., eds), pp. 221–285. John Wiley & Sons: NY,
- Dulvy, N.K. & Reynolds, J.D. (2002) Predicting extinction vulnerability in skates. *Conservation Biology* 16, 440–450.
- Dulvy, N.K. & Forrest, R.E. (2010) Life histories, population dynamics, and extinction risks in Chondrichthyans. In *Sharks and Their Relatives II: Biodiversity, Adaptive Physiology and Conservation* (Carrier, J.C., Musick, J.A., Heithaus, M.R., eds), pp. 639–680. CRC Press: Boca Raton, FL.
- Dulvy, N.K., Metcalfe, J.D., Glanville, J., Pawson, M.G. & Reynolds, J.D. (2000) Fishery stability, local extinctions and shifts in community structure in skates. *Conservation Biology* 14, 283–293.

- Dulvy, N.K., Sadovy, I. & Reynolds, D. (2003) Extinctions vulnerability in marine populations. *Fish and Fisheries* 4, 25–64.
- Ebert, D.A. (2005) Reproductive biology of skates, *Bathyraja* (Ishiyama), along the eastern Bering Sea continental slope. *Journal of Fish Biology* 66, 618–649.
- Ebert, D.A., Compagno, L.J.V. & Cowley, P.D. (2008) Aspects of the reproductive biology of skates (Chondrichthyes: Rajiformes: Rajoidei) from southern Africa. *ICES Journal of Marine Science* 65, 81–102.
- Ellis, J.R. & Shackley, S.H. (1997) The reproductive biology of *Scyliorhinus canicula* in the Bristol Channel, U. K. *Journal of Fish Biology* 51, 361–372.
- Frisk, M.G. (2010) Life History Strategies of Batoids. In *Sharks and Their Relatives II: Biodiversity, Adaptive Physiology and Conservation* (Carrier, J. C., Musick, J. A. & Heithaus, M. R., eds), pp. 283–318. CRC Press: Boca Raton, FL.
- Frisk, M.G., Miller, T.J. & Forgarty, M.J. (2001) Estimation and analysis of biological parameters in elasmobranch fishes: a comparative life history study. *Canadian Journal of Fisheries and Aquatic Sciences* 58, 969–981.
- Frisk, M.G., Miller, T.J. & Forgarty, M. J., (2002) The population dynamics of little skate *Leucoraja erinacea*, winter skate *Leucoraja ocellata*, and barndoor skate *Dipturus laevis*: predicting exploitation limits using matrix analyses. *ICES Journal of Marine Science* 59, 576–586.
- Fuentealba, M., Leible, M. & Morillas, J. (1990) Histología gonádica de *Raja* (*Dipturus*) *flavirostris* Philippi 1892 (Pisces: Chondrichthyes). *Estudios Oceanológicos* 9, 57–62.
- Gálvez, M., Sepúlveda, A., Díaz, C., Miranda, L., Rebolledo, H. & Cuevas, C. (1998) Biomasa estacional de merluza común por área barrida por la flota industrial pesquera en la zona centro-sur. *Instituto de Investigación Pesquera VIII Región Informe técnico* No. 96–33. INPESCA: Concepción. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 September 2011).
- García, M.L. (1984) Sobre la biología de *Discopyge tschudii* (Chondrichthyes, Narcinidae). *Physis (Buenos Aires)* 103, 101–112.
- Girard, M. & Du Buit, M.H. (1999) Reproductive biology of two deep-water sharks from the British Isles, *Centroscymnus coelolepis* and *Centrophorus squamosus* (Chondrichthyes: Squalidae). *Journal of the Marine Association of the United Kingdom* 79, 923–931.
- Hamlett, W.C. & Koob, T.J. (1999) Female reproductive system. In *Sharks, skates and rays: the biology of elasmobranch fishes* (Hamlett, W.C., ed), pp. 398–443. Johns Hopkins University Press: Baltimore, MD.

- Hammer, Ø., Harper, D.A.T. & Ryan, P.D. (2001) PAST: Paleontological Statistics Software Package for Education and Data Analysis. *Palaeontology Electronica* 4, 1–9.
- Holden, M.J. (1977) Elasmobranchs. In *Fish Population Dynamics* (Gulland, J.A., ed), pp. 187–216. John Wiley Press: London.
- Hubbs, C.N. & Ishiyama, R. (1968) Methods for the taxonomic study and description of skates (Rajidae). *Copeia* 3, 483–491.
- Iglésias, S., Toulhoat, L. & Sellos, D.Y. (2009) Taxonomic confusion and market mislabelling of threatened skates: important consequences for their conservation status. *Aquatic Conservation: Marine and Freshwater Ecosystems* 20, 319–333.
- Jennings, S., Greenstreet, S.P.R. & Reynolds, J.D. (1999) Structural change in an exploited fish community: a consequence of differential fishing effects on species with contrasting life histories. *Journal of Animal Ecology* 68, 617–627.
- Kyne, P.M., Courtney, A.J. & Bennett, M.B. (2008) Aspects of the reproduction and diet of the Australian endemic skate *Dipturus polyommata* (Ogilby) (Elasmobranchii: Rajidae), by-catch of a commercial prawn trawl fishery. *Journal of Fish Biology* 72, 61–77.
- Lamilla, J., Pequeño, G. & Figueroa, H. (1984) Aspectos biológicos de *Psammobatis lima*, Poeppig, 1835, en el litoral de Valdivia, Chile (Elasmobranchii, Rajidae). *Revista de la Comisión Permanente del Pacífico Sur* 14, 183–209.
- Lamilla, J., Acuña, E., Araya, M., Oliva, M., Kong, I., Villaroel, J.C., Hernández, S., Concha, F., Vögler, R., Bustamante, C. & Mutche, E. (2005) Lineamientos básicos para desarrollar el Plan de Acción Nacional de Tiburones. *Universidad Austral de Chile Informe técnico No. 2004–18*, Valdivia. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 September 2011).
- Last P.R., White, W.T., Pogonoski, J. & Gledhill, D.C. (2008) New Australian skates (Batoidea: Rajoidae): background and methodology. In *Descriptions of new Australian skates (Batoidea: Rajoidae)* (Last, P.R., White, W.T., Pogonoski, J., Gledhill, D.C., eds), pp. 1–8. CSIRO Marine and Atmospheric Research: Hobart, Australia.
- Licandeo, R.R., Lamilla, J.G., Rubilar, P.G. & Vega, R.M. (2006) Age, growth, and sexual maturity of the yellownose skate *Dipturus chilensis* in the south-eastern Pacific. *Journal of Fish Biology* 68, 488–506.
- Mabragaña, E., Lucifora, L.O. & Massa, A.M. (2002) The reproductive ecology and abundance of *Sympterygia bonapartii* endemic to the south-west Atlantic. *Journal of Fish Biology* 60, 951–967.
- Martin, L.K. & Cailliet, G.M. (1988) Aspects of the reproduction of the Bat Ray, *Myliobatis californica*, in Central California. *Copeia* 3, 754–762.

- Massa, A.M. & Hozbor, N.M. (2003) Peces cartilaginosos de la plataforma argentina: explotación, situación y necesidades para un manejo pesquero adecuado. *Revista del Frente Marítimo* 19, 199–206.
- Menni, R. & López, H. (1984) Distributional patterns of Argentine marine fishes. *Physis (Buenos Aires)* 42, 71–85.
- Mollet, H.F., Cliff, G., Pratt, H.L. Jr. & Stevens, J.D. (2000) Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. *Fishery Bulletin* 98, 299–318.
- Musick, J.A. & Ellis, J.K. (2005) Reproductive evolution of Chondrichthyans. In *Reproductive biology and phylogeny of Chondrichthyes: sharks, batoids, and chimaeras* (Hamlett, W.C., ed), pp. 45–79. Science Publishers: Plymouth, UK.
- Oddone, M.C. & Velasco, G. (2006) Relationship between liver weight, body size and reproductive activity in *Atlantoraja cyclophora* (Elasmobranchii: Rajidae: Arhynchobatinae) in oceanic waters off Rio Grande do Sul, Brazil. *Neotropical Biology and Conservation* 1, 12–16.
- Oddone, M.C., Amorim, A.F., Mancini, P.L., Norbis, W. & Velasco, G. (2007) The reproductive biology of *Rioraja agassizi* (Müller and Henle, 1841) (Chondrichthyes: Rajidae) in southeastern Brazil, SE Atlantic Ocean. *Scientia Marina* 71, 593–604.
- Oddone, M.C., Paesch, L. & Norbis, W. (2005) Size at first sexual maturity of two species of rajoid skates, genera *Atlantoraja* and *Dipturus* (Pisces, Elasmobranchii, Rajidae), from the southwestern Atlantic Ocean. *Journal of Applied Ichthyology* 21, 70–72.
- Paesch, L. & Oddone, M.C. (2008) Change in size-at-maturity of the yellownose skate *Dipturus chilensis* (Guichenot, 1848) (Elasmobranchii: Rajidae) in the SW Atlantic. *Neotropical Ichthyology* 6, 223–230.
- Pequeño, G., Navarro, R. & Oporto, J. (1988) *Discopyge tschudii* Heckel 1845: Aporte a su taxonomía con hincapié en su dimorfismo sexual (Chondrichthyes, Narcinidae). *Estudios Oceanológicos* 7, 41–50.
- Quiroz, J.C., Wiff, R. & Cespedes, R. (2009) Reproduction and population aspects of the yellownose skate, *Dipturus chilensis* (Pisces, Elasmobranchii: Rajidae), from southern Chile. *Journal of Applied Ichthyology* 25, 72–77.
- Quiroz, J.C., Wiff, R., Cubillos, L.A. & Barrientos, M.A. (2011) Vulnerability to exploitation of the yellownose skate (*Dipturus chilensis*) off southern Chile. *Fisheries Research* 109, 225–233.
- Restrepo, V.R. & Watson, R.A. (1991) An approach to modelling crustacean egg-bearing fractions as function of size and season. *Canadian Journal of Fisheries and Aquatic Sciences* 48, 1431–1436.

- Roberts, C.M. & Hawkins, J.P. (1999) Extinction risk in the sea. *Trends in Ecology and Evolution* 14, 241–246.
- Ruocco, N.L., Lucifora, L.O., Diaz de Astarloa, J.M. & Wohler, O. (2006) Reproductive biology and distribution of the white-dotted skate, *Bathyraja albomaculata*, in the southwest Atlantic. *ICES Journal of Marine Science* 63, 105–116.
- SERNAP. (2007) *Anuario Estadístico de Pesca. Servicio Nacional de Pesca*. Ministerio de Economía, Fomento y Reconstrucción, Santiago.
- SERNAP. (2009) *Anuario Estadístico de Pesca. Servicio Nacional de Pesca*, Ministerio de Economía, Fomento y Reconstrucción: Santiago.
- Smith, J.W. & Merriner, J.M. (1986) Observations on the reproductive biology of the Cownose ray, *Rhynoptera bonasus*, in Chesapeake Bay. *Fishery Bulletin* 84, 871–877.
- Sokal, R.R. & Rohlf, F.J. (1987) *Introduction to Biostatistics*, 2nd edn. W.H. Freeman Press: New York.
- Sosebee, K.A. (2005) Maturity of skates in northeast United States waters. *Journal of Northwest Atlantic Fisheries Science* 35, 141–153.
- Stevens, J.D., Bonfil, R., Dulvy, N.K. & Walker, P.A. (2000) The effects of fishing on shark, rays, and chimaeras (Chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Sciences* 57, 476–494.
- Walker, P.A. & Hislop, J.R.G. (1998) Sensitive skates or resilient rays? Spatial and temporal shifts in ray species composition in the central and north-western North Sea between 1930 and the present day. *ICES Journal of Marine Science* 55, 392–402.
- Wetherbee, B.M. (1996) Distribution and reproduction of the southern lantern shark from New Zealand. *Journal of Fish Biology* 49, 1186–1196.

4.2. Insights into the reproductive biology and fisheries of two commercially exploited species, shortfin mako (*Isurus oxyrinchus*) and blue shark (*Prionace glauca*), in the south-east Pacific Ocean

Originally published in Fisheries Research (ISSN: 0165-7836)

Copyright © Carlos Bustamante 2013

Published online: 15 March 2013

License Number: 3303481310532

Abstract

In 2005 and 2010, 1241 *Isurus oxyrinchus* and 1153 *Prionace glauca* were collected from 178 longline sets in a ship-board observer programme in coastal waters off Caldera, Chile (27° S). Catch composition was significantly biased towards *I. oxyrinchus* in 2005, but both species were caught in the same proportion in 2010. The sex ratio for *I. oxyrinchus* and for *P. glauca* did not differ significantly from unity within or between years. Sharks matured (L_{50}) at a total length of 190.3 cm for male and 199.2 cm for female for *P. glauca*, and 180.2 cm for male *I. oxyrinchus*. Size-at-maturity for female *I. oxyrinchus* was not determined due to the near absence of mature specimens examined. Generalised additive models (GAMs) were used to examine catch per unit effort (CPUE) in relation to sea surface temperature, wind speed, time of day, hook depth and soak time. The GAMs revealed a significant effect of depth on *P. glauca* CPUE, and depth and wind speed for *I. oxyrinchus* CPUE. The predominance of small, immature sharks caught in the coastal, artisanal fishery indicates that both species may use the area as a pupping, and possibly a nursery zone during spring and summer. National data on catch composition and annual landings provide evidence of an increasing trend to land *P. glauca*, possibly to satisfy the international shark fin trade. Conservation measures, such as the introduction of a minimum capture size for sharks to protect the recruitment into the population, conservative fishing quotas and delimitation of fishing areas are necessary to ensure the sustainability of both species in the region.

INTRODUCTION

There is global concern about the impact of depletion and possible loss of apex predator fishes in marine ecosystems (Dulvy *et al.*, 2003; Myers *et al.*, 2007; Ferretti *et al.*, 2010). This concern is of particular relevance in relation to sharks as their biological characteristics make them particularly vulnerable to over-exploitation (Stevens *et al.*, 2000; Cailliet *et al.*, 2005). Downward trends in pelagic shark catches have been documented in many oceanic fisheries, for example, in the north-east Atlantic (Pawson & Vince, 1999; Baum *et al.*, 2003; Dulvy *et al.*, 2008), off southern Africa (Petersen *et al.*, 2009), Japan (Nakano, 1999) and in the Mediterranean Sea (Ferretti *et al.*, 2008). The shortfin mako shark, *Isurus oxyrinchus* Rafinesque 1810, is an important component of pelagic shark community, ranging through most tropical and temperate oceans of the world (Compagno *et al.*, 2005). In the south-east Pacific, *I. oxyrinchus* is caught in commercial oceanic longline and gill-net fisheries that target swordfish (*Xiphias gladius* Linnaeus 1758), as well as being caught in the coastal, artisanal longline fishery that operates in northern Chile and southern Peru (Acuña *et al.*, 2001; Gilman *et al.*, 2007). The latter is the only Chilean artisanal fishery that target sharks. In addition to *I. oxyrinchus*, this fishery has a bycatch of blue shark, *Prionace glauca* (Linnaeus 1758) and to a lesser extent, porbeagle, *Lamna nasus* (Bonnaterre 1788) (Lamilla *et al.*, 2010).

In Chilean waters (and outside of the Exclusive Economic Zone) the directed shark fishery, and the associated shark bycatch, has grown substantially in recent years due primarily to a declining abundance of valuable teleost species and management restrictions placed on these teleost fisheries (Cerna & Licandeo, 2009). In contrast to the oceanic fishery, the coastal artisanal fishery has discrete operational boundaries; these are mainly related to the limited autonomy of vessels that restricts the length of trips and hence, fishing areas. This ‘subsistence fishery’, that started in 1979, is focused on the coastal zone from southern Peru (Gilman *et al.*, 2007) to 35° S in Chile where boats of 9–18 m length explore coastal temperate water-masses of about 18–21° C which are associated with a relatively large abundance of sharks (Acuña *et al.*, 2001).

While there are legal minimum sizes for pelagic sharks (which includes *I. oxyrinchus* and *P. glauca*) caught in Peruvian waters, the only regulation of shark fishing in Chilean waters is in the types of gear allowed to be used (Lamilla *et al.*, 2010), despite the fact that Chile has a National Plan of Action to promote the conservation and management of sharks. While *I. oxyrinchus* is retained by both oceanic and coastal fisheries, *P. glauca* is generally discarded after finning which has resulted in under reporting of the latter species in official landings records (Lamilla *et al.*,

2008). Commercial shark landings in the decade 1999–2009 increased four-fold for *I. oxyrinchus*, from 237 to 950 tonnes and almost sixty-fold for *P. glauca*, from 7 to 408 tonnes (SERNAP, 2009).

Isurus oxyrinchus reproduces by oophagic viviparity (Lamniform oophagy), with an average of 12 pups per litter and a 15- to 18-month gestation period (Gilmore, 1990; Snelson *et al.*, 2008). There is a large sexual difference in the size and age at maturity, with males maturing at about 195 cm total length (L_T) at 6 years of age, and females at 265–280 cm L_T at 16 years of age (Stevens, 2008; Semba *et al.*, 2009). While segregation among the developmental stages (Nakano & Nagasawa, 1996) and geographical sexual segregation (Mucientes *et al.*, 2009) have been reported, little is known about stock structure or genetic diversity (Heist *et al.*, 1996) due to the species' large, diffuse, and highly dispersive populations (Schrey & Heist, 2003).

Prionace glauca reproduces by placental viviparity, gives birth to an average of 30 pups after a 9- to 12-month gestation period (Henderson *et al.*, 2001), and females may breed every year (Stevens, 1984; Hazin *et al.*, 1994). Birth usually occurs in spring and summer, with pupping and nursery areas seemingly located in intermediate-latitude oceanic convergences with high prey availability (Nakano & Stevens, 2008). Growth is relatively rapid, with males maturing at 4–6 years and females at 5–7 years of age (Lessa *et al.*, 2004; Manning & Francis, 2005). Distinct sex and size segregation is evident, with size generally decreasing with increasing latitude (Henderson *et al.*, 2001). Blue sharks are a major bycatch of longline and gill-net oceanic fisheries, but because of poor reporting the magnitude of the catch and mortality is not reflected by official statistics (Nakano & Stevens, 2008). Additionally, recent population assessments indicate a moderate to large declining trend in both abundance and size of blue sharks in north-west Atlantic (Baum *et al.*, 2003), central Pacific (Ward & Myers, 2005) and the Mediterranean (Ferretti *et al.*, 2008). To properly manage and conserve pelagic shark species it is necessary to have adequate information on their life-histories in order to understand the ecology and susceptibility to over-exploitation (FAO, 2003; Garcia & Cochrane, 2005). Various analyses suggest that both sharks *I. oxyrinchus* and *P. glauca* may have undergone significant declines in abundance over parts of its distribution (Nakano, 1999; Pawson & Vince, 1999; Baum *et al.*, 2003; Ward & Myers, 2005; Dulvy *et al.*, 2008; Ferretti *et al.*, 2008; Cailliet *et al.*, 2009). Due to estimated and inferred declines, probable increases in fishing pressure, and considering the life history characteristics of *I. oxyrinchus*, the Indo-west Pacific and Atlantic subpopulations have recently been classified as Vulnerable on the IUCN Red List of threatened species; the north eastern Pacific subpopulation as Near Threatened; while the south Pacific population remains without conservation assessment (Cailliet *et al.*, 2009). *P. glauca* is listed as Near Threatened globally (Stevens, 2000). In the south-east Pacific, age and growth (Cerna & Licandeo, 2009) and habitat use (Abascal *et al.*, 2011) of *I. oxyrinchus*, and the

reproductive cycle of *I. oxyrinchus* and *P. glauca* (Acuña et al., 2001) have been examined, although information of the species' reproductive biology in the region is incomplete. The aims of the present study are to estimate life-history traits, including size-at-maturity, sex ratios and catch composition, as well as to describe the species' environmental preferences in Chilean waters. Annual landings and shark fin exports are discussed in relation to fishing practices and factors involved in the commercial fishery of pelagic sharks in Chile.

MATERIALS AND METHODS

Specimens of *I. oxyrinchus* and *P. glauca* were collected during on-board observer surveys in the artisanal longline fishery targeting *I. oxyrinchus* based in Caldera, Chile ($27^{\circ} 04' S$, $70^{\circ} 51' W$) in the Southern Hemisphere summer fishing season (January and February) in two different years (2005 and 2010). Sharks were collected from 78 fishing trips made by 18 vessels of 12–17 m length using 5.5 km monofilament longline gear with wire traces and M/K No. 2 hooks. Sets comprised 200–350 hooks, each suspended from surface buoy spaced every 180–200 m. Hooks were baited using fresh and/or dry-salted chub mackerel (*Scomber japonicus* Houttuyn 1782) or Chilean jack mackerel (*Trachurus murphyi* Nichols 1920). Maximum soak time was 240 min, with sharks hooked during the longline deployment removed, the hook rebaited, and the capture time recorded.

Biological data

Data recorded at the time of collection included sex, maturity and total length (L_T). Measurements were made to the nearest centimetre (cm) in a straight line with the shark lying on its ventral surface (Francis & Duffy, 2005). Left clasper post-cloacal length (L_C) was also recorded.

Three reproductive-stage classifications were determined for each sex as juvenile, adolescent and adult. Changes in the reproductive organs were used to further assess the onset of maturity (Mollet et al., 2000). Males were considered to be adult when the claspers were elongated and the terminal cartilage elements were calcified. Adolescent individuals were those whose claspers extended beyond the posterior edge of the pelvic fins, but lacked calcification of the terminal cartilage elements. Juveniles had short, flexible claspers that did not extend beyond the posterior edge of the pelvic fins. Internally, coiling of the epididymides and testes development were also indicators of maturation (Stevens, 1983). Females were determined to be mature if they

demonstrated one or more of the following characters: presence of pups in utero; large vitellogenic ova; and an oviducal gland distinctly differentiated from the uterus. Adolescent individuals had smaller ovaries, with some differentiation and no mature ova; undeveloped oviducal gland and uteri strap-like in appearance. Juveniles lacked any differentiation of the ovaries, and the oviducal gland was not differentiated from the uterus (Mollet *et al.*, 2000).

Chi-square Goodness-of-Fit (χ^2) (Sokal & Rohlf, 1987), was used to test for significant sex bias between males and females proportion of each species within each year and between the two years sampled. Binomial maturity data (immature 0, mature 1) were determined by sex using 10 cm size class intervals. Size at 50% maturity was calculated by fitting the following logistic curve (by minimization of the least squares), to the relationship between the fraction of mature males or females and L_T , as a function of

$$L_T, Y = [1 + e^{-(a + bX)}]^{-1}$$

Where Y is the fraction of mature individuals in length class X , and a and b are the model coefficients. The ratio $a:b$ represents the size at which 50% of the sharks were mature (Mollet *et al.*, 2000). In addition, the relationship between L_T and L_C were used to further assess the onset of first maturity (Restrepo & Watson, 1991). Comparisons of median L_T for males and females for each species were performed using the Mann-Whitney U test with significance accepted at $P < 0.05$.

Fishery data

Observer-monitored size and catch composition in each set and the final destination of each shark, as target species (whole-body landed), or as bycatch (incidentally caught shark, landed whole), discard (whole shark returned to the sea) or finned (removal of fins from a shark and discard of the body at sea, Hernández *et al.*, 2008). For each longline set five environmental factors were recorded: sea surface temperature (SST) (°C), wind speed (Beaufort scale), soak time (min), depth of hooks (m) and local time for each longline set deployed. Duration of each set was calculated as the length of time from when the first hook entered the water to when the last hook was retrieved. Set duration was multiplied by the number of hooks to give fishing effort in hook-hours. A total of 55,758 hooks were included in the data set. The number of sharks caught in each set was divided by the fishing effort to give the CPUE as sharks per 1000 hook hours. CPUE was log-transformed ($\log(CPUE + 1)$), in order to assess the departure of original data from normality and were calculated separately for each species. To explore the environmental parameters as predictors of the CPUE, generalised additive models (GAMs) were fitted for each species using a

Quasi-Poisson error structure and a log link function to fit the response (Hastie & Tibshirani, 1990; Bigelow *et al.*, 1999):

$$\log(\text{CPUE}+1) = b_0 + f_1(b_1 \text{SST}) + f_2(b_2 \text{Bathymetry}) + f_3(b_3 \text{Soak time}) + f_4(b_4 \text{Time-of-Day}) + f_5(b_5 \text{Wind speed})$$

Where b_i are regression coefficients and f_i is a smoothing function applied to each continuous variable. Analyses were performed using R (R Core Team, 2012), with significance accepted at $P < 0.05$.

Landings

Information on annual commercial landings for the period 1979–2008 was extracted from the Chilean landings database of the Fishery National Service (SERNAP). Data were organised by the three landing categories recognised by the fishing authority: artisanal (vessels under 18 m length), industrial vessels inside EEZ (exclusive economic zone) and industrial vessels in international waters. Also, shortfin mako and blue shark fin exports were extracted from National Customs Service (Servicio Nacional de Aduanas) Foreign Trade Statistics Database for the period 2000–2008. Intentionality of the fishery will be tested considering artisanal and industrial landing records as well on-board observed catches. Target (*I. oxyrinchus*) and bycatch (*P. glauca*) species will be contrasted with an expected 50:50 ratio, as both species shares the same food resources and habitat preferences and seasonal distribution in the region (Acuña *et al.*, 2001).

RESULTS

Catch composition

A total of 1,241 *Isurus oxyrinchus* and 1,153 *Prionace glauca* were caught and examined, and represents the total catch of sharks from 178 longline sets made in two separate years; 2005 and 2010 (Fig. 31). Catch composition (blue and shortfin mako shark proportion) had a significant bias towards shortfin mako sharks in 2005 (1:0.82; $\chi^2 = 5.634$; d.f. = 1; $P = 0.0178$) but no differences were observed in 2010 (0.95:1; $\chi^2 = 0.30$; d.f. = 1; $P = 0.584$).

In 2005, shortfin mako sharks under 80 cm L_T were discarded (dead or alive) due to market restrictions; blue sharks under 100 cm L_T were always discarded (dead or alive), while larger specimens could be retained either whole or as fins only. A 5% discard of shortfin mako over 80 cm L_T was observed during 2005, whereas there was no discard during 2010 of *I. oxyrinchus* of any

size. An increase in the proportion of blue sharks landed rose from 18% in 2005, to 44% in 2010, and there was a related fall in the proportion being finned, which decreased from 60% in 2005 to 38% in 2010. The proportion of blue sharks discarded without use was similar in both years (22% and 18%, respectively).

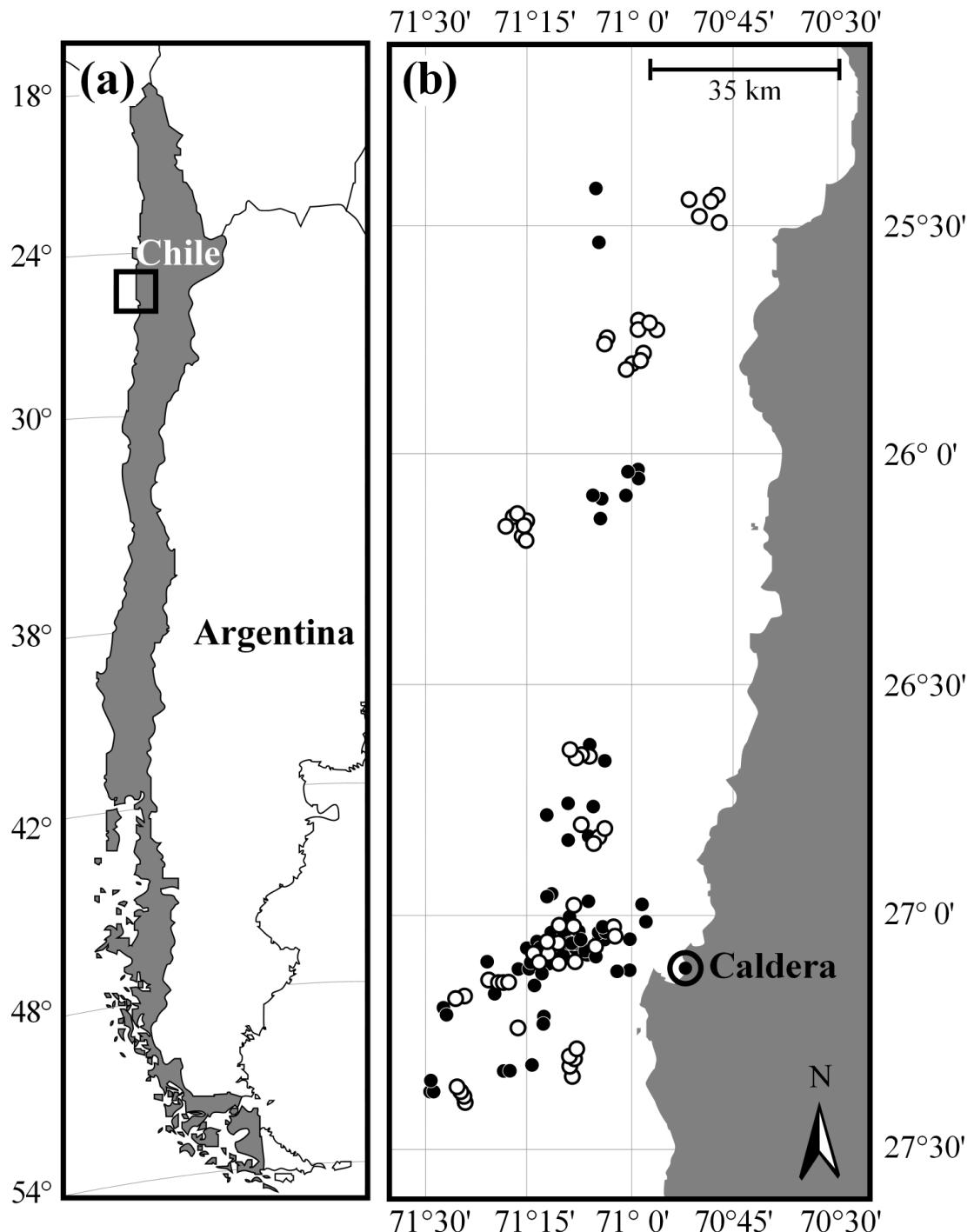


Figure 31 Map of (a) Chile showing location of study area (inset box), and (b) position of longline sets sampled in 2005 (white circles) and 2010 (black circles).

Isurus oxyrinchus

A total of 640 females and 601 male shortfin mako sharks were examined. The male to female sex ratio was similar between years (1:1.16 in 2005; 1:1.03 in 2010) and no differences were observed within years: for 2005 $\chi^2 = 1.786$; d.f. = 1; $P = 0.181$ and for 2010 $\chi^2 = 0.068$; d.f. = 1; $P = 0.794$. Body size of females caught in 2005 ranged from 76 to 213 cm L_T (mean and standard deviation, 121.9 ± 23.7 cm) while males ranged from 75.5 to 240 cm L_T (122.4 ± 25.4 cm). Body size of females in 2010 ranged from 80 to 338 cm L_T (138.7 ± 24.2 cm) and males from 66 to 267 cm L_T (136.3 ± 124.5 cm) (Fig. 32a).

No significant differences were found between median sizes by sex and year (2005: $W = 779.5$; $P = 0.741$; and 2010: $W = -2569.0$; $P = 0.220$); but significant differences were found in the size structure between years ($W = 70954$; $P < 0.0001$) as the modal size increased, but the smallest size-class (70–90 cm L_T) was largely absent in 2010. The smallest free-swimming specimen examined was a 66.1 cm L_T male and there was no sign of an umbilical scar on any specimen in the smallest size class.

For male sharks; juveniles ranged from 66 cm to 182 cm L_T , adolescents from 96 cm to 184 cm L_T and adults from 180 cm to 267 cm L_T . Coiled epididymides were present in specimens over 174 cm L_T and correlated with elongated, partially calcified claspers. There was a sigmoid relationship between clasper and total length (Fig. 33a), with clasper growth in relation to L_T most rapid in adolescent sharks. In female juvenile and adolescent sharks, the oviducal glands were indistinct from the uteri. Juvenile females ranged from 80 cm to 144 cm L_T , adolescents from 164 to 250 cm L_T . Vitellogenic, mature ova were found in a single 338 cm L_T specimen. No gravid females were observed. Using binomial maturity data, the size where 50% of *I. oxyrinchus* males were mature (L_{50}) was 180.2 cm L_T (Fig. 34a), and the equivalent L_{50} for females was not conclusive as no mature females were obtained during surveys.

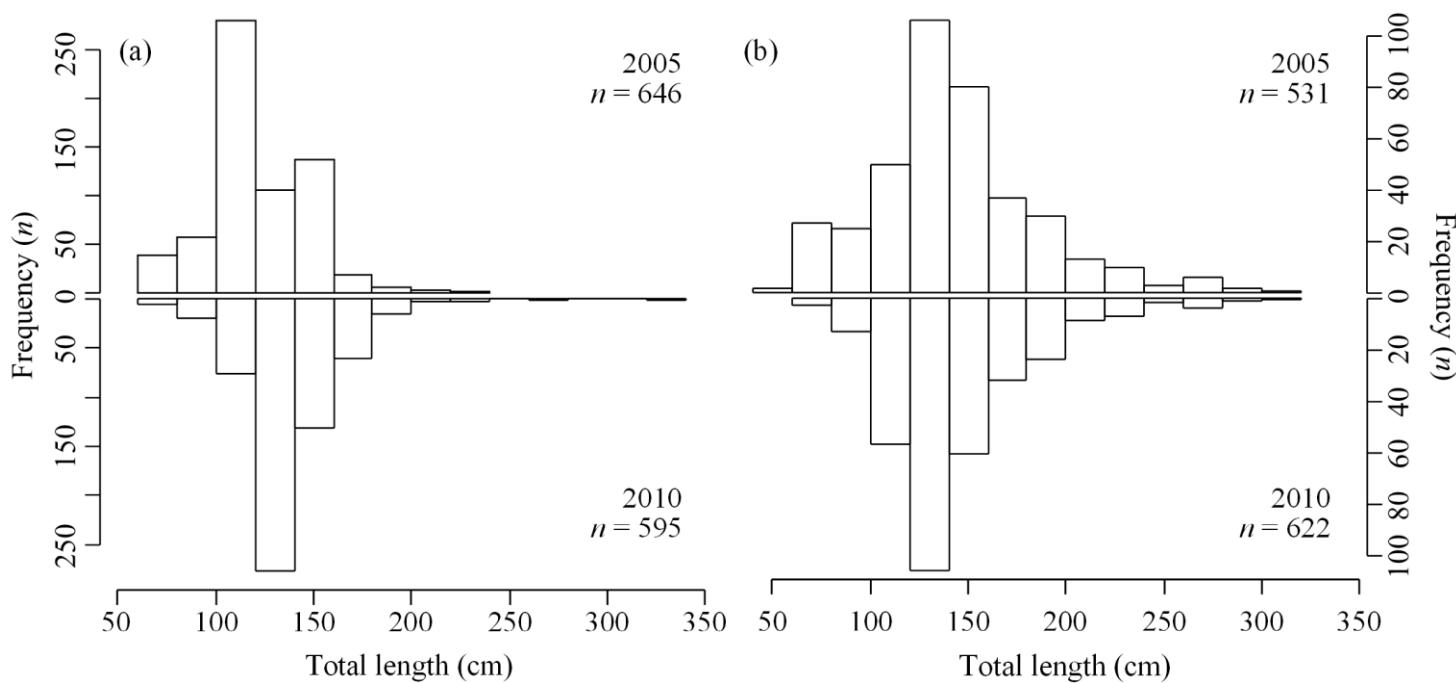


Figure 32 Length frequency distribution of *Isurus oxyrinchus* (a) and *Prionace glauca* (b) in 2005 and in 2010.

Prionace glauca

The male to female sex ratio of blue sharks, based on the examination of 1,153 individuals (576 female, 577 male), was similar between the two years of the study (1:1.12 in 2005; 1:0.94 in 2010) and no differences were observed within 2005 ($\chi^2 = 0.618$; d.f. = 1; $P = 0.431$) and 2010 ($\chi^2 = 0.348$; d.f. = 1; $P = 0.556$). In 2005, the body size ranged from 56 to 249 cm L_T (133.1 ± 35.4 cm) for females, and 52 to 310 cm L_T (152.7 ± 48.6 cm) for males (Fig. 33b). In 2010, body size ranged from 75.5 to 249 cm L_T (139.0 ± 27.5 cm) for females and males 77 to 310 cm L_T (151.3 ± 43.3 cm) for males (Fig. 33b).

Significant differences were found between median body size (L_T) by sex in both study years ($W = 3959.5$; $P < 0.05$ for 2005 and $W = 3204.0$; $P < 0.05$ for 2010), with the size range of females smaller (133 cm and 135 cm L_T in 2005 and 2010, respectively) than that of males (143 cm and 140 cm L_T) despite having similar size structure ($W = 3020$; $P = 0.398$). Juvenile male sharks ranged from 52 to 146 cm L_T , adolescent sharks from 115 cm to 219 cm L_T , and adult sharks from 181 cm to 310 cm L_T . Males over 200 cm L_T had coiled epididymides and well-developed testes, which was consistent with the observation that fully-calcified claspers were found in individuals

over 195 cm L_T (Fig. 33b). The size of juvenile female sharks ranged from 56 and 145 cm L_T ; adolescents from 110 to 180 cm L_T , and mature females from 171 to 249 cm L_T . Using binomial maturity data, the size where 50% of *P. glauca* females were mature (L_{50}) was 199.2 cm L_T (Fig. 34c). Size of 50% of maturity for males was 190.3 cm L_T (Fig. 34d). No gravid females were observed and mature ova were found in 8.4% of the mature female sharks caught.

Environmental preferences and CPUE

Values of CPUE for individual sets ranged from 0 to 230 sharks/1000 hook-hours for shortfin mako sharks and 0 to 662 sharks/1000 hook-hours for blue sharks. In total, there were 14 sets (9%) where *I. oxyrinchus* was not caught and 35 sets (23%) where *P. glauca* was not caught. For shortfin mako, the GAM indicated that there were significant interactions with significant differences in catch rate with depth ($P = 0.009$) and wind speed ($P = 0.036$), but not on the time of day, soak time or SST (Table 22, Fig. 35). For blue shark, the GAM analysis of CPUE data indicated that interaction effects were not significant with the exception of depth ($P = 0.023$). The relationship between *I. oxyrinchus* and *P. glauca* populations, catch rates and environmental variables are shown in Fig. 35.

The maximum catch rate for both shark species were made between 80–100 min of soak time, 10:00–12:00, 20.5–21.5 °C and 8–10 m depth. Wind speed and catch rate relationship is inverse in calm (0 Beaufort); with the highest catch rate for *I. oxyrinchus* and the lowest for *P. glauca*.

National landings

Shark fishing records in Chile began in 1978, when 33 tonnes of *I. oxyrinchus* were landed. Since then, only with the exception of 1981 in which 32 tonnes were landed, annual landings of *I. oxyrinchus* and *P. glauca* increased exponentially to 1991 when 1,118 tonnes were landed (Fig. 36a). After 1990, the bycatch of the industrial fleet was recorded separately to the artisanal fishery landings. Post-1990 the artisanal landings have fluctuated markedly, but with an overall downward trend. From 2000, artisanal and industrial landings have followed a similar pattern, peaking at 1,354 tonnes in 2001, followed by a dramatic decrease to 448 tonnes in 2003; and since then industrial landings have been almost twice that of the artisanal fishery.

The export of shark fin has been recorded since 2001, but the identity of the sharks involved is not known and is likely to include over ten species of cartilaginous fishes (Hernández et al.,

2008). In the period from 2001 to 2006, over 190,000 kg of dry shark fins were exported to Asian markets, but since then the average export of dry fin has decreased to 2,600 kg per annum (Fig. 36b).

Overall, the annual effect evidences a decline after the peak landing during 2000, with low landings levels in subsequent years despite increased fishing effort. Moreover, the blue shark to shortfin mako shark landing ratio has increased 30-fold in the artisanal fishery and about 15–30-fold in the industrial landings over the 1998–2009 period (Fig. 36c).

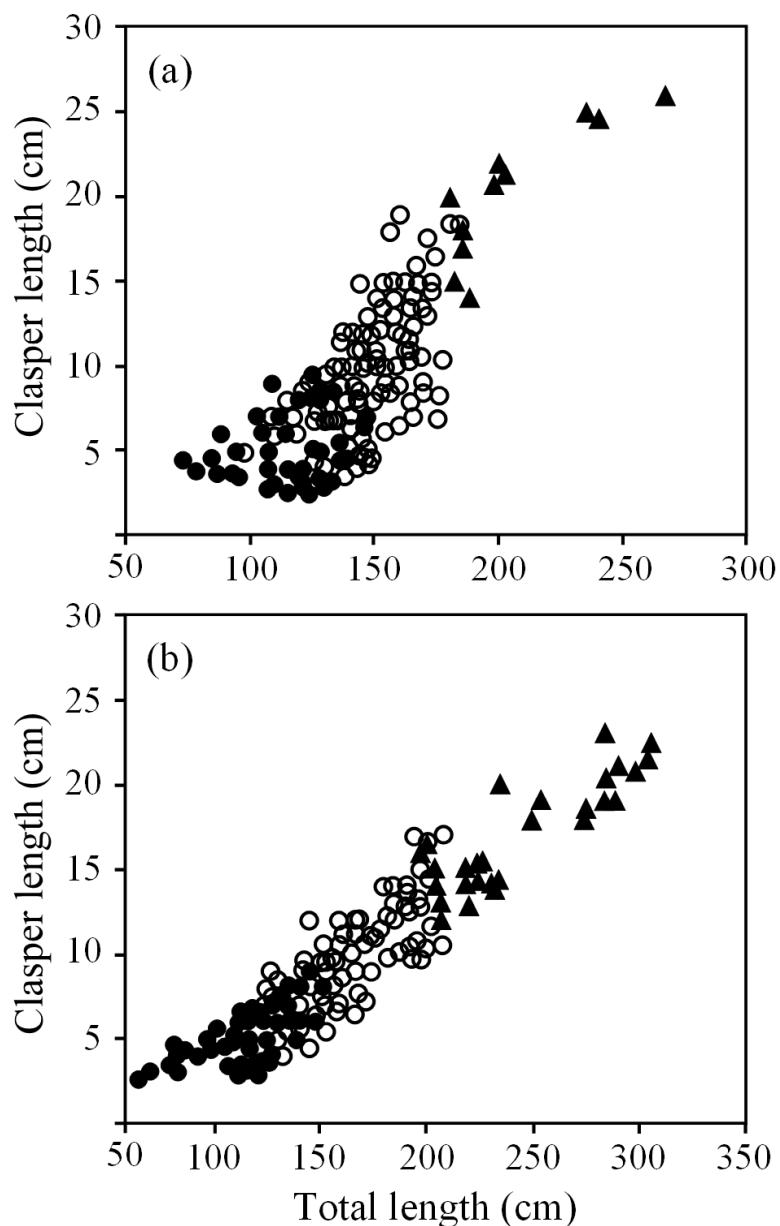


Figure 33 Relationships between inner clasper length and total length based on reproductive classifications of *Isurus oxyrinchus* (a) and *Prionace glauca* (b). Maturity condition is indicated as juveniles (●); adolescents (○) and adults (▲).

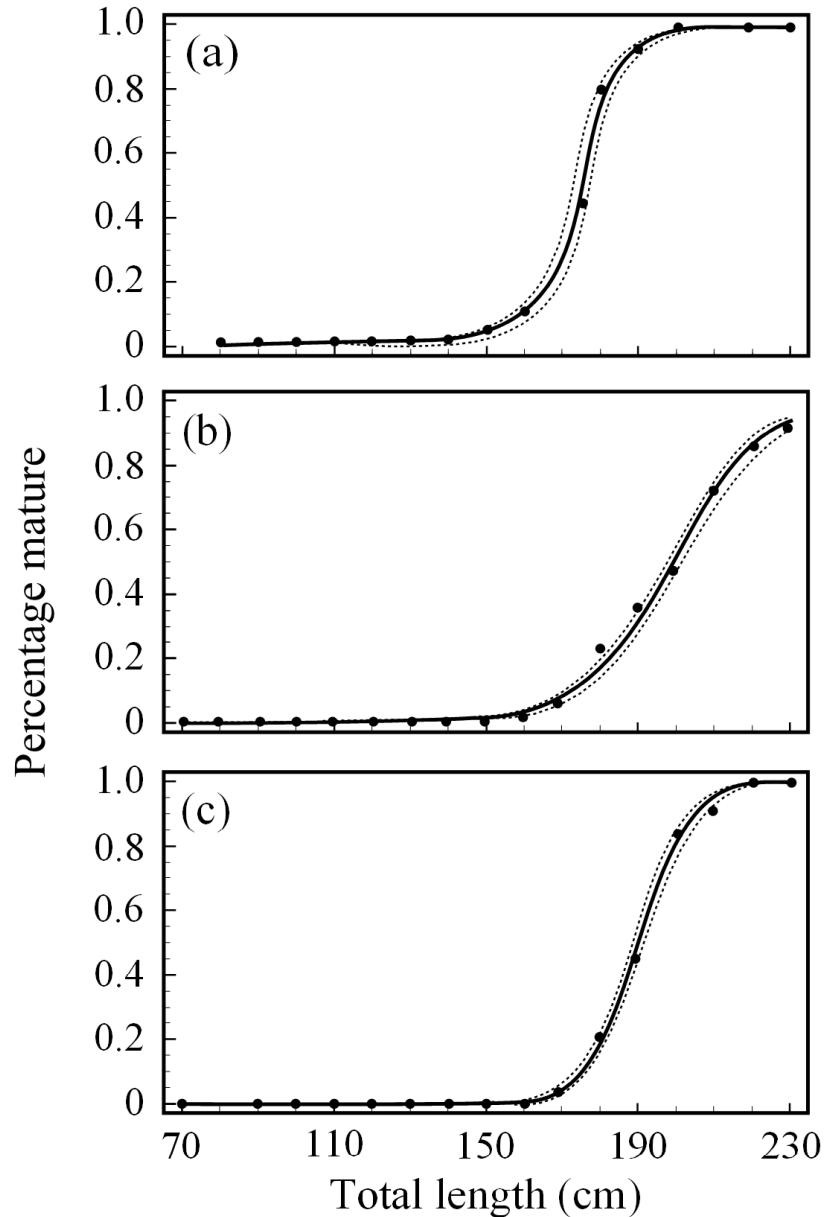


Figure 34 Logistic model (line) fitted for the relationship between total length and percentage of mature *Isurus oxyrinchus* (a) male; and *Prionace glauca* (b) female and (c) male. Circles indicate the observed percentage of mature individual in each size interval. Dashed line indicated 95% confidence interval for the logistic model.

Figure 35 (next page) Generalised Additive Model (GAM) output for *Isurus oxyrinchus* and *Prionace glauca*; and the influence of the each environmental variable on the CPUE. Grey areas represent 95% confidence intervals.

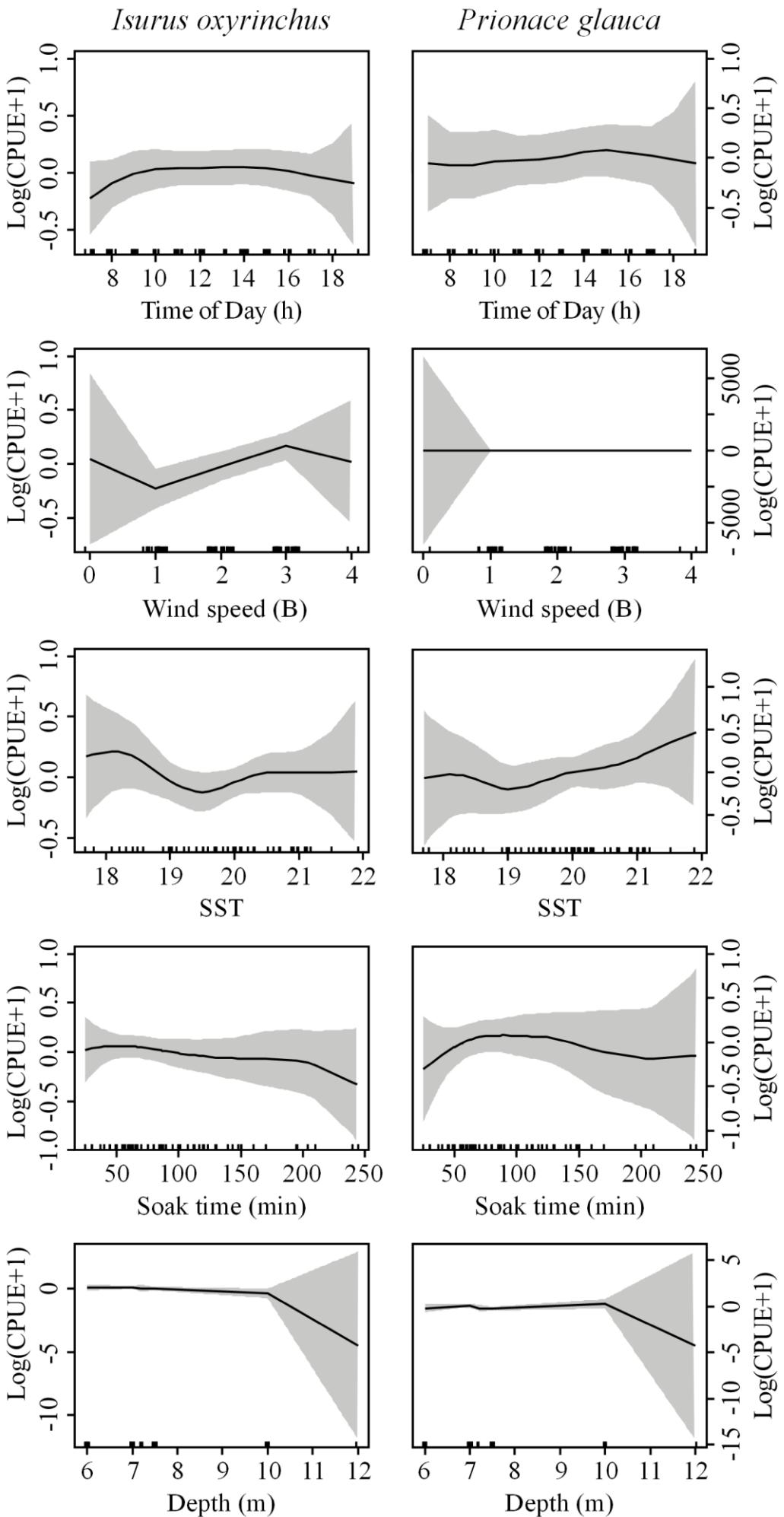


Table 22 Summary of fitting the Generalised Additive Model (GAM), relating *Isurus oxyrinchus* and *Prionace glauca* catches to environmental factors in the artisanal fishery of the south-eastern Pacific Ocean.

Effect	d.f.	F	P-value
<i>Isurus oxyrinchus</i>			
Time of day	3	0.803	0.498
Wind speed	3	3.547	0.038
SST	3	1.502	0.224
Soak time	3	0.379	0.812
Depth	3	4.547	0.019
<i>Prionace glauca</i>			
Time of day	3	0.195	0.899
Wind speed	3	0.230	0.875
SST	3	0.695	0.558
Soak time	3	0.651	0.585
Depth	3	3.879	0.030

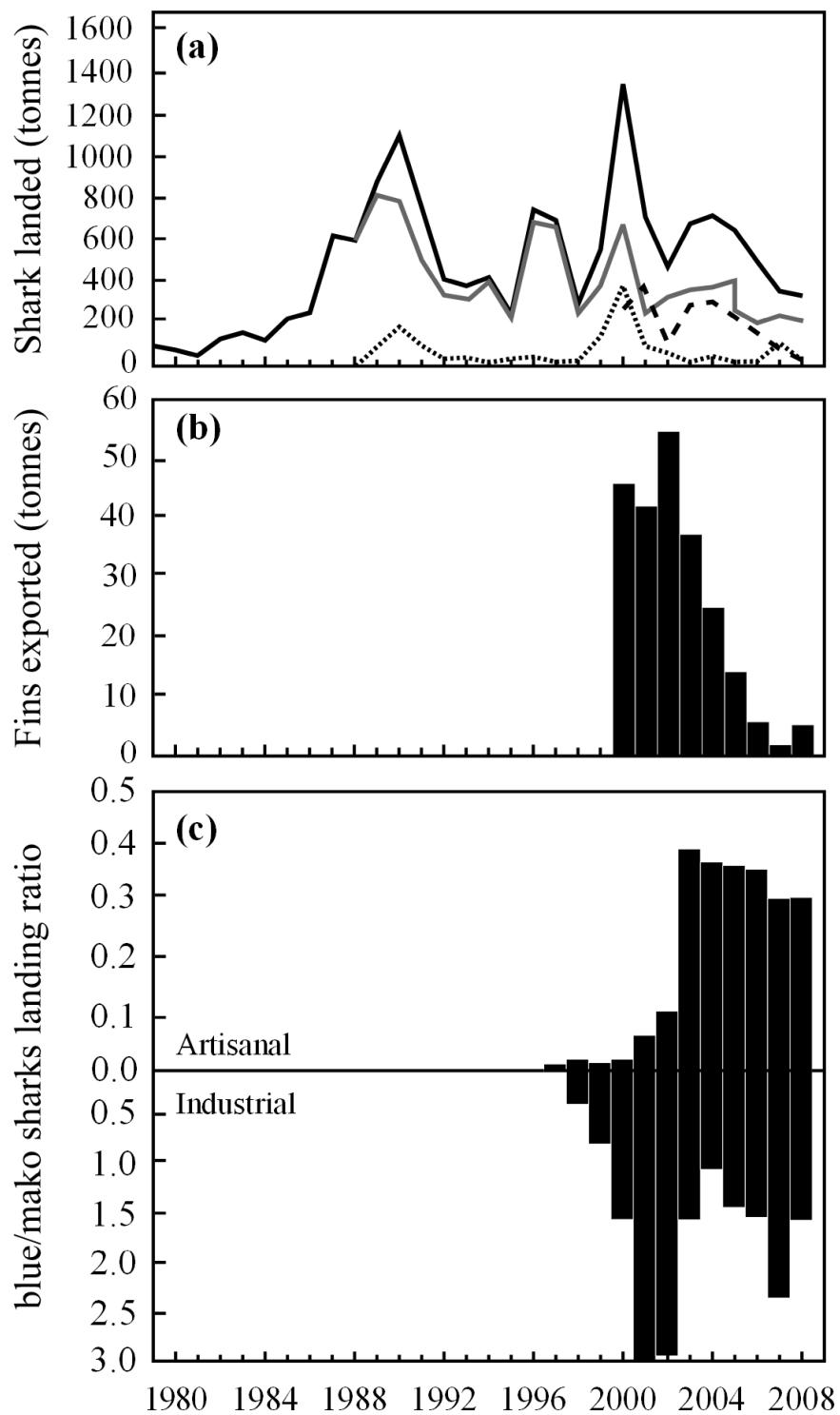


Figure 36 Landings of *Isurus oxyrinchus* and *Prionace glauca* in Chile (a) by fishery type, (b) export of dried shark fins and (c) fishery landing proportion from Chile between 1979 and 2009. Lines in (a) indicates tonnes of sharks landed at overall national (black line), artisanal (grey line), economic exclusive zone industrial (dashed line) and international waters (IW) industrial (dotted line) fisheries.

DISCUSSION

Bycatch and target fisheries are the major source of mortality for oceanic sharks (Dulvy *et al.*, 2008). Information on life-history traits and the constraints these impose on the species' ability to withstand exploitation are required for proper fishing mortality assessments (Stevens, 2008). The attainment of sexual maturity is a major milestone, in an elasmobranch's life-history which governs distribution, behaviour, and biology of pelagic sharks (Francis & Duffy, 2005).

There are many examples of sex-specific traits, such as sex-biased dispersal (Pardini *et al.*, 2001) and sex-specific differences in resource use (Klimley, 1987) and habitat selection (Sims *et al.*, 2001). Various hypotheses have been proposed to explain the phenomenon, such as sexual differences in reproductive strategies (Sims, 2005) and physiological requirements (Wearmouth & Sims, 2008); that are related to sexual maturity. Moreover, reproductive events of mating, gestation and parturition directly influence the physiological condition (King, 1984), migration (Bansemer & Bennett, 2009) and habitat use (Castro, 1993; Heupel *et al.*, 2007) at seasonal or annual scales. Therefore, both the size-at-maturity and the seasonality of reproductive events must be known to understand the spatio-temporal pattern of distribution and behaviour of sharks throughout their lifetime.

The absence of differences in sexual structure for *I. oxyrinchus* and *P. glauca* in the south Pacific Ocean, are in accordance with previous studies for both species in coastal fishing grounds of Mexico (Conde-Moreno & Galván-Magaña, 2006), Brazil (Carvalho *et al.*, 2011), Canada (Campana *et al.*, 2005), Portugal (Maia *et al.*, 2007), USA (Simpfendorfer *et al.*, 2002) and New Zealand (Bishop *et al.*, 2006). Size-at-maturity (L_{50}) in both species appears consistent with previous results despite the relatively absence of mature females in the current study. In both years, the lack of gravid females or those in which the uteri were developed suggest that mature sharks were absent from the fishing grounds during the fishing season (or were not feeding or catchable).

Size-at-birth of *I. oxyrinchus* in the South Pacific Ocean appears to be consistent with reports from other geographical regions, with L_T at birth generally around 65–70 cm (Casey & Kohler, 1992; Duffy & Francis, 2001; Costa *et al.*, 2002; Maia *et al.*, 2007). Habitat use and selection influence population dynamics, intraspecific and interspecific interaction, ecosystem structure and biodiversity (Grubbs, 2010). The predominance of the smaller size-classes (between 70 and 100 cm L_T) in both years of sampling suggests that *I. oxyrinchus* females use the coastal area where the fishery is conducted as a pupping ground and possibly, a nursery zone during spring and summer on an annual basis. If a juvenile growth rate of about 50–61 cm year⁻¹ for the first year of life (Pratt & Casey, 1983; Maia *et al.*, 2007) is considered, two major trends can be recognised in

the catch size distribution: sharks between 60 and 70 cm L_T are likely to be young-of-the-month (YOM); while sharks between 100 and 120 cm L_T represent the young-of-the-year (YOY). The variation in size of the YOY captured during the January/February period of 2005 and 2010 suggests that parturition at the population level may occur over a period of some months, and generally prior to summer with the last recruits of the pupping season represented by the smallest individuals. Assuming an average growth rate for the first year of life of 61.1 cm year⁻¹ (Maia *et al.*, 2007), the main cohort, 52% of the catch, relates to those sharks born in the pupping season (winter to early-summer) just prior to the sampling effort.

A marked decrease in the fraction of YOM and YOY in *I. oxyrinchus* is apparent when the 2005 and 2010 total lengths are compared, which may reflect an additive effect of the capture of juveniles in this fishery or a delayed pupping season in 2010. In both years, thermal anomalies were experienced in ocean surface temperatures due to the effect of the El Niño Southern Oscillation (Sielfeld *et al.*, 2010; Sarachik & Cane, 2010). This natural phenomenon is documented to alter the ‘normal’ structure of marine ecosystems in south Pacific Ocean (Zhang *et al.*, 2008); but by conducting the fishery surveys in similar oceanographic conditions, the environmental effects might be excluded as an explanation of the differences of the pupping season. There was a shift from a relatively high proportion (25.5%) of YOM sharks in the 2005 catch to a low proportion (9.1%) in 2010, and although it is not possible to be certain of the reason(s) for this observation it would be consistent with a decrease in the number of mature females returning to the nursery area to pup in 2010 compared to in 2005.

The lack of large-bodied *I. oxyrinchus* in the catch might be explained by different habitat use of mature sharks. In the current study the shortfin mako catch is dominated by relatively small individuals (<160 cm L_T), which may be explained by an ontogenetic and seasonal spatial segregation in the study area. Spatial segregation between sexes and among ontogenetic stages has been reported for many shark species (Springer, 1967; Klimley, 1987; Cailliet *et al.*, 2005; Dulvy *et al.*, 2008; Bansemer & Bennett, 2009; Mucientes *et al.*, 2009; Abascal *et al.*, 2011); and for example, large adult female sharks are rarely observed in the same, generally inshore locations as conspecific juvenile and immature sharks (Grubbs, 2010). Gilmore (1990) and Compagno (2001) report that *I. oxyrinchus* occupies a depth range from the surface to at least 500 m, and prefers water temperatures around 18° C; while juveniles may spend 90% of their time in the upper mixed layer of the water column without diel activity patterns in horizontal or vertical movements (Holts & Bedford, 1993; Sepulveda *et al.*, 2004; Abascal *et al.*, 2011). Given the preference of juvenile *I. oxyrinchus* for the upper mixed layer (80% of their time was spent in the upper 12 m, based on animals tracked in California (Sepulveda *et al.*, 2004) and taking into account that larger *I.*

oxyrinchus dive deeper (Gilmore, 1990; Compagno, 2001), juvenile shark are likely to be a common component of the catch in a fishery based on surface/shallow set longlines, as in the current study.

Our observations are consistent with those made on eastern North Atlantic (Maia *et al.*, 2007) and eastern North Pacific (Sepulveda *et al.*, 2004) populations, where immature shortfin mako sharks tended to occupy the upper 20 m of the water column, with larger individuals occurring with increasing depth. The upper 30 m of the epipelagic zone in the north of Chile is rich in small scombrid and carangid fishes (Alegria, 1995; Zuleta, 2005), that are a major component of the diets of smaller-sized *I. oxyrinchus* (López *et al.*, 2009) and *P. glauca* (López *et al.*, 2010). Sharks over 180 cm L_T prefer deeper habitat in the mixed layer, located at 30–150 m depth (Abascal *et al.*, 2011), and spend most of their time at environmental temperatures of between 17° C and 24° C. This zone is inhabited and preferred by tunas and related fishes (Block *et al.*, 1997), and thus provides a relative abundance of larger prey for larger sharks (Brill *et al.*, 1999). Cerna & Licandeo (2009) report a large population *I. oxyrinchus* close to our study area in the bycatch of *Xiphias gladius* longline fishery at 40–60 m depth, with mature specimens up to 330 cm L_T . Similar observations have been made in oceanic fisheries bycatch targeting tunas and swordfishes (Gilman *et al.*, 2007).

The GAM output of the environmental factors may not explain the CPUE trend in our results, mainly due to the high heterogeneity of the epipelagic water mass. Depth and wind speed have a significance correlation ($P > 0.05$) in CPUE and this might explain habitat preferences of the smaller size-class in *I. oxyrinchus* although the results are inconclusive for *P. glauca*.

The key factor for habitat selection of juvenile *I. oxyrinchus* appears to be related to a warm SST (Maia *et al.*, 2007). Waters off Caldera had a mean SST of 15.7° C over the last 10 years (SHOA, 2012), with the lowest mean monthly SST of about 14° C in July and the highest SST of about 18° C in January. During our study, SST varied from 17.7° C to 21.9° C following similar conditions described by Maia *et al.* (2007) and despite the lack of significant correlation between SST and CPUE in our study, our interpretation of habitat preferences takes the short, seasonal nature of the fishery into consideration. During the Austral summer, movement of warm water masses due to the position of south Pacific gyre (Ahumada *et al.*, 2000), are coupled with primary production and a small pelagic faunal bloom off north-central Chile (off Caldera) as a consequence of post-upwelling phases during late winter and spring (Vásquez *et al.*, 1998; Camus & Andrade, 1999). This type of ecosystem association has been reported for *I. oxyrinchus* nursery areas in the southern California Bight (Holts & Bedford, 1993; Sepulveda *et al.*, 2004) and Baja California (Conde-Moreno & Galván-Magaña, 2006; Vélez-Marín & Márquez-Farías, 2009).

Habitat occupancy by *I. oxyrinchus* is likely to be a result of broad-scale ecosystemic factors that were outside the scope of the present study that lead to a combination of suitable prey and prey abundance, water temperatures within a preferred range and regions of high primary production as these factors benefit the development and growth of juvenile sharks and their prey (Sepulveda *et al.*, 2004; Heupel *et al.*, 2007; Maia *et al.*, 2007; Abascal *et al.*, 2011). It may be, however, that other factors are also important, as Mucientes *et al.* (2009), suggest that habitat selection for pelagic sharks “does not appear to closely reflect prey, SST or primary productivity” at least over the time scale of their study.

The historic landing records for *I. oxyrinchus* and *P. glauca* show evidence of cycles of increased exploitation followed by collapse, as has occurred in many other fishing areas around the world; e.g. Japan (Nakano, 1999), Portugal (Maia *et al.*, 2007), Brazil (Costa *et al.*, 2002), New Zealand (Bishop *et al.*, 2006), Mediterranean Sea (Boero & Carli, 1979), northeast Pacific (Pawson & Vince, 1999), northwest Atlantic coast of USA (Baum *et al.*, 2003) and Canada (Campana *et al.*, 2005). A major difference between our study area and these other regions is in the measures taken to regulate the catch and landing of sharks. While strong measures have been adopted in many regions of the world, there are no fishing quotas for any shark species in Chilean waters, although annual landings tend to auto-regulate due to the strong seasonal nature of the artisanal fishery.

In Chile, of the few fisheries that record *I. oxyrinchus* and *P. glauca* in their landings, the artisanal longline fishery and industrial longline fishery directed to catch swordfish are the largest; and both share a common fishing area in the Chilean EEZ (Lamilla *et al.*, 2010). The blue shark, caught as bycatch in both fisheries, is the most frequent species (59% of total catch) in the swordfish fishery (Acuña *et al.*, 2001), while it comprises 45–55% of the catch in the artisanal fishery. However, the proportion of blue sharks landed in comparison to shortfin mako sharks has increased markedly in the period spanning 1997–2003, and 1998–2001 in the artisanal and industrial fisheries respectively. The reason for this shift towards landing blue sharks is unknown as there were no changes in relevant fishery regulations, the national market is very limited and there is no export market for blue shark meat. One possibility is that the increase on *P. glauca* landings is related directly to the dried shark fin market. Blue shark is the main species (83.9%) found in the Chilean shark fin market (Hernández *et al.*, 2008), and there has been an upward trend in price and therefore availability of this relatively high revenue commodity in recent years.

As gear selectivity, encounterability of the gear, given the species’ vertical catch distributions, and species’ catchability appear similar, our results suggest that *I. oxyrinchus* and *P. glauca* have similar susceptibilities within the artisanal fishery. Considering the official landings records however, the temporal trend of the *P. glauca*: *I. oxyrinchus* catch ratio suggests that the

target species (*I. oxyrinchus*) may have declined in importance relative to the increasing bycatch of *P. glauca*, which is the opposite of our observations. The reported dry fin export (Fig. 36b) indicates that a decline started in about 2003, which may relate to the reported decline in the reported landings in industrial vessels (Fig. 36a), for which reporting is mandatory. The continued and increasing trend to land blue sharks in both artisanal and industrial fisheries (Fig. 36c) may indicate a change of intentionality of the fisheries and a decline in the availability of shortfin mako shark.

As industrial vessels fish over a broad latitudinal range and across seasons, in contrast to the artisanal fishery for which we present detailed data, it is likely that the annual recruitment of *I. oxyrinchus* may be confronting a significant and ongoing threat. The current absence of management measures in Chile, may be a reflection of the relative paucity of research on highly migratory species (Barría, 2010), but conservation measures in Chile need to address both the artisanal fishery and the bycatch in industrial fisheries. Fishing practices that include minimum catch-sizes for sharks, conservative fishing quotas and delimitation of fishing areas to prevent the continued removal of immature *I. oxyrinchus* should be considered in order to ensure sustainability.

REFERENCES

- Abascal, F. J., Quintans, M., Ramos-Cartelle, A. & Mejuto, J. (2011) Movements and environmental preferences of the shortfin mako, *Isurus oxyrinchus*, in the southeastern Pacific Ocean. *Marine Biology* 158, 1175–1184.
- Acuña E., Araya, M., Cid, L., Kong, I. & Villarroel, J. C. (2001) Estudio biológico de tiburones (marrajo dentudo, azulejo y tiburón sardinero) en la zona norte y central de Chile. *Informes Técnicos FIP*, FIP/IT No. 2000-23. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 September 2011).
- Ahumada, R.B., Pinto, L.A. & Camus, P.A. (2000) The Chilean coast. In *Seas at the Millennium – An Environmental Evaluation* (Sheppard, C.R.C., ed.), pp. 699–717. Elsevier Science: Oxford.
- Alegría, V. (1995) Estudio biológico pesquero sobre el recurso jurel en la zona norte (regiones I y II). *Informes Técnicos FIP*, FIP/IT No. 93-17. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 September 2011).
- Bansemer, C.S. & Bennett, M.B. (2009) Reproductive periodicity, localised movements and behavioural segregation of pregnant *Carcharias taurus* at Wolf Rock south-east Queensland, Australia. *Marine Ecology Progress Series* 374, 215–227.

- Barría, P. (2010) Investigación situación pesquerías de recursos altamente migratorios, 2009. *Informes Técnicos Instituto de Fomento Pesquero*. Available at <http://goo.gl/HxzHU> (accessed 25 Sep 2011).
- Baum, J. K., Myers, R. A., Kehler, D. G., Worm, B., Harley, S. J. & Doherty, P. A. (2003). Collapse and conservation of shark populations in the Northwest Atlantic. *Science* 299, 389–392.
- Bigelow, K.A., Boggs, C.H. & He, X. (1999) Environmental effects on swordfish and blue shark catch rates in the, US North Pacific longline fishery. *Fisheries Oceanography* 8, 178–198.
- Bishop, S. D. H., Francis, M. P., Duffy, C. & Montgomery, J. C. (2006) Age, growth, maturity, longevity and natural mortality of the shortfin mako shark (*Isurus oxyrinchus*) in New Zealand waters. *Marine and Freshwater Research* 57, 143–154.
- Block, B.A., Keen, J., Castillo, B., Dewar, H., Freund, E.V., Marcinek, D., Brill, R.W. & Farwel, C. (1997) Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. *Marine Biology* 130, 119–132.
- Boero, F. & Carli, A. (1979) Catture di Elasmobranchi nella tonnarella di Camogli (Genova) dal 1950 a 1974. *Bollettino dei Musei e degli Istituti Biologici della Regia Universita di Genova* 47, 27–34.
- Brill, R., Block, B.A., Boggs, C.H., Bigelow, K.A., Freund, E.V. & Marcinek, D. (1999). Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. *Marine Biology* 133, 395–408.
- Cailliet G. M., Musick J. A., Simpfendorfer C. A. & Stevens J. D. (2005). Ecology and life history characteristics of chondrichthyan fish. In *Sharks, Rays and Chimaeras: the Status of the Chondrichthyan Fishes* (Fowler S. L., Cavanagh R. D., Camhi M., Burgess G. H., Cailliet G. M., Fordham S. V., Simpfendorfer C. A. & Musick, J. A., eds), pp. 12–18. Cambridge University Press: Cambridge, UK.
- Cailliet, G.M., Cavanagh, R.D., Kulka, D.W., Stevens, J.D., Soldo, A., Clo, S., Macias, D., Baum, J., Kohin, S., Duarte, A., Holtzhausen, J.A., Acuña, E., Amorim, A., Domingo, A. (2009) *Isurus oxyrinchus*. In *IUCN Red List of Threatened Species. Version 2011.2* IUCN 2011. Available at <http://www.iucnredlist.org> (accessed 25 Sep 2011).
- Campana, S. E., Marks, L. & Joyce, W. (2005). The biology and fishery of shortfin mako sharks (*Isurus oxyrinchus*) in Atlantic Canadian waters. *Fisheries Research* 73, 341–352.
- Camus, P.A. & Andrade, Y.N. (1999) Diversidad de comunidades intermareales rocosas del norte de Chile: el supuesto del enriquecimiento por efecto de la surgencia costera. *Revista Chilena de Historia Natural* 72, 389–410.

- Carvalho, F.C., Murie, D.J., Hazin, F.H.V., Hazin, H.G., Leite-Mourato, B. & Burgess, G.H. (2011) Spatial predictions of blue shark (*Prionace glauca*) catch rate and catch probability of juveniles in the Southwest Atlantic. *ICES Journal of Marine Sciences* 68, 890–900.
- Casey, J.G. & Kohler, N.E. (1992) Tagging studies on the shortfin mako shark (*Isurus oxyrinchus*) in the Western North Atlantic. *Australian Journal of Marine & Freshwater Research* 43, 45–60.
- Castro, J.I. (1993) The biology of the fine tooth shark, *Carcharhinus isodon*. *Environmental Biology of Fishes* 36, 219–232.
- Cerna, F. & Licandeo, R. (2009). Age and growth of the shortfin mako (*Isurus oxyrinchus*) in the south-eastern Pacific off Chile. *Marine and Freshwater Research* 60, 394–403.
- Compagno, L.J.V. (2001) *Sharks of the World. An Annotated and Illustrated Catalogue of Shark Species Known to Date*. Volume 2: Bull-Head, Mackerel and Carpet Sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO Species Catalogue for Fisheries Purposes No. 1, vol. 2. Food and Agriculture Organization of the United Nations: Rome.
- Compagno, L., Dando, M. & Fowler, S. (2005). *A Field Guide to the Sharks of the World*. Princeton University Press: Princeton, NJ.
- Conde-Moreno, M. & Galván-Magaña, F. (2006) Reproductive biology of the mako shark *Isurus oxyrinchus* on the south-western coast of Baja California, Mexico. *Cybium* 30, 75–83.
- Costa, F.E.S., Braga, F.M.S., Arfelli, C.A. & Amorim, A.F.D. (2002) Aspects of the reproductive biology of the shortfin Mako, *Isurus oxyrinchus* (Elasmobranchii Lamnidae), in the southeastern region of Brazil. *Brazilian Journal of Biology* 62, 239–248.
- Duffy, C. & Francis, M.P. (2001) Evidence of summer parturition in shortfin mako (*Isurus oxyrinchus*) sharks from New Zealand waters. *New Zealand Journal of Marine and Freshwater Research* 35, 319–324.
- Dulvy, N. K., Sadovy, I. & Reynolds, D. (2003) Extinctions vulnerability in marine populations. *Fish and Fisheries* 4, 25–64.
- Dulvy, N. K., Baum, J. K., Clarke, S., Compagno, L. J. V., Cortés, E., Domingo, A., Fordham, S., Fowler, S., Francis, M. P., Gibson, C., Martinez, J., Musick, J. A., Soldo, A., Stevens, J. D. & Valenti, S. (2008) You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. *Aquatic Conservation: Marine and Freshwater Ecosystems* 18, 459–482.
- FAO (2003) *Fisheries Management II: the ecosystem approach to fisheries*. FAO Technical Guidelines for Responsible Fisheries 4 (Suppl. 2), FAO: Rome.
- Ferretti, F., Myers, R.A., Serena, F. & Lotze, H.K. (2008) Loss of large predatory sharks from the Mediterranean Sea. *Conservation Biology* 22, 952–964.

- Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R. & Lotze, H.K. (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecological Letters* 13, 1055–1071.
- Francis, M. P. & Duffy, C. (2005) Length at maturity in three pelagic sharks (*Lamna nasus*, *Isurus oxyrinchus*, and *Prionace glauca*) from New Zealand. *Fishery Bulletin* 103, 489–500.
- Garcia, S.M. & Cochrane, K.L. (2005) Ecosystem approach to fisheries: a review of implementation guidelines. *ICES Journal of Marine Sciences* 62, 311–318.
- Gilman, E., Clarke, S., Brothers, N., Alfaro-Shigueto, J., Mandelman, J., Mangel, J., Petersen, S., Piovano, S., Thomson, N., Dalzell, P., Donoso, M., Goren, M. & Werner, T. (2007) *Shark depredation and unwanted bycatch in pelagic longline fisheries: industry practices and attitudes, and shark avoidance strategies*. Western Pacific Regional Fishery Management Council: Honolulu, USA.
- Gilmore, G.R. (1990) Reproductive biology of lamnid sharks. *Environmental Biology of Fishes* 38, 95–114.
- Grubbs, R.D. (2010) Ontogenetic shifts in movements and habitat use. In *Sharks and their Relatives II: Biodiversity, Adaptive Physiology and Conservation* (Carrier, J.C., Musick, J.A., Heithaus, M.R., eds.), pp. 319–350. CRC Press: Boca Raton, FL.
- Hastie, T. & Tibshirani, R. (1990) Generalized Additive Models. Chapman & Hall: London.
- Hazin, F. H. V., Couto, A. A., Kihara, K., Otsuka, K., Ishino, M., Boeckman, C. E. & Leal, E. C. (1994). Reproduction of the blue shark *Prionace glauca* in the south-western equatorial Atlantic Ocean. *Fisheries Science* 60, 487–491.
- Heist, E.J., Musick, J.A. & Graves, J.E. (1996) Genetic population structure of the shortfin mako (*Isurus oxyrinchus*) inferred from restriction fragment length polymorphism analysis of mitochondrial DNA. *Canadian Journal of Fisheries and Aquatic Sciences* 53, 583–588.
- Henderson, A. C., Flannery, K. & Dunne, J. (2001) Observations on the biology and ecology of the blue shark in the north-east Atlantic. *Journal of Fish Biology* 58, 1347–1358.
- Hernández, S., Haye, P.A. & Shivji, M.S. (2008) Characterization of the pelagic shark-fin trade in north-central Chile by genetic identification and trader surveys. *Journal of Fish Biology* 73, 2293–2304.
- Heupel, M.R., Carlson, J.K. & Simpfendorfer, C.A. (2007) Shark nursery areas: concepts, definition, characterization and assumptions. *Marine Ecology Progress Series* 337, 287–297.
- Holts, D.B. & Bedford, D.W. (1993) Horizontal and vertical movements of the shortfin mako shark (*Isurus oxyrinchus*) in the southern California bight. *Australian Journal of Marine & Freshwater Research* 44, 901–909.

- King, J.K. (1984) Changes in condition of mature female rig (*Mustelus lenticulatus*) from Golden Bay in relation to seasonal inshore migrations. *New Zealand Journal of Marine and Freshwater Research* 18, 21–27.
- Klimley, A.P. (1987) The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. *Environmental Biology of Fishes* 18, 27–40.
- Lamilla, J., Roa, R., Barría, P., Bustamante, C., Concha, F., Cortes, E., Acuña, E., Balbontín, F., Oliva, M., Araya, M. & Meléndez, R. (2008). Desarrollo metodológico para la estimación del descarte de Condrictios en las pesquerías artesanales. *Universidad Austral de Chile Informe técnico* No. 2008–60, Valdivia. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 September 2011).
- Lamilla J., Bustamante, C., Roa, R., Acuña, E., Concha, F., Meléndez, R., López, S., Aedo, G., Flores, H. & Vargas-Caro, C. (2010) Estimación del descarte de condrictios en pesquerías artesanales. *Universidad Austral de Chile Informe técnico* No. 2008–60, Valdivia. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 Sep 2011).
- Lessa, R., Santana, F.M. & Hazin, F.H. (2004) Age and growth of the blue shark *Prionace glauca* (Linnaeus, 1758) off northeastern Brazil. *Fisheries Research* 66, 19–30.
- López, S., Meléndez, R. & Barría, P. (2009) Alimentación del tiburón marajo *Isurus oxyrinchus* Rafinesque, 1810 (Lamniformes: Lamnidae) en el Pacífico suroriental. *Revista de Biología Marina y Oceanografía* 44, 439–451.
- López, S., Meléndez, R. & Barría, P. (2010) Preliminary diet analysis of the blue shark *Prionace glauca* in the eastern South Pacific. *Revista de Biología Marina y Oceanografía* 45, 745–749.
- Maia, A., Queiroz, N., Cabral, H.N., Santos, A.M. & Correia, J.P. (2007) Reproductive biology and population dynamics of the shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, off the southwest Portuguese coast, eastern North Atlantic. *Journal of Applied Ichthyology* 23, 246–251.
- Manning, M. J. & Francis, M. P. (2005). *Age and growth of blue shark (Prionace glauca) from the New Zealand Exclusive Economic Zone*. New Zealand Fisheries Assessment Report 2005/26. Ministry of Fisheries: Wellington, New Zealand.
- Mollet, H. F., Cliff, G., Pratt Jr, H. & Stevens, J. D. (2000). Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. *Fishery Bulletin* 98, 299–318.
- Mucientes, G.R., Queiroz, N., Sousa, L.L., Tarroso, P. & Sims, D.W. (2009) Sexual segregation of pelagic sharks and the potential threat from fisheries. *Biological Letters* 5, 156–159.
- Myers, R.A., Baum, J.K., Shepherd, T.D., Powers, S.P. & Peterson, C.H. (2007) Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science* 315, 1846–1850.

- Nakano, H. (1999). Fishery management of sharks in Japan. In *Case Studies of the Management of Elasmobranch Fisheries* (Shotton, R., ed), pp. 552–579. FAO Fisheries Technical Paper No. 378/1. FAO: Rome.
- Nakano, H. & Nagasawa, K. (1996) Distribution of pelagic elasmobranch caught by salmon research gillnets in the North Pacific. *Fishery Science* 62, 865–869.
- Nakano, H. & Stevens, J. D. (2009) The biology and ecology of the blue shark, *Prionace glauca*. In *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (Camhi, M. D., Pikitch, E. K. & Babcock, E. A., eds), pp. 140–151.: Blackwell Publishing: Oxford, UK.
- Pardini, A.T., Jones, C.S., Noble, L.R., Kreiser, B., Malcolm, H., Bruce, B.D., Stevens, J.D., Cliff, G., Scholl, M.C., Francis, M., Duffy, C.A. & Martin, A.P. (2001) Sex-biased dispersal of great white sharks. *Nature* 412, 39–40.
- Pawson, M. & Vince, M. (1999) Management of shark fisheries in the Northeast Atlantic. In *Case Studies of the Management of Elasmobranch Fisheries* (Shotton, R., ed), pp. 1–46. FAO Fisheries Technical Paper No. 378/1. FAO: Rome.
- Petersen, S. L., Honig, M. B., Ryan, P. G., Underhill, L. G. & Compagno, L. J. V. (2009) Pelagic shark bycatch in the tuna- and swordfish-directed longline fishery off southern Africa. *African Journal of Marine Science* 31, 215–225.
- Pratt, H.L. & Casey, J.G. (1983) Age and growth of the short mako *Isurus oxyrinchus*. In *Proceedings of the International Workshop on Age Determination of Oceanic Pelagic Fishes: Tunas, Billfishes, and Sharks* (Prince, E.D., Pulos, L.M., eds.), pp. 175–177. NOAA Technical Report NMFS 8: U.S. Department of Commerce.
- R Core Team (2012). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria, <http://www.R-project.org/>
- Restrepo, V. R. & Watson, R. A. (1991). An approach to modelling crustacean egg-bearing fractions as function of size and season. *Canadian Journal of Fisheries and Aquatic Sciences* 48, 1431–1436.
- Sarachik, E.S. & Cane, M.A. (2010) *The El Niño-Southern Oscillation Phenomenon*. Cambridge University Press: Cambridge, UK.
- Schrey, A.W. & Heist, E.J. (2003) Microsatellite analysis of population structure in the shortfin mako (*Isurus oxyrinchus*). *Canadian Journal of Fisheries and Aquatic Sciences* 60, 670–675.
- Semba, Y., Nakano, H. & Aoki, I. (2009) Age and growth analysis of the shortfin mako *Isurus oxyrinchus*, in the western and central North Pacific Ocean. *Environmental Biology of Fishes* 84, 377–391.

- Sepulveda, C.A., Kohin, S., Chan, C., Vetter, R. & Graham, J.B. (2004) Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight. *Marine Biology* 145, 191–199.
- SERNAP (2009) *Anuario Estadístico de Pesca*. Servicio Nacional de Pesca, Ministerio de Economía, Fomento y Reconstrucción: Santiago de Chile.
- SHOA (2012) Servicio Hidrográfico y Oceanográfico de la Armada, Centro Nacional de Datos Hidrográficos y Oceanográficos de Chile. Armada de Chile, available at http://www.shoa.cl/cendhoc_php/index.htm (accessed 25 Sep 2013).
- Sielfeld, W., Laudien, J., Vargas, M. & Villegas, M. (2010) El Niño induced changes of the coastal fish fauna off northern Chile and implications for ichthyogeography. *Revista de Biología Marina y Oceanografía* 45, 705–722.
- Simpfendorfer, C.A., Hueter, R.E., Bergman, U. & Connell, S.M.H. (2002) Results of a fishery-independent survey for pelagic sharks in the western North Atlantic 1977–1994. *Fisheries Research* 55, 175–192.
- Sims, D.W. (2005) Differences in habitat selection and reproductive strategies of male and female sharks. In *Sexual Segregation in Vertebrates* (Ruckstuhl, K.E., Neuhaus, P., eds.), pp. 127–147. Cambridge University Press: Cambridge, UK.
- Sims, D.W., Nash, J.P. & Morritt, D. (2001) Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. *Marine Biology* 139, 1165–1175.
- Snelson, F. F., Roman, B. L. & Burgess, G. H. (2009) The reproductive biology of pelagic elasmobranchs. In *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (Camhi, M. D., Pikitch, E. K. & Babcock, E. A., eds), pp. 24–54. Blackwell Publishing: Oxford, UK.
- Sokal, R. R. & Rohlf, F. J. (1987) *Introduction to Biostatistics*, 2nd edn. W.H. Freeman Press: New York.
- Springer, S. (1967) Social organization of shark populations. In *Sharks, Skates, and Rays*. (Gilbert, P.W., Mathewson, R.F., Rall, D.P., eds.), pp. 149–174. The Johns Hopkins Press: Baltimore, MD.
- Stevens, J.D. (1983) Observations on reproduction in the shortfin mako *Isurus oxyrinchus*. *Copeia* 1983, 126–130.
- Stevens, J.D. (1984) Biological observations on sharks caught by sport fishermen off New South Wales. *Australian Journal of Marine & Freshwater Research* 35, 573–590.

- Stevens, J. D. (2000). The population status of highly migratory oceanic sharks. In *Getting Ahead of the Curve: Conserving the Pacific Ocean's Tunas, Swordfish, Billfishes and Sharks* (Hinman, K., ed), pp. 35–43. National Coalition for Marine Conservation: Leesburg, VA.
- Stevens, J.D. (2008) The biology and ecology of the shortfin mako shark, *Isurus oxyrinchus*. In *Sharks of the Open Ocean: Biology, Fisheries and Conservation* (Camhi, M.D., Pikitch, E.K., Babcock, E.A., eds.), pp. 87–94. Blackwell Publishing: Oxford, UK.
- Stevens, J. D., Bonfil, R., Dulvy, N. K. & Walker. P. A. (2000) The effects of fishing on shark, rays, and chimaeras (Chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Sciences* 57, 476–494.
- Vásquez, J.A., Camus, P. & Ojeda, F.P. (1998) Diversidad estructura y funcionamiento de ecosistemas costeros rocosos del norte de Chile. *Revista Chilena de Historia Natural* 71, 479–499.
- Vélez-Marín, R. & Márquez-Farías, J.F. (2009) Distribution and size of the short-fin mako (*Isurus oxyrinchus*) in the Mexican Pacific Ocean. *Pan-American Journal of Aquatic Science* 4, 490–499.
- Ward, P. & Myers, R.A. (2005) A method for inferring the depth distribution of catchability for pelagic fishes and correcting for variations in the depth of pelagic longline fishing gear. *Canadian Journal of Fisheries and Aquatic Sciences* 62, 1130–1142.
- Wearmouth, V.J. & Sims, D.W. (2008) Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns mechanisms and conservation implications. *Advances in Marine Biology* 54, 107–170.
- Zhang, Q., Guan, Y., Yang, H. (2008) ENSO amplitude change in observation and coupled models. *Advances in Atmospheric Sciences*. 25, 361–366.
- Zuleta, A. (2005) Factores de no sustentabilidad en el manejo de la pesquería de peces pelágicos pequeños en Chile. In *Biodiversidad Marina: valoración, usos y perspectivas* (Figueroa, E., ed.), pp. 473–506. Editorial Universitaria, Santiago de Chile.

CHAPTER 5
GENERAL DISCUSSION



Overview

In many coastal and island civilisations, such as those of the south Pacific islands (Gudger, 1927), sharks, skates, rays and chimaeras have been a mainstay in the culture for many centuries through the provision of food, arms and clothing, and often had a place in ‘religious’ beliefs (Ebert *et al.*, 2013). In contrast, and mainly for cultural reasons, in Chile cartilaginous fishes have only really impinged on the public consciousness from around the second half of the 20th Century, although there are depictions of mythical creatures that feature shark characteristics from ancient coastal civilisations in the region, i.e., south Nazca culture. In effect, Chilean people have recently embraced gastronomic innovations that involve cartilaginous fishes in a traditionalist culture, leaving behind the fear of sharks sown by Hollywood.

Reasons for the inadequate knowledge of cartilaginous fishes in Chile are probably related to the scarce maritime heritage of the Chilean people. Regardless of the experience of the pre-Columbian inhabitants, the society that began to develop after colonisation of South America by the Spaniards was not focused on exploration of maritime resources despite Chilean geography that is characterised by more sea than landmass (Gay, 1848). Modern society has turned its back on the sea, and has based its economic development on the exploitation of copper, wood and paradoxically, freshwater fishes (CAPP, 2010). At the same time, elements of fear and aversion of sharks has grown (Lamilla, 2005). Skates, rays and chimaeras have been even further from the public eye, as they are not as feared or as popular as sharks. However, a subtle and particular interest in skates has occurred since 1980, mainly through Korean immigrants who have an ancestral tradition of trading and eating skates (O’Brien, 1997).

In recent years there has been concern within the scientific community about the sustainable exploitation of cartilaginous fishes. This concern has been driven by reflection on important biological characteristics of this group of fishes that have more in common with mammals than other fishes (Musick & Bonfil, 2005).

These introductory comments (above) provide a necessary vision of how cartilaginous fish knowledge has progressed in Chile from the early works of Molina (1782) and Philippi (1887), and a review of scientific advances in Chilean natural history is provided in Chapter 3.

This thesis represents the first comprehensive study on cartilaginous fishes in the south-eastern Pacific Ocean, and provides new insights into several critical aspects of exploited species in Chile. The purpose of this discussion is to clarify my critical position about cartilaginous fish research in Chile, and complements the discussions provided with each chapter within this thesis, each of which interprets the major findings in both regional and worldwide contexts.

Taxonomy

Taxonomic clarity is a fundamental requirement of biology as it underpins the basis of all other life sciences. In the last decade, taxonomy of cartilaginous fishes (*sensu* Ebert *et al.*, 2013) (the sharks, skates, rays and chimeras) has undergone a scientific revival with >180 new species formally described (White & Last, 2012). At the same time, the rapid expansion of human activities threatens ocean-wide biodiversity (Dulvy *et al.*, 2014). Current research has provided evidence that many cartilaginous fishes have a high potential risk for extinction over the next 100 years (Garcia *et al.*, 2008). Worldwide, cartilaginous fisheries have expanded in response to rising demand, particularly for highly valuable parts such as shark fins and branchial plates of filter-feeders. Advances in gear and equipment (winches, on-board freezing capability, large steel hulled vessels, great range and endurance, sonar, radar, radio, GPS, etc.) also has allowed for more efficient and effective capability to explore new areas, i.e. open ocean waters, sea floor and deep-sea mounts (Barausse *et al.*, 2014).

In Chilean waters, the mortality levels of cartilaginous fish bycatch often exceeds the numbers of targeted bony-fish catch in mid-demersal trawlers, purse-seine nets and longline fisheries (Lamilla *et al.*, 2010). The problem of bycatch is compounded by a broad absence of catch-based records of these fishing interactions. This jeopardises attempts at management of the cartilaginous fish resource, as the catch composition (species affected), timing (seasonality of the interaction) and level of the interaction (fishing impact) are effectively excluded from fishery-dependent assessment activities.

The lack of comparative material or species-specific descriptions of cartilaginous fishes has led to generic, non-specific landing statistics in Chilean waters; mainly due to misidentification and a non-regulated capture record of target species; and non-documented bycatch landings. Erroneous taxonomic determinations are mainly the result of a simple ignorance of local wildlife and the fact that Chile does not consume cartilaginous fishes, which results in a poor general knowledge about fishes within the community (Walsh & Ebert, 2007). In other cases, misidentification of landings is due to variability of morphological characters (e.g., ontogenetic change) and incomplete diagnosis (from original description or available translations). However, species identification in Chile has compromised accuracy with the widespread use of “common sense” categories which may not reflect any species-specific character, as can be observed in the generic categories used to record the landing of shark, skates and rays, as “shark”, “skate” and “ray” (Lamilla *et al.*, 2008). This ‘name confusion’ is especially evident for endemic species; a category that includes many coastal and deep-water species (Lamilla, 2005). If external characteristics alone, such as shape, size and colour, are used to identify landings, this can lead to confused records and, in consequence, erroneous

biodiversity data. This thesis has provided new descriptions of external anatomy based on meristic characters rather than subjective observations of body shape. Also, additional descriptions of key morphological features have been produced for three species; following suggestion made by McEachran & Dunn (1998) and Valenzuela *et al.* (2008), for the use of skeletal structures to aid species identification due to its low intraspecific variability.

In general, Chapter 2 reviewed the taxonomy of Chilean cartilaginous fishes based on case studies, and with new records that supplement biodiversity inventories. Three new species, obtained in relation to different fisheries, have been appended to the Chilean cartilaginous fish fauna. A different issue within the national context is addressed in relation to each of these species, even though none are considered a commercial resource.

Extension of the distribution ranges of *Mobula japanica*, a temperate-tropical species and *Hydrolagus melanophasma*, a deep-water species were made through the respective examination of a stranded carcass and a ‘weird’ fish provided by a curious and friendly fisherman who found it on his vessel. In both cases, serendipity and chance (being in the right place at the right time) played a major role in the discoveries through access to the specimens. The occasional presence of dead marine animals on beaches worldwide often generates public attention, involving curious observers, local agencies, reporters and researchers. The latter, usually report the presence of these stranded animals, i.e., the mass stranding of devil rays *Mobula mobular* (Couturier *et al.*, 2013) or pygmy killer whales *Feresa attenuata* (Mignucci-Giannoni *et al.*, 2000); and have even managed to describe new species (i.e., the Perrin's beaked whale *Mesoplodon perrini*, Dalebout *et al.*, 2002). In other instances, these records serve to rebuild seasonal migrations (i.e., the basking shark *Cetorhinus maximus*, Hernández *et al.*, 2010). These examples illustrate the potential for gaining knowledge about the occurrence and distributions of cartilaginous fishes through interaction between scientists and the general public, be they fishers, divers, snorkelers or just someone walking along a beach and finding something odd and bringing it to the attention of experts. Two recent examples of recreational and commercial fishers bringing unusual specimens to the attention of biologists and have result in the range extension and documented records of the mandarin dogfish *Cirrhigaleus barbifer* (Kempster *et al.*, 2013) in Western Australia, and the sand tiger shark *Carcharias taurus* (Jabado *et al.*, 2013) in United Arab Emirates waters. In recent years there has been a dramatic expansion in ‘citizen science’, in which non-scientists are encouraged to help with the collection of information that is of value to various scientific projects. Australian researchers may have a lead in community engagement and “citizen science” research programs involving cartilaginous fishes. Initiatives such as Project Manta, Grey Nurse Shark Watch, Ecocean, Spot-a-Shark, Reef Watch Australia, etc., have delivered results and attracted new funding sources, and

increase conservation awareness for charismatic elasmobranchs gathering large datasets at reduced cost (Goffredo *et al.*, 2010)

Included in an extended review of bycatch records and descriptions of morphological characteristics, the presence of thickbody skate *Amblyraja frerichsi* was reported in Chilean waters 44 years after its original description in Argentinian waters (Krefft, 1968), and 15 years since Pequeño (1997) provided a clue of its continued presence based on a personal communication “from another person who saw a specimen in southern Chile”.

Recently, a series of comprehensive species descriptions and re-descriptions, has revived taxonomic studies in cartilaginous fishes, for example and just to address a few, the elasmobranchs books series published by CSIRO (Last *et al.*, 2007, 2008a, 2008b, 2010) and the special volumes published by the Journal of Fish Biology (White *et al.*, 2012) and Zootaxa (De Carvalho *et al.*, 2013). The inclusion of morphological characters, skeletal descriptions, radiographic and magnetic resonance images, and genetic sequences from type specimens, are now standard techniques for descriptions and revision of species (White & Last, 2012). The present thesis, have taken advantage of these techniques and the global tendency to revisiting old species descriptions with modern eyes (Ebert *et al.*, 2013a) in one of the “black spot” region in cartilaginous fish science (Compagno, 1984; Ebert *et al.*, 2013b).

Zoogeography

Despite the increase in fishing effort over the last 50 years, there is scant knowledge about geographic and bathymetric distributions, and the relative abundance of cartilaginous fish species in the south-eastern Pacific Ocean. Off the Chilean coast, elasmobranchs and holocephalans are commonly caught as target and bycatch in trawl, coastal gill-nets and longline fisheries, but with the exception of a few target species, capture records (including bycatch and discard) are seldom collected and rarely analysed in detail (Lamilla *et al.*, 2008).

Particular emphasis on the evaluation of the *functional* diversity of cartilaginous fishes was conducted (Chapter 3) to aid future management and conservation planning. This documentation and analysis of species occurrence and species distribution in Chilean waters outlines the regional biodiversity. It provides a tool for use when considering modern threats to marine ecosystems, such as overfishing and climate change that are the likely main causes of disturbances and changes in species composition and distribution ocean-wide (Dulvy *et al.*, 2014). It is hoped that our assessment of the functional diversity of Chilean cartilaginous fishes will act as a catalyst and encourage other researchers to re-evaluate critically their ‘national species checklists’. While

checklists are of some value in furthering the understanding of species' distributions, the transient presence of a single individual is of little importance in the local ecosystem compared to species that are resident and numerous. Clarification of the 'status' of individual species is therefore of considerable importance, as biodiversity records for many countries suffer from similar problems to those identified in the Chilean cartilaginous ichthyofauna.

The current thesis has provided new information related to potential geographic distribution patterns along the southeaster Pacific Ocean. As mentioned by Ebert *et al.* (2013), "species checklists and biological observations may constitute the first approach in the study of the cartilaginous fishes" and, in a following consequent step, the first quantitative assessment of diversity and abundance in the south-east Pacific Ocean has been produced. Fishery-independent surveys provided approximately 6,430 dataset entries, with 20 species represented by 194,705 specimens, in order to assess distribution patterns and habitat affinities of the cartilaginous fish fauna (Chapter 3). Through the use of a novel approach, the regional biodiversity along much of the Chilean continental shelf and slope, and from approximately 100 m to 800 m depth, has been explored.

The functional diversity of each component unit should be assessed before priorities for management and conservation are established (e.g., component units may vary depending the conservation scope, from zoogeographic areas to countries, seas and oceans), before may hypothesize correlations to explain biodiversity patterns and modelling of species richness. As a comparative parallel, Chile and Australia have large coastlines, of 78,563 km and 66,530 km respectively (WRS, 2012), and rank five and six among the world's largest countries by coastline, following Canada, USA, Russia and Indonesia. While Chile has a larger coastline than Australia, species richness of Australian cartilaginous fishes is three-times that of Chile (Last & White, 2011). However, the total species richness between both countries cannot be compared without considering the zoogeographical provinces (8 in Australia v 2 in Chile) and the influence of tropical, temperate and cold water masses. Chile has a larger latitudinal range, as it is a "linear coastline", whereas Australia has latitudinal duplication ("island effect") but separated by cold (south) and warm (north) water masses that restrict longitudinal movements of many species. This thermal barrier related to Ocean influence together with biogeographic barriers (i.e., the Sunda Shelf Barrier) allows for east-west speciation, which is virtually absent in Chile. However, species richness and endemism levels are related between Chile and Australia, when only "cold" Australian species (those species inhabiting cold-temperate waters) are considered (Last & White, 2011; Bustamante *et al.*, 2014).

Life history

Cartilaginous fishes have an important role as top predators in many marine communities (Wetherbee & Cortés, 2004), affecting their structure and function through interactions with other trophic links in food webs to which they belong (Ferretti *et al.*, 2010). The influence of cartilaginous fishes in ecosystems is under increasing threat due to continuing population declines from overfishing and bycatch mortality (Stevens *et al.*, 2000; Ferretti *et al.*, 2010).

While life history may provide considerable insight into the response of cartilaginous fish populations to exploitation, the relatively low importance of shark and shark-related products in Chile has led to a lack of awareness of conservation needs. However, over recent years, there has been an increase in the number of cartilaginous fishes traded, based on catch and mortality statistics for sharks, rays, skates and chimaeras that interact with various fisheries (Lamilla *et al.*, 2010). In the 30 years between 1970 and 2000 landing records comprised only four generic categories for cartilaginous fishes; two for sharks, one for skates and one for chimaeras. In the following decade the numbers of categories increased to 9 and 12 in some years (Lamilla *et al.*, 2008) although independent surveys, that formed the basis of this thesis, provides evidence of 17 species that are landed and traded in Chile. The official records of landings are clearly inadequate to describe the true nature of the commercial catch due to lumping species in generic categories; for example, the category ‘skate’ includes at least five skate and ray species. However, the annual variability of the official landing categories can be correlated (and were supplemented) with to the publication of field guide of Chilean cartilaginous fishes made by Lamilla & Bustamante (2005)

The use of landing categories in fishery records creates particular issues that are evident when information collected through fisheries-independent surveys is compared with national landing records from the National Fisheries Service (SERNAP in Spanish). While such coarse-grained reporting is not unusual in many fisheries around the world (Walsh & Eber, 2007; Iglésias *et al.*, 2010), the confusion of species names and obvious errors and omissions in the official record hampers accurate analysis of catch data. The increase in number of landing categories post 2000 may have been a by-product of a Government requirement to maintain species-specific records, but may simply reflect new species landed as result of coastal fisheries diversification for which coastal sharks and rays are considered a separate economic resource. Former discard species may now be landed (and recorded as catch), or derived products from previously unrecorded bycatch, such as shark fins may now be included in the species-catch mix (Hernández *et al.*, 2008). A fathomless abyss still separates official records from the reality that fishermen face every day, and is urgent to increase skilled human resources to aid data collection from commercial activities, improve landing

statistics through basic use of scientific names, and avoid the use of common names and generic categories.

In Chile, few cartilaginous fishes are captured as target species, either in a directed fishery or bycatch. These target species belong to 10 families, including pelagic sharks caught in the North such as, *Prionace glauca* (Family Carcharhinidae), *Lamna nasus* and *Isurus oxyrinchus* (Family Lamnidae) and *Alopias superciliosus* (Family Alopiidae). In the Chile-Peru border region, a small artisanal fleet catches the Pacific guitarfish *Rhinobatos planiceps* (Family Rhinobatidae) and the Chilean angel shark *Squatina armata* (Family Squatinidae). In a lower proportion than other elasmobranchs, the eagle rays *Myliobatis chilensis* and *M. peruviana* (Family Myliobatidae) are landed in a few locations in North Chile. Between Central and South Chile, the elephantfish *Callorhinchus callorhynchus* (Family Callorhinchidae) and coastal sharks such as, *Mustelus mento* and *Galeorhinus galeus* (Family Triakidae), are caught as bycatch in several teleost gillnet fisheries. Most of artisanal fisheries in South Chile are oriented towards the piked dogfish *Squalus acanthias* (Family Squalidae) and the skates *Zearaja chilensis* and *Dipturus trachyderma* (Family Rajidae). The yellownose skate, *Z. chilensis*, is one of the most economically important batoids in South America.

In this thesis, the life histories of three intensely exploited elasmobranchs, the yellownose skate, shortfin mako and blue shark have been described. Together these species represent about 80% of the total reported cartilaginous fish landing by mass in Chile (SERNAP, 2012). They are also the only elasmobranchs for which official landings records are available. Blue shark and shortfin mako are pelagic species that inhabit open waters off North Chile, while the yellownose skate is a demersal species, present in the Central-South continental shelf at >150 m depth. In spite of their intrinsic differences, each of these species is subject to a similar threat as they are all caught on longlines of about 5 km in length bearing 3,600 hooks, and landings of up to 90% of total catch basically comprise immature and juvenile specimens. The present thesis, have provide evidences that clearly identify the threat posed by the artisanal fisheries for survival of the yellownose skate, shortfin mako and blue shark local populations.

In addition to the obvious concern over possible extinction of some cartilaginous fishes and the ensuing economic hardships caused by fisheries collapse, a further problem is the effects that strong declines in apex predators can have on ecosystems. The removal of species that occupy the position of top predators in their ecosystems can have, not only the expected effect of releasing control over their main prey, but sometimes unexpected second and third degree effects on non-prey species through trophic linkages as have been documented after overexploitation events and stock

collapse (Stevens *et al.*, 2000; Schindler *et al.*, 2002; Ferretti *et al.*, 2013; Barausse *et al.*, 2014; Bornatowski *et al.*, 2014; Dulvy *et al.*, 2014).

There have been a number of studies in recent years, linking life history to risk of overexploitation and extinction in cartilaginous fishes (Hoenig & Gruber, 1990, Kirkwood *et al.*, 1994, Cortes, 1998, Smith *et al.*, 1998, Heppell *et al.*, 1999, Cortés, 2002, Gedamke *et al.*, 2007, Forrest & Walters in review), and considering the natural vulnerability and long life spans most of target species, implications for survival and the signs of an imminent fishery collapse need to be reviewed before local extinctions occur. It may sound daunting the use of words like –extinction– especially considering our human temporal scale, but events of local extinction and extirpation due fishing are not that rare in modern history. Dulvy & Forrest (2010) have reviewed and summarised multiple examples, such as the documented population declines of sharks and rays in the Mediterranean Sea, the steep declines of Australian deepwater sharks, the extirpation of the British Columbia basking shark, the local extinctions of North Atlantic skates, the regional extinction of the angel shark *Squatina squatina* in the NE Atlantic and regional extinctions of guitarfishes and sawfishes.

Future directions for Chilean cartilaginous fish research

The current study has demonstrated that the cartilaginous ichthyofauna of Chile is diverse, but still poorly known. This thesis has collected new information on the fundamental biology of many cartilaginous fishes reported in Chilean waters, allowing for a better understanding of their general ecology particularly in, but not restricted to a national context. Cartilaginous fishes are widely distributed in marine habitats worldwide, occupying demersal, pelagic and coastal habitats in tropical, subtropical, temperate and cold waters. Some shark and ray species also occur in brackish and freshwater habitats (Compagno, 1999; Ebert & Compagno, 2007), having evolved physiological mechanisms that allow them to exploit low salinity environments (Ballantyne & Robinson, 2010).

Only a few studies have provided information in an extensive review as included in the present thesis, especially considering the multi-species approach (rather than a focus on a single species) and the breadth of sampling (species, fisheries, geographic and bathymetric variables). Similar studies have been made by State agencies, i.e., Australian agencies such as the Department of Primary Industries (Rose *et al.*, 2001; Gribble *et al.*, 2005) and the Department of Agriculture, Fisheries and Forestry (Henry & Lyle, 2003; Meekan & Cappo, 2004; DAFF, 2012); overseas agencies such as the US NOAA Fisheries (Hale *et al.*, 2010; Passerotti *et al.*, 2010) and NGOs such as the IUCN Shark Specialist Group (Fowler *et al.*, 1997; Cavanagh *et al.*, 2003; Camhi *et al.*,

2007), where authors review the biodiversity of a nation or a particular region in order to assess a species' conservation status (i.e., IUCN Red List) and management policies (e.g., National Plans of Action; Species' Recovery Programs).

In 2007, Chile issued its National Plan of Action (NPOA) for management and conservation of shark and shark-related species (Decreto Supremo N° 198). Considering limitations of reliable data and research priorities, this plan proposed six research areas to provide the data required to achieve a sustainable equilibrium between conservation and fisheries (e.g., conservation of chondrichthyan fish assets and its environment, access and allocation for the conservation of Chondrichthyes and their environment, governance for conservation of Chondrichthyes and their environment, applied research for conservation of Chondrichthyes and its environment).. At the time of issuance of the NPOA the only Conservation Acts that existed related to primary gear construction and fishery access, highlighting the virtually absence of stock assessment and management for commercially fished species.

The best example of a Chilean conservation paradox, is that after enactment of its NPOA which includes a species checklist, the only Conservation Act passed prior to 2009 was the protection (no-take) of three sharks within national waters, namely the basking shark *C. maximus*, white shark *C. carcharias* and whale shark *R. typus*. Of these, only *C. maximus* is a regular species in Chile, while there have been no records of *C. carcharias* and *R. typus* since 1985 (Bustamante *et al.*, 2014). General ignorance of the functional diversity of species within Chilean waters effectively meant that the Conservation Act related 'exclusively' to the protection of the basking shark. The effectiveness of the Act is questionable, as a lack of enforcement has shown that the 'protection' is basically useless, as this species is seasonally caught (as bycatch), killed and semi-exploited (only 'parts' are harvested from the animal carcass) in South Chile (Hernández *et al.*, 2010).

Considering the NPOA guidelines, the present thesis provides basic information to address four of the six "priority research" areas. Since the present thesis started in 2010 (although data collection began in 2005) and although I cannot take entire credit, one Conservation Act and one Government-funded project have been instigated as a consequence of the results published in Chapter 3. The Act No. 20.525 of August 2011 prohibits the shark finning in any Chilean fishery, considering the magnitude and volume of sharks landed and the fins exported (see Bustamante & Bennett, 2013). Additionally, the first integrated assessment to determinate population units of the yellownose skate *Zearaja chilensis* and roughskin skate *Dipturus trachyderma* will be implemented from 2014, based on sexual maturity data and landing trends analyses made by Bustamante *et al.* (2012). This project, funded by the Fisheries Research Fund in behalf of Ministry of Economy, is expected to strengthen links between The University of Queensland and the Universidad Austral de

Chile, and collaboratively characterise demographic and genetic population units the yellownose and roughskin skates.

In spite of the recent support for research, there is still much to do with respect to research that will assist Chilean cartilaginous fish conservation and management. Enforcement of current legislation is urgently required, especially if scientific data results in further statutory regulations as having a law that is not enforced is no law at all. The Government of Chile needs to invest in professional human resources to oversee the collection of valid catch, bycatch and discard data, landings on both a fisheries and a geographical basis, and to ensure enforcement of fisheries legislation. Fishery scientists can analyse facts and provide guidance based on evidence from current and past fisheries interactions, but cannot make and implement the law. For example, in Chapter 3, minimum catch-sizes have been indicated for the *I. oxyrinchus* based on the species' reproductive biology and likely sustainability of the fishery. However, implementation of this proposal would mean a reduction of approximately 50% in the artisanal landings, with the resulting impact on fishermen and their communities that depend economically on this resource. However, if the fishery undergoes a total collapse then the resulting impact would be much more severe on those communities. Another example was the 'fishing ban' for the yellownose skate that occurred between 2009 and 2011. A prohibition to 'catch and land' one of the most important fish resources in South Chile was issued in order to protect the species and avoid an imminent 'extinction due overexploitation' (Bustamante *et al.*, 2012). Carefully worded, this Administrative Order has been modified 13 times, and has allowed the landing of approximately 1,700 tonnes of *Z. chilensis* which represents over 70% of the total landing of the previous five years. More disturbing is that each of those modifications has been requested by artisanal fishermen through the legal concept of an 'exploratory research quota', each of which would have to be supported by a university or research institute. To request this special quota, outside of the annual total allowable catch, is mandatory to conduct a 'scientific research'. Ironically, not a single publication or technical report has been produced (or is publicly available) from these approved exploratory research quotas. This legal loophole of an exploratory research quota has been extensively criticised by national and foreign scientists, as well as by the Chilean Court of Auditors and Fishing Agencies. There is a recent analogy with the 'scientific whaling program' that has been conducted for many years by Japan to justify their commercial whaling interests, again with little valid scientific justification. In respect to the Chilean situation the actions can be understood as "a simple mechanism to extinguish -social fires- granting quotas to artisanal fishermen arguing humanitarian reasons" to quote a former chair of the Fisheries Authority. This kind of social pressure has limited the implementation of moderate- to high-impact management measurements, limiting *actual* conservation actions towards

the protection of sharks that 'do not inhabit' Chilean waters and inoperable, artificial paper-based fishing quotas.

While Chile as a nation may find it difficult to resolve social issues related to the fishermen who seemingly rely on government indifference towards natural (fisheries) resources for their economic dependence, the implementation of management and conservation actions will not be accomplished efficiently. However, this reality must not restrain researchers to provide basic and applied science. Perhaps one day legislators and managers will come to us on a quest for answers, and humbly with a mischievous smile, we can tell them: "I told you so".

REFERENCES

- Ballantyne, J.S. & Robinson, J.W. (2010) Freshwater elasmobranchs: a review of their physiology and biochemistry. *Journal of Comparative Physiology B* 180, 475–493.
- Bustamante, C. & Bennett, M.B. (2013) Insights into the reproductive biology and fisheries of two commercially exploited species, shortfin mako (*Isurus oxyrinchus*) and blue shark (*Prionace glauca*), in the south-east Pacific Ocean. *Fisheries Research* 143, 174–183.
- Bustamante, C., Vargas-Caro, C., Oddone, M.C., Concha, F., Flores, H., Lamilla, J. & Bennett, M.B. (2012) Reproductive biology of *Zearaja chilensis* (Chondrichthyes: Rajidae) in the south-east Pacific Ocean. *Journal of Fish Biology* 80, 1213–1226.
- Bustamante, C., Vargas-Caro, C. & Bennett, M.B. (2014). Not all fish are equal: Functional biodiversity of cartilaginous fishes (Elasmobranchii and Holocephali) in Chile. *Journal of Fish Biology (In Press)*.
- Barausse, A., Correale, V., Curkovic, A., Finotto, L., Riginella, E., Visentin, E., & Mazzoldi, C. (2014) The role of fisheries and the environment in driving the decline of elasmobranchs in the northern Adriatic Sea. *ICES Journal of Marine Science* (Advance Access), DOI: 10.1093/icesjms/fst222.
- Bornatowski, H., Navia, A. F., Braga, R.R., Abilhoa, V. & Correa, M.F.M. (2014) Ecological importance of sharks and rays in a structural foodweb analysis in southern Brazil. *ICES Journal of Marine Science* (Advance Access), DOI: 10.1093/icesjms/fsu025.
- Camhi, M., Valenti, S.V., Fordham, S.V, Fowler, S.L. & Gibson, C. (2007) *The Conservation Status of Pelagic Sharks and Rays*. Report of the IUCN Shark Specialist Group Pelagic Shark Red List Workshop. IUCN Species Survival Commission Shark Specialist Group: Newbury, UK.

- Cavanagh, R., Kyne, P., Fowler, S.L., Musick, J.A. & Bennett, M.B. (2003) *The conservation status of Australasian Chondrichthyans*. Report of the IUCN Shark Specialist Group Australia and Oceania Regional Red List Workshop. The University of Queensland, School of Biomedical Sciences: Brisbane.
- CAPP (2010) *Informe País: Estado del Medio Ambiente en Chile, 2008*. Centro de Análisis de Políticas Públicas: Santiago de Chile.
- Compagno, L.J.V. (1984). FAO species catalogue, Sharks of the world, An annotated and illustrated catalogue of the shark species known to date. Part 1. Hexanchiformes to Lamniformes. *FAO Fishery Synopsis* 125, 1–250.
- Compagno, L.J.V. (1999) An overview of chondrichthyan systematics and biodiversity in southern Africa. *Transactions of the Royal Society of South Africa* 54, 75–120.
- Cortés, E. (1998) Demographic analysis as an aid in shark stock assessment and management. *Fisheries Research* 39, 199–208.
- Cortés, E. (2002) Incorporating uncertainty into demographic modelling: application to shark populations and their conservation. *Conservation Biology* 18, 1048–1062.
- Couturier, L.I.E., Bennett, M.B. & Richardson, A.J. (2013) Mystery of giant rays off the Gaza strip solved. *Oryx* 47, 480.
- DAFF (2012) *National Plan of Action for the Conservation and Management of Sharks 2012*. Shark-plan 2, Australian Government Department of Agriculture, Fisheries and Forestry: Canberra.
- Dalebout, M. L., Mead, J. G., Baker, C. S., Baker, A. N. & Van Helden, A. (2002) A new species of beaked whale *Mesoplodon perrini* sp. n. (Cetacea: Ziphiidae) discovered through phylogenetic analyses of mitochondrial DNA sequences. *Marine Mammal Science* 18, 577–608.
- De Carvalho, M.R., Ebert, D.A., Ho, H. & White, W.T. (2013) Systematics and biodiversity of sharks, rays, and chimaeras (Chondrichthyes) of Taiwan. *Zootaxa* 3752, 1–386.
- Dulvy, N.K. & Forrest, R.E. (2010) Life histories, population dynamics, and extinction risks in Chondrichthyans. In *Sharks and Their Relatives II: Biodiversity, Adaptive Physiology and Conservation* (Carrier, J.C., Musick, J.A. & Heithaus, M.R., eds), pp. 639–680. CRC Press: Boca Raton, FL.
- Dulvy, N. K., Fowler, S. L., Musick, J. A., Cavanagh, R. D., Kyne, P. M., Harrison, L. R., *et al.* (2014) Extinction risk and conservation of the world's sharks and rays. *eLife*, 3, e00590.
- Ebert, D.A. & Compagno, L.J.V. (2007) Biodiversity and systematics of skates (Chondrichthyes: Rajiformes: Rajoidei). *Environmental Biology of Fishes* 80, 111–124.

- Ebert, D.A., Ho, H., White, W.T., & De Carvalho, M.R. (2013a) Introduction to the systematics and biodiversity of sharks, rays, and chimaeras (Chondrichthyes) of Taiwan. *Zootaxa* 3752, 5–19.
- Ebert, D.A., Fowler, S. & Compagno, L.V.J. (2013b). *Sharks of the World*. Wild Nature Press: Plymouth.
- Ferretti, F., Worm, B., Britten, G.L., Heithaus, M.R. & Lotze, H.K. (2010) Patterns and ecosystem consequences of shark declines in the ocean. *Ecology Letters* 13, 1055–1071.
- Ferretti, F., Osio, G.C., Jenkins, C.J., Rosenberg, A.A. & Lotze, H.K. (2013) Long-term change in a meso-predator community in response to prolonged and heterogeneous human impact. *Scientific Reports* 3, 1057.
- Forrest, R.E. & Walters, C.J. (2009) Estimating thresholds to optimal harvest rate for long-lived, low-fecundity sharks accounting for selectivity and density dependence in recruitment. *Canadian Journal of Fisheries and Aquatic Sciences* 66, 2062–2080.
- Fowler, S.L., Reed, T.M. & Dipper, F.A. (1997) *Elasmobranch Biodiversity, Conservation and Management: Proceedings of the International Seminar and Workshop, Sabah, Malaysia, July 1997*. IUCN SSC Shark Specialist Group. IUCN: Gland, Switzerland and Cambridge, UK
- Garcia, V.B., Lucifora, L.O. & Myers, R.A. (2008) The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Proceedings of the Royal Society B* 275, 83–89.
- Gay, C. (1848) *Historia Fisica y Politica de Chile, Zoología* vol. 2. Museo de Historia Natural de Santiago: Santiago.
- Gedamke, T., Hoenig, J.M., Musick, J.A., DuPaul, W.D. & Gruber, S.H. (2007) Using demographic models to determine intrinsic rate of increase and sustainable fishing for elasmobranchs: pitfalls, advances, and applications. *North American Journal of Fisheries Management* 27, 605–618.
- Gudger, E. (1927) Wooden hooks used for catching sharks and *Ruvettus* in the south seas; a study of their variation and distribution. *The American Museum of Natural History* 28, 199–348.
- Goffredo, S., Pensa, F., Neri, P., Orlandi, A., Gagliardi M.S., Velardi, A., Piccinetti, C. & Zaccanti, F. (2010) Unite research with what citizens do for fun: “recreational monitoring” of marine biodiversity. *Ecological Applications* 20, 2170–2187.
- Gribble, N.A., Whybird, O., Williams, L. & Garrett, R. (2005) *Fishery assessment update 1988–2003: Queensland east coast shark*. Department of Primary Industries and Fisheries: Brisbane, Queensland.
- Hale, L.F., Gulak, S.J.B. & Carlson, J.K. (2010) *Characterization of the shark bottom longline fishery*, 2009. NOAA Technical Memorandum NMFS-SEFSC-596.

- Henry, G.W. & Lyle, J.M. (2003) *The National Recreational and Indigenous Fishing Survey*. FRDC Project No. 99/158. Australian Government Department of Agriculture, Fisheries and Forestry: Canberra.
- Heppell, S.S., Crowder, L.B. & Menzel, T.R. (1999) Life table analysis of long-lived marine species with implications for conservation and management. In *Life in the slow lane: ecology and conservation of long-lived marine animals* (Musick, J.A., ed.), pp. 137–147. American Fisheries Society: Bethesda, Maryland.
- Hernández, S., Haye, P.A. & Shivji, M.S. (2008) Characterization of the pelagic shark-fin trade in north-central Chile by genetic identification and trader surveys. *Journal of Fish Biology* 73, 2293–2304.
- Hernández, S., Vögler, R., Bustamante, C. & Lamilla, J. (2010) Review of the occurrence and distribution of the basking shark (*Cetorhinus maximus*) in Chilean waters. *Marine Biodiversity Records* 3, 1–6.
- Hoenig, J.M. & Gruber, S.H. (1990) Life-history patterns in the elasmobranchs: implications for fisheries management. In *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of fisheries* (Pratt, Jr., H.L., Gruber, S.H. & Taniuchi, T., eds.) pp. 1–16. U.S. Department of Commerce, NOAA Technical Report NMFS (National Marine Fisheries Service) 90.
- Iglésias, S.P., Toulhoat, L. & Sellos, D.Y. (2010) Taxonomic confusion and market mislabelling of threatened skates: important consequences for their conservation status. *Aquatic Conservation: Marine and Freshwater Ecosystems* 20, 319–333.
- Jabado, R.W., Al Ghais, S.M., Hamza, W., Henderson, A.C. & Ahmad, M.A. (2013) First record of the sand tiger shark, *Carcharias taurus*, from United Arab Emirates waters. *Marine Biodiversity Records* 6, e27.
- Kempster, R.M., Hunt, D.M., Human, B.A., Egeberg, C.A. & Collin, S.P. (2013) First record of the mandarin dogfish *Cirrhigaleus barbifer* (Chondrichthyes: Squalidae) from Western Australia. *Marine Biodiversity Records* 6, e25.
- Kirkwood, G.P., Beddington, J.R. & Rossouw, J.A. (1994) Harvesting species of different lifespans. In *Large-scale ecology and conservation biology* (Edwards, P.J., May, R.M. & Webb, N.R., eds), pp. 199–227. Blackwell Science: Oxford.
- Lamilla, J. (2005) Bycatch: tiburones en peligro. *Oceana* 11, 1–14.
- Lamilla, J. & Bustamante, C. (2005) Guía para el reconocimiento de: tiburones, rayas y quimeras de Chile. *Oceana* 18, 1–71.

- Lamilla, J., Roa, R., Barría, P., Bustamante, C., Concha, F., Cortes, E., Acuña, E., Balbontín, F., Oliva, M., Araya, M. & Meléndez, R. (2008) Desarrollo metodológico para la estimación del descarte de Condriictios en las pesquerías artesanales. *Universidad Austral de Chile Informe técnico* No. 2008–60, Valdivia. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 March 2014).
- Lamilla J., Bustamante, C., Roa, R., Acuña, E., Concha, F., Meléndez, R., López, S., Aedo, G., Flores, H. & Vargas-Caro, C. (2010) Estimación del descarte de condriictios en pesquerías artesanales. *Universidad Austral de Chile Informe técnico* No. 2008–60, Valdivia. Available at <http://www.fip.cl/Proyectos.aspx> (accessed 25 March 2014).
- Last, P.R., White, W.T. & Pogonoski, J.J. (2007) *Descriptions of new dogfishes of the genus Squalus (Squaloidea: Squalidae)*. CSIRO Marine and Atmospheric Research: Hobart.
- Last, P.R., White, W.T. & Pogonoski, J.J. (2008a) *Descriptions of New Australian Chondrichthyans*. CSIRO Marine and Atmospheric Research: Hobart.
- Last, P.R., White, WT., Pogonoski, J.J. & Gledhill, D.C. (2008b) *Descriptions of new Australian skates (Batoidea: Rajoidae)*. CSIRO Marine and Atmospheric Research: Hobart.
- Last, P.R., White, W.T. & Pogonoski, J.J. (2010) *Descriptions of New Sharks and Rays from Borneo*. CSIRO Marine and Atmospheric Research: Hobart.
- McEachran, J.D. & Dunn, K.A. (1998) Phylogenetic analysis of skates, a morphologically conservative clade of Elasmobranchs (Chondrichthyes: Rajidae). *Copeia* 2, 271–290.
- Meekan, M.G. & Cappo, M. (2004) *Non-destructive Techniques for Rapid Assessment of Shark Abundance in Northern Australia*. Australian Government Department of Agriculture, Fisheries and Forestry: Camberra.
- Mignucci-Giannoni, A.A., Toyos-González, G.M., Pérez-Padilla, J., Rodríguez-López, M.A. & Overing, J. (2000) Mass stranding of pygmy killer whales (*Feresa attenuata*) in the British Virgin Islands. *Journal of the Marine Biological Association of the UK* 80, 383–384.
- Molina, J.I. (1782) *Saggio sulla storia naturale del Chili*. Stamperia di S Tomase D'Aquino: Bologna, Italia
- Musick, J.A. & Bonfil, R. (2005) *Management techniques for elasmobranch fisheries*. Food and Agriculture Organization: Rome.
- O'Brien, B. (1007) *Let's Eat Korean Food*. Hollym Press: Elizabeth, NJ.
- Passerotti, M., Carlson, J.K. & Gulak, S.J.B. (2010) *Catch and Bycatch in U.S. Southeast Gillnet Fisheries*, 2009. NOAA Technical Memorandum NMFS-SEFSC-600.
- Pequeño, G. (1997) Peces de Chile. Lista sistemática revisada y comentada: addendum. *Revista de Biología Marina, Valparaíso* 32, 77–94.

- Philippi, R. A. (1887). Sobre los tiburones y algunos otros peces de Chile. *Anales de la Universidad de Chile* 71, 535–537.
- Rose, C., Gribble, N. & Stapley, J. (2001) *Northern Australian sharks and rays: the sustainability target and bycatch fisheries*. Phase I. Final Report to Fisheries Research and Development Corporation. Department of Primary Industries and Fisheries: Brisbane, Queensland.
- Schindler, D.E., Essington, T.E., Kitchell, J.F., Boggs, C. & Hilborn, R. (2002) Sharks and tunas: fisheries impacts on predators with contrasting life histories. *Ecological Applications* 12, 735–748.
- SERNAP. (2012) *Anuario Estadístico de Pesca. Servicio Nacional de Pesca*. Ministerio de Economía, Fomento y Reconstrucción: Santiago de Chile
- Smith, S.E., Au, D.W. & Show, C. (1998) Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research* 49, 663–678.
- Stevens, J.D., Bonfil, R., Dulvy, N.K. & Walker, P.A. (2000) The effects of fishing on shark, rays, and chimaeras (Chondrichthyans), and the implications for marine ecosystems. *ICES Journal of Marine Science* 57, 476–494.
- Valenzuela, A., Bustamante, C. & Lamilla, J. (2008) Morphological characteristics of five bycatch sharks caught by southern Chilean demersal longline fisheries. *Scientia Marina* 72, 231–237.
- Walsh, J.H. & Ebert, D.A. (2007) A review of the systematics of western North Pacific angel sharks, genus *Squatina*, with redescriptions of *Squatina formosa*, *S. japonica*, and *S. nebulosus* (Chondrichthyes: Squatiniformes, Squatinidae). Zootaxa 1551, 31–47.
- Wetherbee, B.M. & Cortés, E. (2004). Food consumption and feeding habits. In *Biology of Sharks and Their Relatives* (Carrier, J. C., Musick, J. A. & Heithaus, M. R., eds), pp. 223–244. CRC press: Boca Raton, FL.
- White, W.T. & Last, P.R. (2012) A review of the taxonomy of chondrichthyan fishes: a modern perspective. *Journal of Fish Biology* 80, 901–917.
- White, W.T., Blaber, S.J.M. & Craig, J.F. (2012) The current status of elasmobranchs: biology, fisheries and conservation. *Journal of Fish Biology* 80, 897–900.
- WRI (2010) Coastal and Marine Ecosystems, Marine Jurisdictions: Coastline length. World Resources Institute. Available at: <http://web.archive.org/web/20120419075053/http://earthtrends.wri.org/text/coastal-marine/variable-61.html> (Accessed 25 March 2014).

