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ECOLOGICAL RELATIONSHIPS OF THE FISH FAUNA ON CORAL REEFS OF THE MARSHALL ISLANDS¹

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INTRODUCTION

The greatly increased attention paid to scientific aspects of the central Pacific by American scientists following the close of World War II brought sharply into focus our exceedingly meager knowledge of this region. Problems faced by administrators of the

newly created Trust Territory of the Pacific, and by those responsible for maximum safety during and after atomic weapons testing operations stimulated many studies of this vast portion of the globe, of which the study reported here was a part. Significant marine problems such as the nature and distribution of the poisonous fishes of the tropical Pacific islands, the effect of nuclear explosions and radioactive con-

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tamination from weapons testing, and the possibility of commercial sources of marine food products required a thorough knowledge of the nature, extent, and community relationships of the marine fauna and flora. More significant, perhaps, in the long run will be the opportunity for learning more about the optima for utilizing sunlight and raw materials in this relatively isolated, but complex, ecosystem which apparently fluctuates in composition very little, if at all, from year to year, and has over a long period of time acquired a biota successfully adjusted competitively in the relatively constant environment of the tropical west-central Pacific Ocean. It has already been realized by Odum & Odum (1955) that important information might be secured on the relationship between organic productivity, energetic efficiency, and the standing crop structure of such coral reef communities. Moreover, the answers as to how steady state equilibria, such as the reef ecosystem, are self adjusted may be more easily revealed by more critical, comprehensive examination.

To reach reasonable interpretations of the energetics of production and utilization it is necessary, among other things, to determine the relationship between the standing crop, defined as the biomass of existing organisms per unit area, and productivity, defined as the rate of manufacture of this biomass per unit area (Odum 1953). Odum & Pinkerton (1955) indicate that, on a theoretical basis, systems of many types when in open steady state tend to adjust to maximum output of energy consistent with available input energy and a correspondingly low but optimum efficiency. Therefore, if the apparently steady state coral reef ecosystems tend to be similarly self adjusted regarding efficiency of energy utilization between trophic levels, and if the biota remains rather constant in composition as it certainly seems to do, then the pyramids of biomass should be roughly proportional to the standing crop for a particular coral reef area. It becomes paramount in importance, therefore, not only to know the taxonomic composition of the biota of reef areas under intensive study, but to have a rather clear concept of the biotic interaction of the species present to categorize them in proper trophic levels, and to know the community relationships in the various physiographic environments characteristic of the coral reef biotope. The importance of the type of information embodied in this paper may best be illustrated by the following statement made by Odum & Odum (1955), "Although the trophic relationships of most of the higher organisms on the reef are very imperfectly known, an attempt has nevertheless been made to make rough groupings by trophic level as to herbivores, carnivores, and decomposers."

PREVIOUS RESEARCH

Although numerous workers have reported on the feeding habits of Pacific fishes, only two authors report in any comprehensive manner and neither makes any attempt to express his results as meaningful eco-

logical aspects. In a very painstaking study of the digestive system and feeding habits of fishes of Japan, Suyehiro (1942) provided far more information on these subjects than had theretofore been available. Moreover, he included an extensive review of the literature which now makes it unnecessary to discuss this matter for the period preceding his publication. Suyehiro based his study on 88 families, 132 genera, and 150 species, providing a firm basis for many of the central Pacific families and genera. Only a few species reported by Suyehiro reach the central Pacific area. Al-Hussaini (1947) reported on a similar study of some 60 species in the vicinity of the Marine Biological Station at Ghardaqa, Red Sea, and included many of the widespread Indo-Pacific types. Randall (1955) reported on the fishes of the Gilbert Islands and included notes on food habits for a few of the specimens collected. Only two papers dealing with the Indo-Pacific fish fauna (Hiatt 1947a, 1947b), and these dealing with a special type of ecosystem, have approached the problem of food and feeding habits of fishes from the point of view of biotic interaction. Scattered accounts of feeding habits of Pacific fishes occur incidentally in other papers, and these will be mentioned in the species accounts where pertinent.

SCOPE OF THE PRESENT STUDY

Reported herein are accounts of the food and feeding habits and ecological relationships of 56 families of Marshallese fishes, covering 127 genera and 233 species. Some idea of the completeness of coverage of the study may be gained from the fact that in the Marshall Islands there are about 225 genera and about 600 species of fish. We have examined therefore somewhat more than half of the genera and slightly less than half of the species known to be present. Because the Marshallese fauna is part of the widespread Indo-Pacific faunal complex, the significance and applicability of this study extends a great deal further than the west-central Pacific Ocean islands.

The study was initiated at Bikini Atoll in the summer of 1947, as part of the Bikini Scientific Resurvey to determine what changes had resulted, if any, from Operations Crossroads, continued at Arno Atoll during the summer of 1950 as part of the Coral Atoll Project of the Pacific Science Board, and completed at Eniwetok Atoll during the summer of 1955 as part of the regular studies being carried out at the U. S. Atomic Energy Commission's Eniwetok Marine Biological Laboratory. The total number of individual fish stomachs examined was 2,051, of which 209 were examined at Bikini, 1,185 at Arno, and 657 at Eniwetok.

A systematic list of the families, genera, and species covered by this food study follows, and a few species, not examined for food, are cited elsewhere in the text.

- Family Carcharinidae (gray sharks)
Carcharinus melanopterus (Quoy and Gaimard)
C. menisorrh (Müller and Henle)
- Family Triakidae (smooth dogfishes)
Triadenodon obesus (Rüppell)
- Family Orectolobidae (carpet sharks)
Ginglymostoma ferrugineum (Lesson)
- Family Mobulidae (manta rays)
Manta alfredi (Krefft)
- Family Dussumieridae (round herrings)
Sprattelloides delicatulus (Bennett)
- Family Clupeidae (sardines)
Harengula kunzei Bleeker
- Family Ophichthidae (snake eels)
Leiuranus semicinctus (Lay and Bennett)
Brachysomophis sauropsis Schultz
- Family Muraenidae (moray eels)
Echidna zebra (Shaw)
E. leucotaenia Schultz
E. polyzona (Richardson)
Uropterygius xanthopterus Bleeker
Rabula marshallensis Schultz
Gymnothorax pictus (Ahl)
G. petelli (Bleeker)
G. javanicus (Bleeker)
G. flavimarginatus (Rüppell)
G. buroensis (Bleeker)
G. undulatus (Lacepede)
G. margaritophorus Bleeker
G. rupelli (McClelland)
G. fimbriatus (Bennett)
G. sp.
- Family Congridae (conger eels)
Conger noordzieki Bleeker
- Family Moringuidae (whip eels)
Moringua macrochir Bleeker
- Family Synodontidae (lizard fishes)
Synodus variegatus (Lacepede)
Saurida gracilis (Quoy and Gaimard)
- Family Belonidae (needle fishes)
Strongylura gigantea (Temminck and Schlegel)
S. incisa (Cuvier and Valenciennes)
- Family Hemiramphidae (halfbeaks)
Hyporhamphus laticeps (Günther)
H. affinis (Günther)
- Family Bothidae (flounders)
Bothus mancus (Broussonet)
- Family Holocentridae (squirrel fishes)
Myripristis berndti Jordan and Evermann
M. microphthalmus Bleeker
M. sp.
Holocentrus sammara (Forskål)
H. lacteoguttatus Cuvier and Valenciennes
H. microstomus Günther
H. laevis Günther
H. diadema Lacepede
H. spinifer (Forskål)
H. sp.
- Family Syngnathidae (pipe fishes)
Corythoichthys flavofasciatus conspicillatus (Jenyns)
C. intestinalis waitei (Jordan and Seale)
- Family Aulostomidae (trumpet fishes)
Aulostomus chinensis (Linnaeus)
- Family Fistulariidae (cornet fishes)
Fistularia petimba Lacepede
- Family Atherinidae (silversides)
Stenatherina temminckii (Bleeker)
Allanetta ovalaua (Herre)
Pranesus pinguis (Lacepede)
- Family Mugilidae (mulletts)
Neomyxus chapali (Eyedoux and Souleyet)
Crenimugil crenulabris (Forskål)
- Family Sphyraenidae (barracudas)
Sphyraena qenie Klünzinger
- Family Polynemidae (threadfins)
Polydactylus sexfilis (Cuvier and Valenciennes)
- Family Scombridae (tunas)
Gymnosarda nuda (Günther)
Euthynnus affinis yaito Kishinouye
Katsuwonus pelamis (Linnaeus)
- Family Carangidae (jacks)
Trachurus crumenophthalmus (Bloch)
Trachinotus bailloni (Lacepede)
Carangoides ferdau jordani Nichols
Caranx melampygus Cuvier and Valenciennes
C. lessoni Bleeker
Elagatis bipinnulatus (Quoy and Gaimard)
- Family Apogonidae (cardinal fishes)
Apogon novemfasciatus Cuvier and Valenciennes
A. snyderi Jordan and Evermann
A. exostigma (Jordan and Starks)
A. nigrofasciatus Lachner
A. novaeguineae Cuvier and Valenciennes
A. erythrinus Snyder
Apogon sp.
Gymnapogon philippinus (Herre)
Paramia quinquelineata Cuvier and Valenciennes
Cheilodipterus macrodon (Lacepede)
- Family Priacanthidae (bigeyes)
Priacanthus cruentatus (Lacepede)
- Family Serranidae (groupers)
Epinephelus merra Bloch
E. fuscoguttatus (Forskål)
E. kohleri Schultz
E. hexagonatus (Bloch and Schneider)
E. macrospilos (Bleeker)
E. spilotos Schultz
Variola louti (Forskål)
Cephalopholis urodelus (Bloch and Schneider)
C. miniatus (Forskål)
C. argus Bloch and Schneider
- Anyperodon leucogrammicus* (Cuvier and Valenciennes)
Plectropomus truncatus Fowler
- Family Pseudochromidae
Plesiops melas Bleeker
P. nigricans (Rüppell)
Pseudogramma polyacantha (Bleeker)
Pseudochromis tapeinosoma Bleeker
- Family Pempheridae (sweepers)
Pempheris ovalensis Cuvier and Valenciennes
- Family Lutjanidae (snappers)
Lutjanus monostigmus (Cuvier and Valenciennes)
L. bohar (Forskål)
L. vitta (Quoy and Gaimard)
L. vaigiensis (Quoy and Gaimard)
L. gibbus (Forskål)
Scolopsis cancellatus (Cuvier and Valenciennes)
Gymnocranius griseus (Schlegel)
Lethrinus microdon Cuvier and Valenciennes
Aprion virescens Cuvier and Valenciennes
Gnathodentex aureolineatus (Lacepede)
- Family Leleognathidae (Silver perch)
Gerres argyreus (Bloch and Schneider)
- Family Sparidae (snappers)
Monotaxis grandoculis (Forskål)
- Family Mullidae (goat fishes)
Mulloidichthys samoensis (Günther)
Parupeneus trifasciatus (Lacepede)
P. barberinus (Lacepede)
P. cyclostomus (Lacepede)
Upeneus arge Jordan and Evermann
- Family Cirrhitidae (hawkfishes)
Amblycirrhitus arcatus (Cuvier and Valenciennes)
Paracirrhites forsteri (Bloch)
Cirrhitichthys aprinus (Cuvier and Valenciennes)
Cirrhitus pinnulatus (Bloch)
- Family Siganidae (rabbit fishes)
Siganus rostratus (Cuvier and Valenciennes)
- Family Kyphosidae (pilot fishes)
Kyphosus cinerascens (Forskål)
- Family Chaetodontidae (butterfly fishes)
Chaetodon lunula (Lacepede)
C. citrinellus Cuvier and Valenciennes
C. ephippium Cuvier and Valenciennes
C. vagabundus Linnaeus
C. reticulatus Cuvier and Valenciennes
C. auriga Forskål
Megaprotodon strigangulus (Gmelin)
Centropyge flavissimus (Cuvier and Valenciennes)
- Family Acanthuridae (surgeon fishes)
Acanthurus mata Cuvier and Valenciennes
A. xanthopterus Cuvier and Valenciennes
A. gahhm (Forskål)
A. olivaceus Schneider
A. triostegus triostegus (Linnaeus)
A. achilles Shaw
A. aliala Lesson
A. nigroris Cuvier and Valenciennes
A. guttatus Bloch
A. lineatus (Linnaeus)
Otenochaetus striatus (Quoy and Gaimard)
Naso lituratus (Schneider)
N. unicornis (Forskål)
Zebrasoma veliferum (Bloch)
- Family Scorpaenidae (scorpion fishes)
Scorpaenodes parvipinnis (Garrett)
Scorpaenodes sp.
Scorpaenopsis gibbosa (Bloch)
Pterois radiata Cuvier and Valenciennes
P. volitans (Linnaeus)
Synanceja verrucosa Bloch
- Family Caracanthidae
Caracanthus unipinnus (Gray)
- Family Platycephalidae (flatheads)
Thysanophrys sp.
- Family Pomacentridae (damselfishes)
Abudefduf sordidus (Forskål)
A. septemfasciatus (Cuvier and Valenciennes)
A. leucopomus (Lesson)
A. saxatilis (Linnaeus)
A. dicki (Lienard)
A. biocellatus (Quoy and Gaimard)
A. amabilis (DeVis)
A. glaucus (Cuvier and Valenciennes)
A. lacrymatus (Quoy and Gaimard)
Chromis atripectoralis Welander and Schultz
O. caeruleus (Cuvier and Valenciennes)
Dascyllus aruanus (Linnaeus)
Pomacentrus pavo (Bloch)
P. nigricans (Lacepede)
P. jenkinsi Jordan and Evermann
P. albofasciatus Schlegel and Müller
P. vaudii Jordan and Seale
- Family Labridae (wrasses)
Epibulus insidiator (Pallas)
Gomphosus varius Lacepede
Pseudochelinus hexataenia (Bleeker)
Labroides dimidiatus (Cuvier and Valenciennes)
Novaculichthys taeniourus (Lacepede)
Stethojulis axillaris (Quoy and Gaimard)
Stethojulis sp.
Halichoeres hoeveni (Bleeker)
H. marginatus Rüppell
H. hortulanus (Lacepede)

<i>H. trimaculatus</i> (Quoy and Gaimard)	<i>Scarus bicolor</i> Rüppell	Family Parapercidae (sand perch)	<i>Pseudobalistes flavimarginatus</i> (Rüppell)
<i>H. margaritaceus</i> (Cuvier and Valenciennes)	<i>S. sordidus</i> Forskål	<i>Parapereis cephalopunctatus</i> (Seale)	<i>P. fuscus</i> (Bloch)
<i>Macropharyngodon meleagris</i> (Cuvier and Valenciennes)	<i>S. sp.</i>	<i>P. clathrata</i> Ogilby	<i>Melichthys vidua</i> (Solander)
<i>M. pardalis</i> (Kner)	<i>S. sp.</i>	Family Blenniidae (blennies)	Family Monacanthidae (file fishes)
<i>Thalassoma umbrostigma</i> (Rüppell)	<i>S. sp.</i>	<i>Aspidontus taeniatus</i> Quoy and Gaimard	<i>Amanses carolae</i> (Jordan and McGregor)
<i>T. quinquevittata</i> (Lay and Bennett)	Family Gobiidae (gobies)	<i>Istiblennius coronatus</i> (Günther)	<i>Oxymonacanthus longirostris</i> (Bloch)
<i>T. lucasanum marnae</i> Schultz	<i>Gnatholepis anjerensis</i> (Bleeker)	<i>I. paulus</i> (Bryan and Herre)	<i>Monacanthus</i> sp.
<i>T. hardwicki</i> (Bennett)	<i>Gobius ornatus</i> Rüppell	<i>Exallias brevis</i> (Kner)	Family Ostracionidae (trunk fishes)
<i>T. lutescens</i> (Lay and Bennett)	<i>Bathygobius fuscus fuscus</i> (Rüppell)	<i>Cirripectus variolosus</i> (Cuvier and Valenciennes)	<i>Ostracion cubicus</i> Linnaeus
<i>Cheilinus oxycephalus</i> Bleeker	<i>Gobiodon erythrospilus</i> Bleeker	<i>C. sebæ</i> (Cuvier and Valenciennes)	Family Tetraodontidae (puffers)
<i>C. chlorourus</i> (Bloch)	<i>G. rivulatus</i> (Rüppell)	Family Brotulidae	<i>Arothron mappa</i> (Lesson)
<i>C. trilobatus</i> Lacepede	<i>Paragobiodon echinocephalus</i> (Rüppell)	<i>Dinematichthys lucoosteoides</i> Bleeker	<i>A. hispidus</i> (Linnaeus)
<i>Coris angulata</i> Lacepede	Family Eleotridae (sleepers)	Family Balistidae (trigger fishes)	<i>A. meleagris</i> (Lacepede)
<i>C. gaimardi</i> (Quoy and Gaimard)	<i>Valenciennæa violifera</i> Jordan and Seale	<i>Rhinecanthus rectangulus</i> (Bloch)	<i>A. nigropunctatus</i> (Bloch)
<i>Hemigymnus melapterus</i> (Bloch)	<i>V. strigata</i> (Broussonet)	<i>R. aculeatus</i> (Linnaeus)	<i>Arothron</i> sp.
Family Scaridae (parrot fishes)	Family Microdesmidae	<i>Balistapus undulatus</i> (Mungo Park)	Family Canthigasteridae (sharp-backed puffers)
<i>Cryptotomus spinidens</i> (Quoy and Gaimard)	<i>Paragobioides grandoculis</i> Kendall and Goldsborough	<i>Balistoides viridescens</i> (Bloch and Schneider)	<i>Canthigaster solandri</i> (Richardson)
	Family Echeiseidae		Family Diodontidae (spiny puffers)
	<i>Echeis naucrates</i> Linnaeus		<i>Diodon hystrix</i> Linnaeus

During the course of this study the authors were supported by several agencies all of which generously provided both funds, supplies, equipment, transportation, and shelter. The United States Atomic Energy Commission supported the studies at Bikini and at Eniwetok, the latter studies being carried out under the auspices of the A.E.C. Division of Biology and Medicine at the Eniwetok Marine Biological Laboratory. The study at Arno Atoll was part of the Coral Atoll Program sponsored by the Pacific Science Board of the U. S. National Research Council, under its major project Scientific Investigations in Micronesia. Funds to support the Coral Atoll Project were provided by the U. S. Office of Naval Research. Special acknowledgment is due to the Military Air Transport Service and to officials of the Civil Administrative Staff of the Trust Territory (Navy) for logistical support of this work.

The University of Hawaii through its Pacific Islands Research Fund provided generously for all the equipment and supplies for the work at Arno Atoll, and provided technical assistance in working up the mass of data collected for this study. Marian Adachi Kohn, staff artist for the Hawaii Marine Laboratory, drew the figures depicting habitat associations on the Marshallese coral reefs.

DESCRIPTION OF THE STUDY AREAS

The Marshall Islands are a group of atolls lying north of the Gilbert Islands and east of the Caroline Islands. All are enclosed in an area bounded by the parallels of latitude 4°30'N and 15°N and the meridians of longitude 161°E and 174°E (Fig. 1). They are about 2,500 statute miles west-southwest of Honolulu, Hawaii, and 4,700 statute miles from San Francisco. Most of the atolls are distributed along two chains which are nearly parallel and trend north-westward. The eastern is named the Ratak Chain (which includes Arno Atoll near its southern end)

and the western the Ralik Chain (which includes Bikini at its northern end). Besides the two main chains there are several isolated outlying atolls, of which Eniwetok Atoll is one, lying west of the chain. Bikini Atoll is located between the parallels of latitude 11°30' to 11°40'N and between the meridians of longitude 165°10' and 165°40'E. Eniwetok Atoll is located between the parallels of latitude 11°20' to 11°40'N and between the meridians of longitude 162° to 162°30'E. Arno Atoll is located between the parallels of latitude 7° to 7°30'N and between the meridians of longitude 171°30' to 172°E. The physiographic features of Bikini Atoll and Eniwetok Atoll are set forth in great detail by Emery, Tracey, & Ladd (1954), and these features for Arno Atoll were described by Wells (1951).

The major ocean current systems in the Marshall Islands area are the westerly-flowing North and South Equatorial Currents and the easterly-flowing Equatorial Countercurrent lying between them. Most of the Marshall Islands lie athwart the North Equatorial Current which extends north of latitude 6°-8°N and occupies the zone of the northeast trade winds. The Equatorial Countercurrent lies south of the North Equatorial Current and usually has its southern boundary just north of the equator. Thus Arno Atoll is located in the divergence of these current systems which brings about upwelling and resultant high organic productivity. These hydrographic conditions, coupled with a higher rainfall and resultant terrestrial productivity, make the reefs of Arno Atoll more productive than those of Bikini and Eniwetok Atolls lying farther to the north.

Water temperatures at the surface in the Marshall Islands are among the highest found anywhere in the open ocean far from large land masses. During summer average temperatures range between 82° and 85°F. The average annual range of temperature along the entire island chain down to a depth of about 300 feet is only 3° to 4°F.

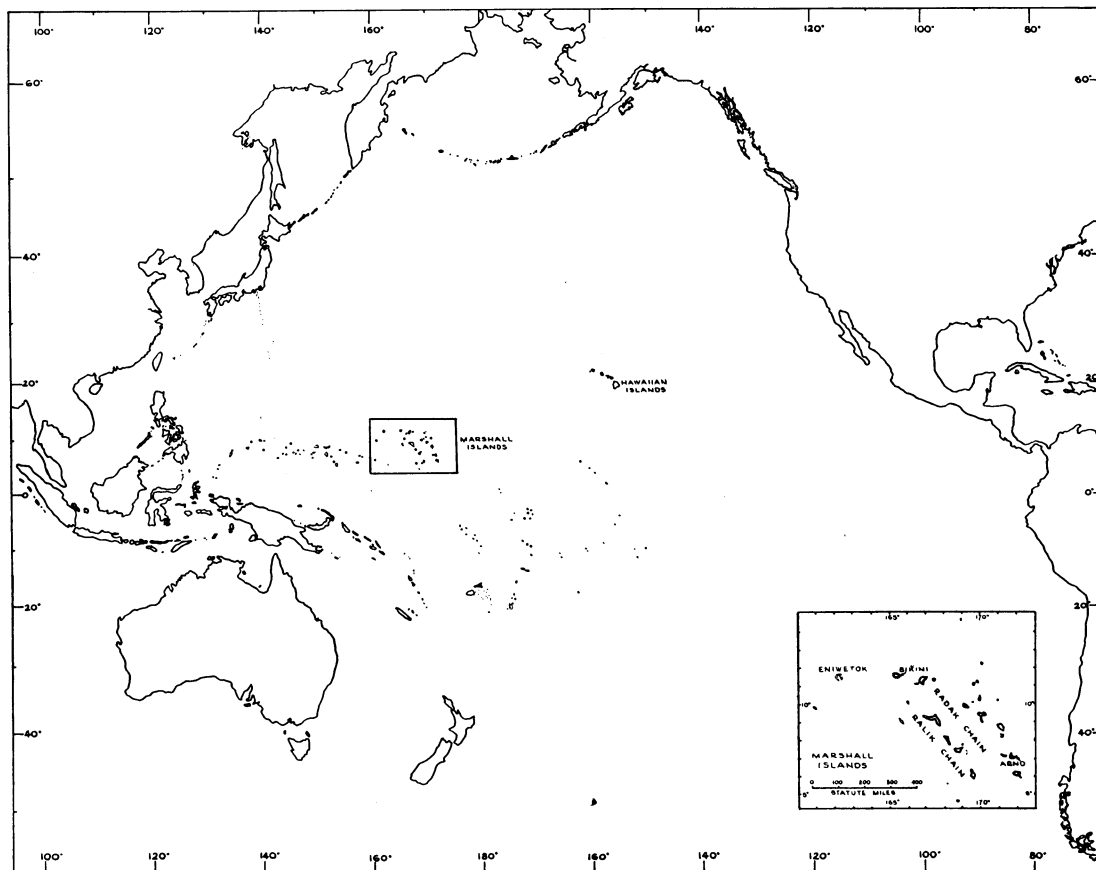


FIG. 1. The Pacific Ocean showing the location of Arno, Bikini, and Eniwetok Atolls.

Rainfall along the island chains varies considerably from north to south. At Arno the average rainfall is about 200 in, whereas at Bikini and Eniwetok it is about 50 in. The difference in rainfall is reflected in the surface oceanic salinity values which range from about 33.7 ‰ in the southern Marshall Islands to about 35.3 ‰ in the northern area of the chains. Although no data have been collected regarding tidal cycle effects on the salinity values across the reefs of Bikini and Eniwetok Atolls, such data from Arno Atoll indicate that a gradient occurs during low tides across the seaward reefs from about 50% oceanic salinity near shore to 100% oceanic salinity just off the seaward reef front. This phenomenon, associated with the runoff of fresh water from the Ghyben-Herzberg lens under the island, has a profound effect on the distribution of corals, and indirectly, if not directly, the distribution of fish on these seaward reefs (Hiatt 1958).

The tidal amplitude varies somewhat from the northern islands in the chains to those of the southern end. At Arno Atoll the mean tidal range is 3.8 ft and the mean spring tide range is about 4.1 ft. At Eniwetok and Bikini Atolls the mean tidal range is about 2.7 ft, while the mean spring tide range is about 3.9 ft. This tidal range is sufficiently extensive

to change almost completely the biotic composition of the fish fauna on the flat, table-like seaward reefs which are virtually uncovered during low tides, but which are covered by about 2-4 ft of water during high tides.

Rather detailed descriptions of the reefs of Bikini and Eniwetok Atolls are given by Tracey, Ladd & Hoffmeister (1948), Ladd, Tracey, Wells, & Emery (1950), and Emery, Tracey, & Ladd (1954). Wells (1951) has described those of Arno. Consequently, only a brief summary will be presented here. The reefs of the Marshall Islands, like those elsewhere, are highly complicated structures which can be only roughly classified into three primary types, windward, leeward, and lagoon reefs. Most of these reefs exhibit well-developed zonation, the zones tending to parallel the reef front. The nature and extent of these zones depends on many factors, e.g., prevailing winds and currents, fresh water runoff from islands, and ecological factors determining the suitability of the environment for particular species. Although no two atoll reefs are identical, the major features which are controlled by wind, waves, and temperatures, have much in common.

The windward reefs, exposed to the prevailing trades that blow from the east and northeast during

most of the year, differ markedly from the leeward reefs. The reef surface is comparatively flat and is covered with adequate water for most fishes only during periods of high tides. The outer marginal zones are usually flourishing and most often are bordered by a coralline ridge which receives the main impact of the waves. These reefs flats may be up to a half-mile in width, with several distinctive shoreward zones in which characteristic faunal and floral associations appear.

The leeward reefs are narrow, being only 200-500 ft in width. Their seaward margins are usually made irregular by surge channels which frequently extend inward 10-30 yds. No coralline ridge is present, and corals grow in great profusion, covering half or more of the reef surface. Usually, the leeward reefs are less elevated than those of the windward type so that the biota is resident. Only the largest of the roving carnivores slip over the reef front at high tide to forage on the reef flat.

Lagoon reefs vary depending upon their exposure to the prevailing wind. In protected areas there is a discontinuous series of irregular reef patches which extend from near shore to the outer slope leading to the deeper parts of the lagoon. These reef patches are not subjected to heavy wave impact, the only water movement aside from prevailing currents which affects them is the slow ocean swells which enter the lagoons through passages. Usually these conditions favor a luxuriant growth of coral in its more delicate form, imparting to these coral patches striking beauty. The fauna and flora are largely unaffected by tides and remain closely associated with the coral patches. Extensive sand and rubble flats separate the coral patches, and characteristic animal communities there contrast with those ecologically more closely tied to coral patches. On the leeward side of these atolls the lagoon reefs are better developed and frequently are continuous, because they receive fairly strong waves engendered by the prevailing winds which have a fetch of up to 20 miles or more across the lagoon. In some instances, these reefs come to resemble those characteristic of the windward side of the atoll, in that they frequently have an elevated algal ridge bordering the reef margin and may be flattened shoreward of the reef margin. However, they usually lack the distinct zonation characteristic of the seaward reefs of the windward side.

METHODS

Most of the fishes collected for this study were taken by poisoning sections of the reefs with rotenone. However, many were taken with spears, hook and line, explosives, and other techniques suitable for the occasion. The advantage of rotenone is that it almost simultaneously kills all fish in an area, and causes those deep in interstices of the corals and rocks, as well as those in burrows to come to the surface. In this way all members of a fish community can be collected and analyzed for their interrelationships as all niches filled give up their fish fauna for study.

The following data were recorded for each specimen examined: (1) standard length, (2) sex, (3) extent of development of the gonads, (4) nature of the alimentary tract, i.e., length, thickness of intestinal wall, presence or absence of a gizzard, (5) nature of the dentition and gill rakers, position and special features of the mouth, and (6) type of food items contained in the stomach, or, if empty, those found in the intestine.

For the food habits analysis the particular food items were listed and the numbers of fish containing the items were tallied. This method was used because it gives essentially the predilection of each fish species for particular items of diet. In studies of food and feeding interrelationships these types of data are most important. Such methods of analysis as the comparative quantities of different food items ingested become significant only when sufficient specimens are analyzed to ensure that one or a few large items taken by only one or a few fish do not give spurious percentages for the total. In most cases in the present study neither time nor specimens were available to add biomass or volume measurements. However, in those instances when a fish had consumed a great preponderance of a particular item, along with numerous other incidental items, it was noted in our records. For many species sufficient specimens were examined so that the percentage of fish containing the item became significant, and these are so listed in the systematic analysis of the food and feeding habits. If too few fish were available the results were recorded simply as the number of fish containing the item.

Naturally, collecting fish by means of rotenone poisoning resulted in many of the large carnivorous and predaceous species consuming smaller species which had succumbed earlier to the poison. Fish found in the stomachs which appeared too freshly caught were therefore discarded.

It will be obvious to the reader that biotic interrelationships and community groupings based solely on circumstantial evidence presented by food items in stomachs and structural features adapted for food getting, while exceedingly important, could not provide all the evidence needed to interpret data such as are presented in this paper. Consequently, it will be reassuring to state that hundreds of hours of underwater observations using skin-diving equipment have contributed very substantially to our results and interpretations. As a matter of fact, the analyses of natural aggregations in the various habitats on the reefs, to be presented later in this paper, were only possible by combining our field observations with the stomach analyses.

The results of our studies will be presented first by a systematic analysis and discussion of the food and feeding habits of the species, genera, and families represented. Following these data an analysis will be made of the major feeding habits characteristic of the species studied. Discussions will include such natural groupings as algal feeders, plankton feeders,

omnivores, detritus feeders and scavengers, coral polyp feeders, and large roving carnivores. The interrelationships of naturally occurring assemblages on the reefs will be discussed also. In this section accounts will cover fish associated with mid-water and surface fauna, fish associated with the bottom, fish associated with rock and coral ledges and caverns, fish associated with branching corals and their dead bases, fish associated with solid coral heads, fish

associated with the surf zone, fish associated with the windward sea reef flats, and fish associated with tide pools.

Discussions of the trophic levels represented by the fish studied will be presented also. Following this section the study will be summarized by a consideration of the results in the form of the food chains and the food web found on these coral reefs of the Marshall Islands.

FOOD AND FEEDING HABITS BY TAXONOMIC CATEGORIES

Family Carcharhinidae

Species: *Carcharhinus melanopterus* (black-tipped shark)
Number examined: Eniwetok, 3 specimens: 2 empty
Sex: 1 male; 1 female
Standard length: 690-1,200 mm

Two specimens were caught near the garbage dump; one stomach was empty and one contained garbage only. One specimen taken on the seaward reef flats had a partly digested fish in its stomach. This is the most common shark on the seaward reefs both on the windward and leeward sides of the atolls. It moves onto the reef flat as the tide rises, and forages widely. It also occurs on the lagoon reefs, but there the individuals are usually of larger size and are less numerous than on the seaward reefs. This shark seems to have a rather curious nature and many encounters with it in the water indicate that it has poor vision. Consequently, it usually approaches very closely to persons wading or swimming before it suddenly darts away. It habitually enters recently poisoned areas to devour small fish rendered moribund by rotenone, and is itself rather resistant to this poison. It is classed as a roving carnivore and scavenger.

Species: *C. menisorrhah* (gray shark)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 1,450 mm

One specimen was caught at the garbage dump, but the stomach was empty. This species is more common in the lagoons than is *C. melanopterus*, and is also found along the outer edge of the seaward reef front cruising in water 15-20 ft in depth. It frequently enters surge channels along the seaward reef. On numerous occasions this species has competed with us in picking up fish during poison station operations. At such times, individuals up to 7-8 ft in length enter water only 2-3 ft deep. It is classed as a roving carnivore and scavenger.

Family Summary

Members of the Family Carcharhinidae are by far the most abundant sharks on Marshallese reefs, and certainly occupy an important position among the carnivores as well as the scavengers of the coral reef community.

Family Triakidae

Species: *Triaenodon obesus* (white-tipped shark)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 1,150 mm

One specimen caught near the garbage dump had no food in its stomach. Next to *C. melanopterus* this shark is the most abundant on Marshallese reefs both in the lagoon and in lee seaward reefs. It is ubiquitous in surge channels and competes lively in picking up fish

killed by rotenone. It is not timid and approaches disconcertingly close to humans before turning away. As with *C. melanopterus*, its vision seems to be poor and its apparent boldness is probably just exploratory.

Family Orectolobidae

Species: *Ginglymostoma ferrugineum* (nurse shark)
Number examined: Eniwetok, 3 specimens: 2 empty
Sex: Males and females
Standard length: 2,100-2,500 mm

Two of the specimens were empty and the third contained partly digested remains of a rabbit fish (*Siganus* sp.). Since the nurse sharks were taken near the garbage dump, it is probable that the *Siganus* may have been dead before it was eaten. The species is a very sluggish, bottom-dwelling scavenger which rarely comes into water less than 50 ft deep. It was never seen on the reefs by us in the Marshall Islands, but a small individual was taken in shallow water in the Gilbert Islands.

Family Mobulidae

Species: *Manta alfredi* (manta ray)
Number examined: Bikini, 1 specimen
Sex: Female
Standard breadth: 2,950 mm

The stomach of this specimen contained approximately one quart of copepods and other crustacean plankters. Its planktonic feeding habits are well known. These rays were seen daily swimming about near the center of Enyu Channel, Bikini, and occasionally at various other places at Eniwetok and Arno. At Arno one approached us very closely while we were swimming just seaward of the reef margin near Ine Village, coming to within 20-30 ft of the reef edge.

Family Dussumieridae

Species: *Spratelloides delicatulus* (round herring)
Number examined: Arno, 20 specimens
Sex: Both males and females
Standard length: 20-70 mm
Digestive tract: Gill rakers very long; Y-shaped stomach; short, straight intestine.

Food item	Percentage of fish containing the item
Crustacea	
Copepods	85
Shrimp larvae	80
Ostracods	50
Crab zoeae	20
Mollusca	
Protoconchs	10
Polychaeta	10

This species is a typical plankton feeder, and shows a strong predilection for planktonic crustaceans. It occurs at all three atolls in very large schools on the lagoon reefs and on sheltered seaward reefs, occurring even in very shallow water just off the beaches. It is

especially common around piers and ships' hulls. Tunas, belonids, and the carangid, *Scomberoides sanctipetri*, frequently are seen slashing through these dense schools of round herrings. Terns hover above the schools to catch the fish whenever they swim close to the surface.

Family Clupeidae

Species: *Harengula kunzei* (sardine)
Number examined: Arno, 20 specimens
Sex: Both males and females
Standard length: 37-82 mm.
Digestive tract: Y-shaped stomach; straight, short intestine

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	55
Ostracods	50
Copepods	15
Shrimp larvae	10
Unidentified crustacean fragments	40
Polychaeta	15
Foraminifera	
<i>Calcarina</i> sp.	5

This species, seen only at Arno, occurred in large schools in shallow water near the lagoon beaches. Unlike its counterpart in Japan, *H. zunasi*, which is exclusively a plankton feeder (Suyehiro 1942) taking diatoms and copepods, the Arno species is carnivorous and feeds on the shallow bottom fauna.

Family Ophichthidae

Species: *Leiuranus semicinctus* (snake eel)
Number examined: Eniwetok, 5; Bikini, 1 specimen: 5 empty
Sex: Undeveloped
Standard length: 215-490 mm
Digestive tract: short, straight intestine

The single specimen with food in its stomach contained a partly digested fossorial hemichordate, *Ptychodera* sp. It apparently feeds under the sand where it is common in areas of fine gravel-like deposits on the shallow reefs. It does not live in permanent burrows, but is capable of burying itself rather rapidly.

Species: *Brachysomophis sauropsis* (snake eel)
Number examined: Eniwetok, 2 specimens
Sex: Males
Standard length: 260-400 mm
Digestive tract: short, straight intestine

The food found in these two specimens consisted of unidentified fish fragments, a very small *Octopus* sp., several specimens of the ubiquitous foraminiferan, *Calcarina* sp., and sand grains. Like *L. semicinctus*, this species lives buried in gravelly sand without permanent burrows. It was taken commonly on all reef areas where sandy bottoms occurred. Unlike *L. semicinctus*, which has the eyes normally located on the head, *B. sauropsis* has the eyes almost at the tip of the snout, which, together with the food items taken, suggests that the latter species probably lies under the sand with just the tip of the snout protruding, keeping watch for prey inadvertently crawling or swimming close to it.

Family Muraenidae

Species: *Echidna zebra* (moray eel)
Number examined: Arno, 2 specimens
Sex: Male
Standard length: 375-575 mm
Digestive tract: teeth molariform; short, straight intestine

The specimens examined had all consumed crabs of the genus *Etisus* and other unidentified xanthids, and one contained, in addition, the crushed shell of the common reef urchin, *Echinometra mathaei*.

Species: *Echidna leucotaenia* (moray eel)
Number examined: Arno, 2 specimens
Sex: Male
Standard length: 365 mm
Digestive tract: Teeth molariform; short, straight intestine.

The specimens examined had crab fragments in their stomachs; one had fragments of a swimming crab (Portunidae) and the other contained fragments of a xanthid crab.

Species: *Echidna polyzona* (moray eel)
Number examined: Eniwetok, 1 specimen
Sex: Undeveloped
Standard length: 520 mm
Digestive tract: Teeth molariform; short, straight intestine

This specimen had consumed a large shrimp, *Saron marmoratus*, which habitually secludes itself under rocks and ledges.

Generic Summary

None of the species of *Echidna* is common, but some specimens are usually collected in extensive poison stations. All live very secretively in crevices or under rocks on the shallow reefs and are almost never seen by skin divers. Structurally unique in this genus is the extensive, flattened, cobble-like dentition well adapted for crushing, rather than the shearing and stabbing teeth found in other genera of moray eels. Their prey is apparently seized as it crawls into or near the crevices in which the morays lie concealed. The sea urchin taken by one specimen is a rock dwelling species which usually is difficult to extricate from its tightly fitting depression.

Species: *Uropterygius xanthopterus* (moray eel)
Number examined: Arno, 8 specimens; 4 empty
Sex: Males and females
Standard length: 187-315 mm
Digestive tract: Teeth conical, pointed, canine-like; short straight intestine.

All four eels with food had crustacean fragments only. Three contained xanthid crab fragments and three contained alpheid shrimp fragments. This eel lives in interstices of coral mounds and masses of coralline rubble. It is strongly demersal and seldom is seen outside its place of refuge.

Species: *Rabula marshallensis* (moray eel)
Number examined: Arno, 2 specimens
Sex: Male and female
Standard length: 147-159 mm
Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Both specimens contained fragments of small crabs. This moray lives in interstices of coral mounds and rocky debris.

Species: *Gymnothorax pictus* (moray eel)
Number examined: Arno, 4; Eniwetok, 2: 2 empty
Sex: Males and females
Standard length: 400-725 mm
Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Of the four fish having food in their stomachs three had unidentified fish fragments and two had small crab fragments. This is the common moray found near the beach under rocks on the seaward reef flats. It is frequently encountered moving about reefs exposed by the receding tide, and commonly secludes itself under the nearest rock when startled by waders. Often it mistakes the shoes of the intruder for a rock and tries to seclude itself there, most often unsuccessfully, because humans can outrun it. Like most morays, it is vicious when teased with a stick.

Species: *Gymnothorax petelli* (moray eel)
 Number examined: Arno, 14; Bikini, 1 specimen: 13 empty
 Sex: Males and females
 Standard length: 108-520 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, heavy-walled, straight intestine

Each of the two specimens containing food had crab fragments, while one had, in addition, a hippolytid shrimp, and the other contained a partly digested small fish, *Pomacentrus jenkinsi*. This comparatively small moray has habits similar to most of the others. However, it seems clear that it must feed predominantly at night, because of the small proportion of those with food in their stomachs to those without.

Species: *Gymnothorax javanicus* (moray eel)
 Number examined: Arno, 4 specimens: 2 empty
 Sex: Undeveloped
 Standard length: 102-287 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

One of the two specimens containing food items had an alpheid shrimp, and the other contained fragments of unidentified gobies. This moray attains a very large size, some of those observed having a length of 6-7 ft. Like other morays it is seldom seen on the reefs because of its habit of secreting itself in interstices of large coral heads and coral rubble. When observed while skin-diving this eel usually has the head and forepart of the body extended from its hiding place. It is probably a night feeder.

Species: *Gymnothorax flavimarginatus* (moray eel)
 Number examined: Arno, 9; Eniwetok, 2 specimens: 7 empty
 Sex: Males and females
 Standard length: 185-690 mm
 Digestive tract: Conical, pointed, canine-like teeth; short, straight intestine

Only four of the 11 specimens examined contained food. In two of them, crab fragments were found; fragments of a blenny (*Cirripectus variolosus*), a damselfish (*Abudefduf dicki*), and other unidentified species of fish were found in three of them. The habits of *flavimarginatus* are similar to those of *G. javanicus*, and like the latter, it also attains large sizes.

Species: *Gymnothorax buroensis* (moray eel)
 Number examined: Arno, 21; Eniwetok, 4 specimens: 8 empty
 Sex: Males and females
 Standard length: 125-310 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments, unid.	64
Xanthid crab fragments	11
<i>Trapezia</i> sp.	5
Shrimp fragments	8
Stomatopod fragments	5
Fish	
Fish fragments, unid.	5
Labrid, unid.	5

This is the most abundant moray on the reefs of the Marshall Islands. It is a comparatively small species which has habits similar to other morays as regards seclusion and feeding habits.

Species: *Gymnothorax undulatus* (moray eel)
 Number examined: Eniwetok, 6 specimens: 4 empty
 Sex: Males and females
 Standard length: 600-700 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Only two of these specimens contained food items, and these were small pomacentrids and labrids which

undoubtedly had succumbed earlier to the rotenone. Like most other morays, this species probably feeds at night. It is very large and seems especially vicious. Its habits are similar to the other morays.

Species: *Gymnothorax margaritophorus* (moray eel)
 Number examined: Eniwetok, 8 specimens: 4 empty
 Sex: Females and undeveloped
 Standard length: 160-420 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Of the four specimens containing food, two had only gurry, another contained crustacean fragments, and the fourth contained unidentified fish fragments. This common species of the interisland reefs and seaward reef shallows does not grow large. It frequently may be found in the interstices of dead coral heads.

Species: *Gymnothorax rupelli* (moray eel)
 Number examined: Eniwetok, 4 specimens: all empty
 Sex: Females and undeveloped
 Standard length: 300-550 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

The lack of food in the stomachs examined probably indicates a night feeding habit. However, this species appears to have habits similar to other comparatively small morays, so it doubtless feeds on crustaceans and small fish. It is particularly common on the seaward reef flats and on the interisland reefs where it hides in any crevice or under any rock available.

Species: *Gymnothorax fimbriatus* (moray eel)
 Number examined: Eniwetok, 1 specimen: empty
 Sex: Undeveloped
 Standard length: 250 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

This moray is especially common in coral heads on the interisland reefs and leeward seaward reefs. It is a small species, frequently found when cracking open coral heads carried ashore. Its digestive tract and teeth indicate that it feeds like the other members of the genus.

Species: *Gymnothorax* sp. (moray eel)
 Number examined: Bikini, 14 specimens: 7 empty
 Sex: Males and females
 Standard length: 230-700 mm
 Digestive tract: Teeth conical, pointed, canine-like; short, straight intestine

Food item	Percentage of fish containing the item
Crustacea	
<i>Odontodactylus</i> sp.	28
Xanthid crabs, unid.	28
<i>Etisus</i> sp.	14
Fish	
<i>Siganus rostratus</i>	14
<i>Abudefduf leucopomus</i>	14
Unid. fragments	14
Foraminifera	
Foraminiferans and sand	14

This large moray apparently feeds also mostly by night, but a sufficient number contained food to indicate that its food and feeding habits are similar to the other morays.

Family Summary

Except for the genus *Echidna* the moray eels have very similar habits of concealment and food getting. A few become very large and are certainly the most vicious of the reef fishes, although, if unprovoked, will do little more than watch human intruders, with the head and forepart of the body protruding from a hole or crevice in the reef. Crustaceans appear to be the

food type most frequently taken, doubtless because these crustaceans, like the eels, become active at night and leave their diurnal hiding places in crevices and under the sand to forage. Moray eels appear to be predominantly night feeders, as judged by the high proportion of them without food in their stomachs during the day. Small fish species which habitually remain close to coral heads and rubble are also taken commonly. The kinds of food items found suggest that morays do not forage widely, but apparently catch their prey by watchful waiting methods.

An observation made in Hawaii indicates that morays are also adept at stalking prey. One swam slowly along the edge of a rocky pool watching a lined shore crab, *Grapsus grapsus tenuicrustatus*, walking along the rock about two feet above the water's surface. Suddenly the moray slithered up the rock in pursuit of the crab, caught it and fell back into the water. Likewise, the actions of *G. pictus* slithering along on just a film of water on the seaward reef flats suggest that it seeks prey both in and out of the water.

The fang-like canine teeth, some of which are depressible, are admirably suited to predacious habits.

Family Congridae

Species: *Conger noordzieki* (conger eel)
Number examined: Arno, 4; Bikini, 1; Eniwetok, 1 specimen: 1 empty
Sex: Males and undeveloped
Standard length: 151-620 mm
Digestive tract: Teeth short, conical, very numerous and point backwards; stomach elongate, Y-shaped; intestine short, and nearly straight

Each specimen contained different food items among which were shrimp fragments, unidentified crustacean fragments, polychaete worms, unidentified fish fragments, and fish eggs. Like other eels, the conger is cryptic and is seldom seen during the day. Its night feeding forays were observed several times when the eels came into very shallow water seeking prey.

Family Moringuidae

Species: *Moringua macrochir* (whip eel)
Number examined: Arno, 20; Eniwetok, 2 specimens: 12 empty
Sex: Males and females
Standard length: 128-260 mm
Digestive tract: Short, straight intestine

Food item	Percentage of fish containing the item
Polychaeta	60
Foraminifera	
<i>Calcarina</i> sp.	40
Fish	
Unid. fragments	10
Sand	30

The whip eels are quite common in sandy bottoms of the reefs shallows on all atolls. They construct no permanent burrows, but lie below the sand completely out of sight during the day. Whip eels apparently forage for prey species just under the sand and on the bottom.

Family Synodontidae

Species: *Synodus variegatus* (lizard fish)
Number examined: Arno, 8; Bikini, 4; Eniwetok, 5 specimens: 10 empty
Sex: Males and females
Standard length: 72-220 mm
Digestive tract: Teeth canine-like, numerous on both jaws and tongue; stomach heavy-walled; intestine short, straight

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	71
<i>Epinephelus</i> sp.	14
<i>Abudefduf</i> sp.	14

Five specimens collected at Eniwetok had picked up recently poisoned fish and were considered as empty for this study. This species is ubiquitous on sandy patches in all reefs areas. It lies mostly buried in the sand, with only the eyes and forepart of the head exposed watching for prey which may venture too closely. It is obliteratedly colored for sandy bottom, so that its habit of lying perfectly motionless until it darts out after its victim is very effective. It is a voracious, small carnivore.

Species: *Saurida gracilis* (lizard fish)
Number examined: Arno, 16 specimens: 4 empty
Sex: Males and undeveloped
Standard length: 45-131 mm
Digestive tract: Teeth canine-like in profusion on both jaws, palatines, vomer, and tongue; teeth on jaws not covered by lips; stomach heavy-walled; intestine short, straight

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	67
Unid. juvenile fish	17
<i>Apogon novemfasciatus</i>	8
<i>Allanetta ovalaua</i>	8
Fish scales	8

This species is distributed widely about all reefs, and has habits very similar to *Synodus variegatus*.

Family Summary

Lizard fish have obliterated color patterns so that when they lie motionless on sandy bottoms, or are partially buried in the sand, they are virtually impossible to detect. When prey species, mostly small fish, come within a few feet of them they dart upward very rapidly and seize their victim. Rarely have they been observed to swim more than 3-4 ft upward while attacking prey species. The profuse and powerful canine-like dentition provides a very effective mechanism for catching small fish. Our analyses and observations indicate that only fish were taken as food. However, Suyehiro (1942) reports that *Saurida undosquamis* in Japan will take shrimps and squid in addition to its more usual diet of small fish.

Family Belonidae

Species: *Strongylura gigantea* (needle fish; "Gar fish")
Number examined: Eniwetok, 2 specimens: both empty
Sex: Male and female
Standard length: 840-1,030 mm
Digestive tract: Jaws extremely long and needle-like toward the tip, mouth large, teeth canine-like arranged in villiform bands with inner row of enlarged canines; alimentary tract a straight, heavy-walled tube divided into an oesophagus and intestine, no stomach.

Both specimens examined had been caught by hook and line near the garbage dump, and one contained only garbage in its stomach. Observations indicate that this surface swimming species is a voracious carnivore, feeding on small fish by drifting up to them and then suddenly lashing out with its jaws.

Species: *Strongylura incisa* (needle fish)
Number examined: Arno, 1 specimen
Sex: Undeveloped
Standard length: 143 mm
Digestive tract: Jaws and teeth similar to *S. gigantea*; alimentary tract a straight tube, no stomach.

This specimen, a very small one, contained a small fish, *Allanetta ovalaua*.

Family Summary

Members of the Family Belonidae apparently feed by drifting into schools of fish or crustaceans (Randall 1955), whereupon they suddenly lash out with their

long, tooth-lined jaws to capture their prey. In our observations, and in those of Al-Hussaini (1947), small schooling species such as round herrings and silversides were most often the object of these carnivores which travel in small schools just below the surface. However, Suyehiro (1942) mentions that a closely related species in Japan, *Athlennes anastomella*, contained the remains of a rather large fish. Japanese fishermen also report that this species uses its long, powerful jaws very effectively in attacking larger prey species.

Family Hemiramphidae

Species: *Hyporhamphus laticeps* (halfbeak)
Number examined: Bikini, 8; Eniwetok, 12 specimens: 1 empty
Sex: Males and females
Standard length: 215-320 mm
Digestive tract: Lower jaw elongate and pointed, upper jaw short, teeth in both jaws minute, mouth large; a straight tube from the oesophagus to the anus, no stomach

Food item	Percentage of fish containing the item
Fish	
Unid. small fish (probably round herrings)	47
Crustacea	
Shrimp larvae	21
Mysids	15
Shrimp fragments	10
Crab zoeae	5
Polychaeta	
Unid. swimming polychaetes	26

This species swims in midwater or near the surface in small schools on all reefs investigated. It is a small, midwater carnivore which feeds on whatever prey species are available, showing comparatively little predilection for small fish species over swimming crustaceans or polychaetes.

Species: *Hyporhamphus affinis* (halfbeak)
Number examined: Arno, 16 specimens: 3 empty
Sex: Unknown
Standard length: Unmeasured
Digestive tract: Similar to *H. laticeps*

Food item	Percentage of fish containing the item
Crustacea	
Copepods	30
Crab zoeae	23
Crab fragments	15
Fish	
Unid. fragments	30
Foraminifera	
Several pelagic species	30
Gastropoda	
Veliger larvae	8
Gurry	23

This species apparently feeds predominantly on plankton, but it is capable also of taking small fish.

Family Summary

The halfbeaks are comparatively small, mid-water and surface dwellers where they occur in rather large schools. Younger individuals are primarily zooplankton feeders, but as they become larger their predilection turns to small, densely schooling surface fishes such as round herrings and silversides.

Earlier accounts (Jordan 1907) suggest that the halfbeaks are phytoplankton feeders, but this seems to be in error as our studies, as well as those of Uchida, reported by Suyehiro (1942), indicate that they are carnivores. No particular function can be ascribed to the elongate lower jaw by us, although it may be used to stun small fishes by a slashing action. Uchida believes that not only is the lower jaw useless when taking food, but actually is a hindrance.

Family Bothidae

Species: *Bothus mancus* (flounder)
Number examined: Arno, 5; Bikini, 6; Eniwetok, 12 specimens: 4 empty
Sex: Males and females
Standard length: 97-300 mm
Digestive tract: Short, nearly straight intestine

Food item	Percentage of fish containing the item
Fish	
Unid. gobies	21
Unid. fragments	21
<i>Acanthurus t. triostegus</i> (juvenile)	10
Unid. balistid (juvenile)	10
Unid. labrid	10
<i>Parupeneus trifasciatus</i>	5
<i>Otenogobius</i> sp.	5
<i>Abudefduf amabilis</i>	5
Pomacentrid (juvenile)	5
<i>Apogon novemfasciatus</i>	5
<i>A. erythrinus</i>	5
<i>Istiblennius paxillus</i>	5
<i>Tripterygion minutus</i>	5
Crustacea	
<i>Odontodactylus</i> sp.	15
<i>Trapezia</i> sp.	10
<i>Thalamita</i> sp. fragments	10
Portunid fragments	5
Xanthid crab fragments	5
Palaemonid shrimp fragments	5
Amphipod	5

With a very effective obliteratively colored upper surface this flounder lies motionless on rocks or sandy bottoms on all reefs studied. At times it covers itself, except for the eyes, with sand, thus becoming almost impossible to discern. After thus lying in wait for prey species to venture close enough, it seizes any fish or crustacean possible for it to ingest. Insofar as we could ascertain it responds only to moving prey. All the food items taken are species which frequent the bottom in sandy areas adjacent to coral mounds or rubble.

Family Holocentridae

Species: *Myripristis berndti* (squirrel fish)
Number examined: Arno, 7 specimens: 2 empty
Sex: Females and undeveloped
Standard length: 40-99 mm
Digestive tract: Teeth short, rather weak; stomach moderately heavy-walled; intestine short, straight

All five of the specimens containing food had only fragments of shrimps. This species and all other holocentrids examined had very little food in their stomachs, which is to be expected, since they are well known night feeders. All specimens of this species examined by Randall (1955) in the Gilbert Islands were empty of food.

Species: *Myripristis microphthalmus* (squirrel fish)
Number examined: Eniwetok, 17 specimens: 5 empty
Sex: Males and females
Standard length: 135-170 mm
Digestive tract: Similar to *M. berndti*

Food item	Percentage of fish containing the item
Crustacea	
Unid. crab fragments	58
Portunid crabs	16
Crab megalopa	8
Crab zoeae	8
Unid. shrimps	25
Alpheid shrimp	8
Stomatopod fragments	16
<i>Galathea</i> sp.	8
Amphipods	8
Polychaeta	
Unid. tube dwellers in sand near coral mound	16
Algae	
<i>Turbinaria</i> sp. tips	8
Sand grains	8

This species takes a great variety of crustaceans which are associated with, or swim near, the coral mounds in which this spelean fish secludes itself. Two specimens had the gut filled with hundreds of polychaetes which inhabit membranous tubes forming a dense network just beneath the surface of the rather compacted sandy bottoms on the protected lagoon reefs. The lack of sand in the gut indicates that the worms were pulled from their tubes, rather than being excavated from the sand by rooting actions of the fish.

Species: *Myripristis* sp. (squirrel fish)
Number examined: Bikini, 7 specimens: 5 empty
Sex: Males and females
Standard length: 70-210 mm
Digestive tract: Similar to *M. berndti*

Stomach contents of the two specimens containing food consisted of the following crustaceans: *Odontodactylus* sp., inachid crab fragments, and amphipods; and the following small fish: *Ctenochaetus striatus*, labrids, and unidentified larval stages.

Species: *Holocentrus sammara* (squirrel fish)
Number examined: Arno, 5; Eniwetok, 8 specimens: 2 empty
Sex: Males and females
Standard length: 34-165 mm
Digestive tract: Teeth short, weak; stomach moderately heavy-walled; intestine medium in length with one loop.

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	36
Parthenopiid crab	27
<i>Thalamita</i> sp.	18
<i>Pachygrapsus plicatus</i>	9
Portunid crab	9
Maiid crab	9
Unid. crustacean fragments	18
Copepods	9
Coelenterata	
Pieces of unid. coral, partly digested	18
Polychaeta	
Unid. polychaetes	9
Gastropoda	
<i>Cerithium</i> sp.	9
Algae	
Algal frond, bitten off	9

This species, like other squirrel fish, hides under rocks or in small coral caverns during the day, and feeds primarily at night. However, it is the most commonly observed squirrel fish during the day, as it frequently comes out of its hiding place and seems less secretive than the others.

Species: *Holocentrus lacteoguttatus* (squirrel fish)
Number examined: Arno, 4 specimens: 1 empty
Sex: Females
Standard length: 59-82 mm
Digestive tract: Similar to *H. sammara*

Shrimp fragments, small gastropods, and gurry were found in the three specimens containing food in their stomachs.

Species: *Holocentrus microstomus* (squirrel fish)
Number examined: Arno, 24; Eniwetok, 5 specimens: 3 empty
Sex: Males and females
Standard length: 45-191 mm
Digestive tract: Similar to *H. sammara*

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	42
Shrimp fragments	23
Alpheid shrimp	6
<i>Gonodactylus</i> sp.	3
Fish	
Unid. fragments	15
<i>Chromis caeruleus</i>	3

Gastropoda	
Small unid. gastropods	3
Coelenterata	
Hydroid fragments	3
Polychaeta	
Unid. polychaetes	3
Gurry	6

Species: *Holocentrus laevis* (squirrel fish)
Number examined: Eniwetok, 4 specimens: 1 empty
Sex: Males and females
Standard length: 125-150 mm
Digestive tract: Similar to *H. sammara*

In the three fish containing food in their stomachs the following crustaceans were found: crab fragments, a portunid crab, a maiid crab, and shrimp fragments.

Species: *Holocentrus diadema* (squirrel fish)
Number examined: Eniwetok, 14 specimens: 1 empty
Sex: Males and undeveloped
Standard length: 75-120 mm
Digestive tract: Similar to *H. sammara*

Food item	Percentage of fish containing the item
Gastropoda	
<i>Atys</i> sp.	46
Unid. gastropods	14
Polychaeta	
Unid. polychaetes	46
Crustacea	
Xanthid crab fragments	38
Isopods	23
Unid. fragments	14
Shrimp fragments	7
Alpheid shrimp	7
Pelecypoda	
Small coral-dwelling clams	14
Amphineura	
Solenogastroid	7

Species: *Holocentrus spinifer* (squirrel fish)
Number examined: Eniwetok, 9 specimens: 1 empty
Sex: Males and females
Standard length: 150-280 mm
Digestive tract: Similar to *H. sammara*

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crabs	50
<i>Charybdis</i> sp.	12
Portunid crab	12
Maiid crab	12
Stomatopod	12
Fish	
Unid. fragments	12

Species: *Holocentrus* sp. (squirrel fish)
Specimens examined: Bikini, 5 specimens
Sex: Males and females
Standard length: 80-140 mm
Digestive tract: Similar to *H. sammara*

Three of the five specimens contained only fragments of the small coral crab, *Trapezia* sp., while the remaining two specimens contained only shrimp fragments.

Family Summary

Food and feeding habits of all members of this family appear to be very similar. All are carnivores, taking a wide variety of crustaceans, polychaetes, small fish, and gastropods. During the day squirrel fish are cryptic, secluding themselves to a great extent in holes, under ledges, or in larger caverns in coral mounds or rubble. All have comparatively large eyes, and feed almost exclusively at night. Food remains are infrequent in the stomachs during the day, persistent items being generally the hard parts of prey taken the previous night. In many instances the intestines had to be searched for traces of food items because the stomachs were empty. Randall (1955) reported that most of the stomachs of holocentrids in the Gilbert Islands were

also empty, and those containing food had remains of crustaceans and small fish.

The fact that many of the squirrel fish contained polychaetes which were tube dwellers on sandy bottoms indicates that they do forage well away from their day time hiding places. None were observed feeding on these polychaetes during daylight hours. Further evidence of their foraging on sand bottoms is shown by the presence of sand dwelling gastropods (*Atys* sp.) and the fossorial solenogastrid amphineurans. The few broken, partly digested tips of coral branches in the stomach of *H. sammara* may have been taken inadvertently while the fish was seeking small crabs wedged in interstices. We do not believe that any holocentrid feeds habitually on living coral.

Family Syngnathidae

Species: *Corythoichthys flavofasciatus conspicillatus* (pipefish)
Number examined: Eniwetok, 3 specimens
Sex: Males and females
Standard length: 82-95 mm
Digestive tract: Snout long, pipette-like; mouth cavity small, teeth absent; alimentary canal straight, no stomach.

All three pipefish examined contained copepods; one had, in addition, some small isopods, and another had taken several ostracods along with the copepods. This pipefish is very common on all reefs studied in the northern Marshalls, and frequently is seen lying on coral heads, rubble, or sand.

Species: *Corythoichthys intestinalis waitiei* (pipefish)
Number examined: Arno, 1 specimen
Sex: Female
Standard length: 85 mm
Digestive tract: Similar to *C. f. conspicillatus*

This specimen contained copepods, copepod nauplii, and ostracods in about equal abundance. Although this pipefish was not seen at either Eniwetok or Bikini, it was locally abundant at Arno and Majuro Atolls in the southern Marshalls. Its habits are very much like those of *C. f. conspicillatus*.

Generic Summary

The food getting structures and the food items eaten by the two species of *Corythoichthys* suggest that these pipefish probably use their snout as a sort of pipette to take up minute crustaceans so abundant on the surface of coral rubble and compacted sand bottoms. Al-Hussaini (1947) suggests that the pipefishes take mostly planktonic crustaceans, but we believe that the species ingested are benthonic. There is no evidence that the snout is distensible or that they can swallow prey larger than might be expected, as Bigelow & Welsh (1924) have described for the related species *Siphostoma fuscum* of the east coast of North America.

Family Aulostomidae

Species: *Aulostomus chinensis* (trumpet fish)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 600 mm
Digestive tract: Snout very long, tubular, with jaws at end, mouth capable of bellows-like dilation; intestine short, straight

The single specimen examined was taken by spear, and contained a small silverside (Atherinidae) in its stomach. Because rotenone was not used it appears likely that the silverside was a normal dietary item. This solitary trumpet fish has frequently been observed to swim slowly over open areas and near coral heads and rubble. It appears to glide about, seldom seeking

cover. Although it has never been seen to capture food, its structural features suggest that it captures small prey by a rapid dilation of its mouth, particularly prey secluded in shallow holes or interstices into which it could probe with its long, tubular snout.

Family Fistulariidae

Species: *Fistularia petimba* (cornet fish)
Number examined: Bikini, 9 specimens
Sex: Males and females
Standard length: 500-700 mm
Digestive tract: Snout, long, tubular, jaws at end, very short and with an extremely small mouth opening, but capable of being broadened or narrowed, teeth small; alimentary tract straight.

Food item	Percentage of fish containing the item
Fish	
Labrids	77
Pomacentrids	33
Unid. small fish	33
<i>A. t. triostegus</i>	11
Balistids	11

This cornet fish occurs rather commonly in schools swimming near the surface, and occasionally in mid-water or near the bottom, in the quiet waters of the lagoon reef and leeward sea reefs. Frequently the schools lie quite motionless. It is obvious from the food items found that they frequent the vicinity of coral heads as well as cruise over the reef flats, and that they are capable of taking small fishes which are larger than the mouth opening of dead specimens. Hence, the extension of its flute-like snout is very important. We cannot agree with Suyehiro (1942) that this species takes only minute, floating creatures by utilizing its snout as a pipette. Our specimens contained nothing but small fish, although it is certain that swimming crustaceans, etc., would be taken if available. One of us has seen the species taken on a large bass plug in Hawaii.

Family Atherinidae

Species: *Stenatherina temmincki* (silverside)
Number examined: Bikini, 8 specimens: 1 empty
Sex: Males and females
Standard length: 85 mm
Digestive tract: Mouth moderately large, teeth weak; stomach absent, intestine moderately short, one loose coil

Food item	Percentage of fish containing the item
Crustacea	
Shrimp larvae	57
Copepods	28
Stomatopod larvae	14
Foraminifera and sand	57
Gastropoda	
Unid. small species	14
Fish	
Unid. fragments	14

This species occurs in very large schools near the surface or in mid-water. Some have been observed feeding from the bottom in very shallow water. Thus, observations as well as an analysis of the food items ingested indicate that this silverside feeds both on planktonic and benthonic forms.

Species: *Allanetta ovalaua* (silverside)
Number examined: Arno, 12 specimens: 3 empty
Sex: Males and females
Standard length: 66-74 mm
Digestive tract: Similar to *S. temmincki*

Food item	Percentage of fish containing the item
Crustacea	
Calanoid copepods	88
Crab zoeae	44
Gastropoda	
Veliger larvae	11

This species swims near the surface and in mid-water in very large schools on all reefs visited. It behaves primarily as a selective feeder on zooplankton.

Species: *Pranesus pinguis* (silverside)
Number examined: Arno, 5 specimens: 3 empty
Sex: Males and females
Standard length: 66-74 mm
Digestive tract: Similar to *S. temminckii*

Both specimens containing food items had copepods and crab zoeae. This species has habits similar to *A. ovalaua*, and is often found schooling with that species.

Family Summary

Atherinids are ubiquitous in large schools on virtually all reefs visited. For the most part they subsist on zooplankton, being rather selective in that they take mostly crustaceans and larval gastropods. At least one species, *S. temminckii*, feeds on the benthonic types of minute organisms when the school moves into very shallow, protected areas of the reefs.

Family Mugilidae

Species: *Neomyxus chaetali* (mullet)
Number examined: Bikini, 3 specimens
Sex: Males and females
Standard length: 160-190 mm
Digestive tract: Teeth trifid setiform; stomach heavy-walled, but not gizzard-like; intestine very long, coiled

The three specimens examined all contained diatoms, desmids, and fine filamentous algae, some foraminiferans and detritus. This species apparently strains sandy bottom material from which it gets the minute algal forms and, perhaps only by inadvertence, picks up some minute animal species from the surface of the substrate.

Species: *Orenimugil crenilabris* (mullet)
Number examined: Arno, 11; Eniwetok, 2 specimens
Sex: Females and undeveloped
Standard length: 112-400 mm
Digestive tract: Stomach heavy-walled and a gizzard, but less heavy and with a greater lumen than in *Mugil cephalus*; intestine very long, coiled

Food item	Percentage of fish containing the item
Detritus and sand (fine)	92
Algae	
<i>Oscillatoria</i> sp.	84
Diatoms (<i>Nitzschia</i> sp. mostly)	61
Fine filamentous algae (appears scraped from compacted sandy bottoms)	15
Foraminifera	76

This species feeds quite similarly to the well known gray mullet, *Mugil cephalus*, except that larger items pass into the gut of *C. crenilabris*. It is frequently solitary or forms small schools in the less turbulent waters of the lagoon and seaward reefs. It is often seen feeding in very shallow water on compacted sandy or muddy bottoms.

Family Summary

Probably as much has been written about the digestive tract and food habits of the mullet as for any other group of fishes. The peculiar digestive tract of *Mugil cephalus* has been reported on in detail by many writers, since Cuvier and Valenciennes described it in the early nineteenth century. More recently Ghazzawi (1933, 1935) studied both morphological and histological features as well as the feeding habits of *M. cephalus* and *M. capito* in Egypt, and Al-Hussaini (1947) reported on a similar study for *M. auratus*; Suyehiro (1942) did likewise for *M. cephalus* in Japan; and

Hiatt (1947a) described feeding habits and alimentary tract morphology for *M. cephalus* in Hawaii. All agree that mullets feed predominantly on unicellular algae composing the benthos. Inadvertently, perhaps, they also ingest a considerable amount of the microfauna associated with the same habitat. The exceptionally long intestine and the triturating gizzard containing fine sand as an abrasive are evidence of mullets' primary dependence upon such forms as diatoms and desmids.

Family Sphyraenidae

Species: *Sphyraena genie* (barracuda)
Number examined: Eniwetok, 2 specimens: both empty
Sex: Female
Standard length: 1,220-1,240 mm
Digestive tract: Mouth large, pointed; large canine teeth; intestine short, straight

Both specimens examined were caught by hook and line near the garbage dump, and had no natural food items in their stomachs. Although this species is uncommon in the Marshall Islands it has been observed several times drifting solitarily near the surface stalking its prey. It surprises its victim with a sudden lunge. Barracuda probably also feed at mid-depth or near the bottom. Its main food is undoubtedly fish.

Family Polynemidae

Species: *Polydactylus sexfilis* (threadfin)
Number examined: Arno, 18 specimens: 12 empty
Sex: Undeveloped
Standard length: 57-86 mm
Digestive tract: Moderately short intestine

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	50
Crab fragments	33
Polychaeta	16
Foraminifera	
<i>Calcarina</i> sp.	16

Small specimens of this schooling species are found commonly on the reef shallows over sandy bottoms in protected areas. Larger fish are found along sandy beaches where the surf is rather strong. It feeds strictly on the benthonic fauna.

Family Scombridae

Species: *Gymnosarda nuda* (dogtooth tuna)
Number examined: Eniwetok, 2 specimens: both empty
Sex: Unknown
Standard length: 44-45 inches
Digestive tract: Several conical, pointed, canine-like teeth in jaws; stomach thick-walled; intestine short, almost straight

Neither of these specimens, caught by hook and line near a pass in the Eniwetok lagoon, had food in their stomachs, although others were often seen in small schools slashing through the dense schools of round herring near the pier. This species seems to swim more deeply than species of either *Katsuwonus* or *Euthynnus* which also occur inside the lagoons and in the surrounding seas. Dogtooth tuna are pelagic, rapid-swimming carnivores which grow to a large size. Woods (1953) mentions that this species had taken seads (*Decapterus muroadsi*) in the northern Marshalls, and the senior author noted the stomachs of this species at Bikini to contain seads (*Decapterus sanctaehelenae*) as well as pelagic squid, flying fishes, and other small schooling types (Hiatt & Brock 1948).

Species: *Euthynnus affinis yaito* (little tunny)
Number examined: Observations only

No specimens of this species were available for food analysis, but small schools were observed repeatedly at

Eniwetok to slash through the dense schools of round herrings swimming near the pier. It is a rapid swimming, schooling, pelagic carnivore which feeds most often near the surface. It is known to take small fish, pelagic crustaceans, and pelagic squid (Welch 1950). The senior author has observed this species feeding among a dense school of atherinids at Arno which had surrounded him while skin-diving near the outer slope of the lagoon reef. The tunny showed no concern whatever for the swimmer while slashing with great speed through the silversides, frequently as close as 5-6 ft from him. In another instance three medium-sized tunny were observed herding a large school of several hundred scads, *Decapterus sanctaehelenae*, over a large coral knoll for over three hours in Rongerik Atoll in the northern Marshall Islands (Hiatt & Brock 1948). One lagging scad was captured by one of the tunny. The entire performance was extraordinary, but probably typical, as Kishinouye (1923) also reports, although he singles this species out among the bonitos as the one which does not engage in herding prey.

Species: *Katsuwonus pelamis* (oceanic skipjack)
Number examined: Observations only

As with the other tunas reported herein, this schooling species was observed to slash repeatedly through the dense school of round herrings around the pier at Eniwetok. Because of its great economic importance and wide range the food and feeding habits of this species have been studied intensively. In Hawaii, Welch (1950) reports that this species subsists mainly on cephalopods, stomatopod larvae, and small fish, while Suyehiro (1942) and others in Japan have found this genus to feed principally on small or juvenile fishes, cuttle-fish, shrimps, schizopods, and amphipods.

Family Summary

The tunas are large, pelagic, fast-swimming, schooling carnivores which take virtually any prey of the proper size. Because of their pelagic nature, the food of the ones caught at sea consists mainly of schooling fishes, crustaceans, and squid which they capture by visual means. Those taken in lagoons or close to land appear to contain larval fishes and crustaceans which are produced by reef- and shore-dwelling adults. This type of food, supplementing the usual high seas forage species, probably is significant in attracting tunas close to mid-ocean islands.

Family Carangidae

Species: *Trachurops crumenophthalmus* (scad)
Number examined: Arno, 23; Bikini, 1; Eniwetok, 3 specimens: 4 empty
Sex: Males and females
Standard length: 85-245 mm
Digestive tract: Mouth moderately large, teeth small; stomach rather thick-walled; intestine rather short, with one loop

Food item	Percentage of fish containing the item
Foraminifera	
<i>Calcarina</i> sp.	47
<i>Marginopora</i> sp.	13
Gastropoda	
<i>Cerithium</i> sp.	26
Unid. small gastropods	17
Fish	
Unid. fragments	17
Crustacea	
Pelagic shrimps	8
Miscellaneous items	
Sand grains	30
Pebbles	26
Gurry	21

All specimens containing food were juvenile fish taken at Arno Atoll where they formed large schools which frequented the protected lagoon reef and inter-island reefs. Unlike most carangids (and this is perhaps an age characteristic) these scads fed principally on the benthonic fauna of the reef shallows, particularly the forms occurring on compacted sand. In all cases the foraminiferans eaten were enveloped in a viscous fluid which was probably associated with the digestive process. The adults of a closely related species in Japan, *Decapterus muroadsi*, were found by Suyehiro (1942) to have taken mostly larval fishes.

Species: *Trachinotus bailloni* (pompano)
Number examined: Arno, 9 specimens: 4 empty
Sex: Undeveloped
Standard length: 56-101 mm
Digestive tract: Mouth small; stomach thick-walled; intestine moderately short

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	100
<i>T. bailloni</i> , juveniles	20
Crustacea	
Isopods	20
Crab fragments	20

This species is a slow-cruising carnivore which occurs in pairs or small schools. It lives rather close to shore in the lagoon shallows. The specimens examined were all juveniles, so the food of the adult of this pompano is unknown, but fish probably predominate in their diet as they do with the juveniles.

Species: *Carangoides ferdau jordani* (jack)
Number examined: Arno, 2; Eniwetok, 3 specimens: 2 empty
Sex: Males and females
Standard length: 250-395 mm
Digestive tract: Intestine short, straight

The three specimens containing food had eaten the following fish: *Bathygobius f. fuscus*, *Parupeneus trifasciatus*, unidentified goby, and unidentified fish fragments. This species grows rather large, and is a fast-swimming, roving carnivore on all reefs visited. It sometimes is seen schooling with other types of fish.

Species: *Caranx melampygus* (jack)
Number examined: Arno, 1; Eniwetok, 1 specimen
Sex: Females
Standard length: 555 mm
Digestive tract: Intestine very short, straight

One specimen contained a small scad, *Trachurops crumenophthalmus*, and the other an unidentified fish fragment. This species, like *Carangoides ferdau jordani*, is a large, rapid-swimming, roving carnivore which prefers reef areas with considerable open water, either in lagoons, or in surge channels of the seaward reefs. It apparently feeds in mid-water close to coral mounds where it catches small coral-dwelling fish. In the Gilbert Islands Randall (1955) found the species to take coral-dwelling fish such as small wrasses.

Species: *Caranx lessoni* (jack)
Number examined: Eniwetok, 1 specimen: empty
Sex: Female
Standard length: 640 mm
Digestive tract: Intestine very short, straight

The single specimen was empty, but its observed habits are very much like *C. melampygus*.

Species: *Elagatis bipinnulatus* (rainbow runner)
Number examined: Eniwetok, 2 specimens: 1 empty
Sex: Male and female
Standard length: 535-590 mm
Digestive tract: Mouth comparatively small, teeth in villiform bands; intestine short

The one specimen containing food in its stomach had a pelagic shrimp, a crab megalops, and some unidentified fish fragments. This species is a fast-swimming carnivore which is more or less pelagic. It is abundant around the pier at Eniwetok where it may be chummed to the surface easily. At intervals small schools of 5-10 individuals slash through the dense school of round herring near the pier. Its usual food is probably pelagic fish although it certainly will take swimming crustaceans or squid.

Family Summary

Many differences in feeding methods and predilections for food items occur among the several genera in this family, although all are carnivores. The smaller species, e.g., scads, frequently forage for benthonic fauna in very shallow water, although adult scads are seen most often in large schools in mid-water where they doubtless take small fish and pelagic invertebrates. The larger carangids, e.g., *Trachinotus*, *Carangoides*, and *Caranx*, feed mostly as roving carnivores, with *Trachinotus* inhabiting the more open water in small schools, and the other two genera inhabiting reef shallows and channels, mostly in a solitary fashion, where they feed upon small fish associated with the coral heads. They typically inhabit the deeper water just off the seaward reef edge during low tides, and move up onto the reef proper when the tide rises. *Elegatis bipinnulatus* is more pelagic than the other species and occupies a mid-water or surface position, usually in small schools. The small mouth suggests that only very small pelagic fishes and swimming crustaceans serve them as food.

Although no specimens were collected for examination, three separate observations of the jack, *Gnathodon speciosus*, two at Arno, and one at Eniwetok are worthy of reporting. At Arno two fish of this species were observed swimming along-side the head of a large white-tipped shark, *Triaenodon obesus*, near the outer edge of the lagoon reef, at Eniwetok one fish was seen hovering about the head of a large nurse shark, *Ginglymostoma ferrugineum*, and three were observed at very close range swimming about the head of a giant sea bass, *Promicrops lanceolatus*. In no case were the sharks or the bass following the brilliantly yellow and black barred carangid, but the latter remained close to the head of the larger fish at all times.

The larger carangids are certainly one of the most important of the roving carnivores over all Marshallese reefs.

Family Apogonidae

Species: *Apogon novemfasciatus* (cardinal fish)
Number examined: Arno, 21; Bikini, 3 specimens: 7 empty
Sex: Males and females
Standard length: 34-70 mm
Digestive tract: Mouth large, small villiform teeth; stomach large, Y-shaped; intestine moderately short with one loop

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	35
Damsel fish	11
Wrasses	11
Unid. gobies	11
<i>Bathygobius f. fuscus</i>	5
<i>Amphiprion melanopus</i>	5
<i>Apogon frenatus</i>	5
Fish eggs	11
Crustacea	
Shrimp fragments	17
Xanthid crab fragments	17

This species is perhaps the most ubiquitous cardinal fish in the Marshall Islands. It lives beneath ledges or in caverns in rather large coral heads, and often aggregates into loose schools of several individuals. It is a voracious carnivore taking fish and crustaceans closely associated with the same coral head. These apogonids have never been observed more than a few feet away from their hiding place.

Species: *Apogon snyderi* (cardinal fish)
Number examined: Arno, 6; Bikini, 4; Eniwetok, 11 specimens: 3 empty
Sex: Males and females
Standard length: 54-110 mm
Digestive tract: Similar to *A. novemfasciatus*

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	38
Xanthid crabs	22
Ostracods	11
Copepods	5
<i>Alpheus</i> sp.	5
Isopods	5
Fish	
Unid. fragments	27
Gastropoda	
<i>Cerithium</i> sp.	5

This solitary species lives mostly around coral mounds on the lagoon reefs near the outer slope at depths of 10-15 ft; but some have been taken in protected ocean reef shallows. It dwells in crevices and caverns in the coral, and subsists mainly on small fish and crustaceans in the immediate vicinity of its hiding place. Randall (1955) found this species to have taken small fish and crustaceans in the Gilbert Islands.

Species: *Apogon exostigma* (cardinal fish)
Number examined: Arno, 5 specimens: 1 empty
Sex: Females
Standard length: 45-53 mm
Digestive tract: Similar to *A. novemfasciatus*

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crab fragments	50
Fish	
<i>Eviota</i> sp.	25
Polychaeta	25

Species: *Apogon nigrofasciatus* (cardinal fish)
Number examined: Eniwetok, 3 specimens
Sex: Female and undeveloped
Standard length: 52-68 mm
Digestive tract: Similar to *A. novemfasciatus*

Two of the specimens examined contained unidentified shrimps; one contained, in addition, and unidentified polychaete. The remaining specimen contained an alpheid shrimp. This species is common on both the seaward reef shallows and on the lagoon reefs, living under ledges and in interstices of coral mounds. Its food consists of items closely associated with the same coral heads.

Species: *Apogon novaeguineae* (cardinal fish)
Number examined: Eniwetok, 2 specimens
Sex: Undeveloped
Standard length: 36-41 mm
Digestive tract: Similar to *A. novemfasciatus*

Both specimens examined had taken shrimp, and one had, in addition, the abundant foraminiferan, *Calcarina* sp. This species, common both on seaward and lagoon reefs, in crevices and holes in coral mounds, is sometimes found in close association with echinoids. The foraminiferan in one specimen suggests that at times it feeds on benthonic fauna.

Species: *Apogon erythrinus* (cardinal fish)
 Number examined: Eniwetok, 1 specimen
 Sex: Female
 Standard length: 34 mm
 Digestive tract: Similar to *A. novemfasciatus*

This specimen contained unidentified fish fragments and an unidentified polychaete. This species is common about crevices and caves in coral mounds on both seaward and lagoon reefs down to depths of at least 18 feet.

Species: *Apogon* sp. (cardinal fish)
 Number examined: Bikini, 3 specimens
 Sex: Males and females
 Standard length: 85-90 mm
 Digestive tract: Similar to *A. novemfasciatus*

All specimens contained remains of shrimps, one an alpheid shrimp, another a *Leander* sp., and the third had unidentified shrimp fragments.

Species: *Gymnapogon philippinus* (cardinal fish)
 Number examined: Arno, 3 specimens: 2 empty
 Sex: Females
 Standard length: 35-40 mm
 Digestive tract: Mouth large, teeth erect, large canine teeth on vomer; intestine short

The single fish with food items in its stomach contained fish eggs. We cannot be certain that these are not eggs of this species which may have been "incubating" in the mouth of the fish, as some of the cardinal fish are known to do. Its large canines suggest that it is a voracious carnivore. This species lives beneath ledges and in interstices of living or dead coral heads, particularly on the protected seaward reefs. It has never been seen alive by the authors, despite many hours of intensive observation in its habitat. Thus, it is probably very secretive during the day and forages at night. The empty stomachs add evidence to this suggestion.

Species: *Paramia quinquelineata* (cardinal fish)
 Number examined: Arno, 8 specimens
 Sex: Males and females
 Standard length: 36-55 mm
 Digestive tract: Mouth large, canines weak; intestine short

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	37
<i>Eriota</i> sp.	12
Wrasses	12
Crustacea	
Shrimp fragments	25
Crab fragments	12
Gastropoda	
<i>Atys</i> sp.	12

This species is very shy, seldom seen, and lives under ledges and in caves, rarely in interstices of coral heads. It apparently forages on the benthonic fauna of sandy areas adjacent to its hiding place, as the eleotrid, *Eriota* sp., and the gastropod, *Atys* sp., are benthonic, sandy-substrate dwellers.

Species: *Cheilodipterus macrodon* (cardinal fish)
 Number examined: Bikini, 1 specimen
 Sex: Male
 Standard length: 90 mm
 Digestive tract: Mouth large, numerous fang-like canines in jaws; intestine short.

The single specimen examined had eaten a blenny, *Istiblennius* sp. This species was common in the deeper reef areas of the lagoon at Bikini, but uncommon or rare in a similar habitat at Eniwetok. It is solitary and lives under ledges near mounds of rubble or living coral. This species is one of the largest apogonids in the Marshall Islands.

Family Summary

The cardinal fishes all have rather similar habits, although the dental armature varies appreciably among the several genera found in the Marshall Islands. All are voracious carnivores, taking fish, crustaceans, and other invertebrates if they are of the proper size. Suyehiro (1942) reports that *Apogon lineatus* and *A. semilineatus* of Japan take small crustacea and larval fish. Suyehiro also points out an interesting situation, with which our observations also agree, that when the ovaries are well developed the females cease to take food. We found this to be the case with every species in which the females had eggs nearing maturity. Most species apparently forage diurnally, although at least one species appears to be a nocturnal feeder.

Ordinarily cardinal fishes occur solitarily, or in rather small schools, although some species not covered in this study form dense schools over and in patches of certain living, branching corals, and others form large schools confined to coral mounds with large caverns in which they hide if disturbed. *A. novaeguineae* has been observed to swim among the long spines of diademid sea urchins, particularly *Echinothrix diadema*, when both the urchin and fish are secluded in crevices or holes in coral mounds. When the urchin is moved outside the hole a short distance some of the cardinal fish venture out and take station among the spines. However, they will not do this if the urchin is moved too far away from the hole or crevice.

Several specimens were found with fish eggs in their stomachs. The presence of these could have resulted from the accidental convulsive swallowing of "incubating" eggs held in the mouth during rotenone poisoning.

Family Priacanthidae

Species: *Priacanthus cruentatus* (big-eye)
 Number examined: Eniwetok, 13 specimens
 Sex: Males and females
 Standard length: 100-235 mm
 Digestive tract: Teeth villiform, short; intestine short

Food item	Percentage of fish containing the item
Cephalopoda	
<i>Octopus</i> sp.	84
Crustacea	
Pelagic shrimps	53
Shrimp fragments	15
Alpheid shrimps	7
Stomatopod fragments	53
Xanthid crab fragments	15
Portunid crab	7
Crab megalopa	7
Isopods	7
Fish	
Unid. fragments	46
Polychaeta	
Unid. polychaetes	23

This species is locally abundant, particularly on lagoon reefs where there are large crevices or caverns in living coral or coral rubble. Because of its especially large eyes and spelean habitat, most marine biologists have considered this genus to comprise nocturnal feeders. However, the bulk of the food taken by the specimens examined were octopi (*Octopus* sp.) and many had retained the beaks of previously digested ones in their stomachs. It is therefore conceivable that the cryptic habits of both octopi and big-eyes combine to provide these fish a source of food during the daytime. The fact that no stomachs of this species were empty, yet many stomachs of the associated holocentrids (squirrel fish) were empty, leads us to suspect that the big-eye is an active day feeder, but may also forage at night.

Both swimming and bottom-dwelling organisms are taken in amounts which indicate that this species is not restricted in its foraging habits to any particular locality on the reef, but rather is an opportunist. The polychaetes found so abundantly in a few stomachs were a type common in the sandy bottoms adjacent to coral and rubble mounds. Members of this family are abundant carnivores, feeding in caverns, in mid-water and on coral mounds and sandy bottoms.

Family Serranidae

Species: *Epinephelus merra* complex (grouper)
Number examined: Arno, 25; Bikini, 6 specimens: 6 empty
Sex: Males and females
Standard length: 99-360 mm
Digestive tract: Mouth large, outer teeth on jaws villiform, inner rows larger and depressible, short canines at symphysis of each jaw; stomach large, heavy-walled; intestine medium length with a long loop

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	28
<i>Gymnothorax margaritophorus</i>	4
<i>Allanetta ovalaua</i>	4
<i>Parupeneus trifasciatus</i>	4
<i>Holocentrus sammara</i>	4
Holocentrid fragments	4
Unid. goby	4
Larval fish	4
Unid. small fish	8
Crustacea	
Crab fragments	24
Portunid fragments	8
<i>Petrolisthes</i> sp.	4
Hippolytid shrimp	4
Shrimp fragments	4
Stomatopod fragments	8
<i>Galathea</i> sp.	4

Essentially, four species are grouped together here which were not segregated taxonomically until after our food analyses had been made and the specimens thrown away. The species involved are *merra*, *hexagonatus*, *spilotus*, and *elongatus*. All four have similar appearance and behavior, and occupy essentially the same habitat.

These species are very abundant, demersal, small carnivores which live under ledges near the bottom of coral mounds and rubble. Frequently, they are seen lying motionless on the surface of massive coral formations. They occurred on all reef shallows visited. These groupers forage by lying in wait for prey species to move sufficiently close to them at which time they dash out and seize the victim in their large mouths. No particular selection is made among prey species; they take any small fish or crustaceans which happen by.

Species: *Epinephelus fuscoguttatus* (grouper)
Number examined: Arno, 4; Eniwetok, 4 specimens: 3 empty
Sex: Females
Standard length: 240-360 mm
Digestive tract: Similar to *E. merra*

Food item	Percentage of fish containing the item
Fish	
<i>Holocentrus diadema</i>	20
<i>Parupeneus trifasciatus</i>	20
<i>Spratelloides delicatulus</i>	20
Unid. fragments	20
Crustacea	
<i>Thalamita</i> sp.	20
Shrimp fragments	20
Gurry	20

This large solitary grouper is commonly observed lying motionless on the bottom, frequently some distance from protective cover. It also commonly hides under large corals such as *Acropora reticulata* and under rock ledges. This species is one of the commonest large carni-

vores found on all reefs where the water is six or more feet in depth.

Species: *Epinephelus kohleri* (grouper)
Number examined: Arno, 1; Eniwetok, 1 specimen: 1 empty
Sex: Males
Standard length: 325-370 mm
Digestive tract: Similar to *E. merra*

The one specimen with food contained fish fragments. This species is a large, strongly demersal grouper which usually lies on the bottom near the base of a coral mound in water from 6 to 30 feet in depth. It does not stay away from its refuge place as does *E. fuscoguttatus*. At no place was this species common.

Species: *Epinephelus hexagonatus* (grouper)
Number examined: Bikini, 6 specimens: 2 empty
Sex: Males and females
Standard length: 105-290 mm
Digestive tract: Similar to *E. merra*

Each of the four specimens had taken different species of food items although three of them contained only fish, *Pempheris ovalensis*, a juvenile trigger fish, and *Pseudocheilinus* sp. The other specimen had many polychaete fragments in its stomach. This species has the same habits and is found in the same localities on the reefs as is *E. merra*, described earlier.

Species: *Epinephelus macrospilos* (grouper)
Number examined: Eniwetok, 2 specimens: 1 empty
Sex: Female
Standard length: 240-290 mm
Digestive tract: Similar to *E. merra*

The specimen containing food had only fragments of polychaetes. This species, uncommon on most reef areas, grows to about one foot in length, and lurks under expansive coral heads and rock ledges, seldom venturing far from protective cover. Although the specimen examined contained only polychaetes, it is reasonable to expect this species to have food habits similar to other groupers and to take fish, crustaceans, and other invertebrates on occasion.

Species: *Epinephelus spilotus* (grouper)
Number examined: Eniwetok, 12 specimens: 4 empty
Sex: Males and females
Standard length: 170-315 mm
Digestive tract: Similar to *E. merra*

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	75
Crustacea	
Crab fragments	25
Shrimp fragments	12
<i>Stenopus hispidus</i>	12
Cephalopoda	
Octopus beaks	12
Sand and pebbles	37

This was a common grouper on all reefs visited. It appears sluggish, often hiding in coral heads or under ledges, but sometimes is seen lying motionless on the bottom well away from protective cover. Its food and feeding habits are similar to other groupers of similar size.

Species: *Variola louti* (grouper)
Number examined: Bikini, 2 specimens: 1 empty
Sex: Female
Standard length: 400 mm
Digestive tract: Similar to *E. merra*

The one specimen with food in its stomach had taken a juvenile surgeon fish, *Naso* sp. This species was uncommon on most reefs visited, preferring lagoon reefs to seaward ones, and was found in deeper water than most

other groupers, usually depths in excess of 10 ft. It is solitary, and lives around the deeper coral heads, but frequently is seen hovering in mid-water. It attains a length of about 3 ft, and seems much more agile than other groupers.

Species: *Cephalopholis urodelus* (grouper)
Number examined: Eniwetok, 17; Arno, 3 specimens: 7 empty
Sex: Females and undeveloped
Standard length: 65-190 mm
Digestive tract: Similar to *E. merra*

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	42
Crustacea	
Alpheid shrimp fragments	28
Xanthid crab fragments	14
Porcellanid crab fragments	7
Sand grains	7

This species attains about one foot in length, and lurks in holes and crevices of coral heads in all reef areas at depths of 10-12 ft. It is strongly demersal and seldom ventures more than a few feet from its place of refuge.

Species: *Cephalopholis miniatus* (grouper)
Number examined: Eniwetok, 1 specimen: empty
Sex: Undeveloped
Standard length: 280 mm
Digestive tract: Similar to *E. merra*

This is a large, demersal carnivore which lives at considerable depths in the lagoons. It was never observed on the reefs, but several individuals frequented the garbage dump at Eniwetok. Its structure and habits indicate that it is predaceous and probably feeds, like other large groupers, mostly on fish and crustaceans.

Species: *Cephalopholis argus* (grouper)
Number examined: Arno, 3; Bikini, 1; Eniwetok, 8 specimens: 3 empty
Sex: Males and females
Standard length: 130-430 mm
Digestive tract: Similar to *E. merra*

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	33
Unid. fragments	11
Fish	
<i>Abudefduf dicki</i>	11
Mullid fragments	11
Unid. fragments	22
Polychaeta	
Unid. polychaetes	11

This medium-sized grouper is common around coral heads from depths of 3-30 ft or more on most reefs. It is a rather active, demersal species which lies in wait for its prey beneath ledges and coral heads. In the Gilbert Islands one specimen of this species examined had taken a shrimp (Randall 1955).

Species: *Anypserodon leucogrammicus* (grouper)
Number examined: Eniwetok, 5 specimens: 2 empty
Sex: Males and females
Standard length: 230-350 mm
Digestive tract: Similar to *E. merra*

One of the three specimens with food had unidentified fish fragments in its stomach; another had a goat fish and the third had only the foraminiferan, *Calcarina* sp., along with sand grains of the same size, caught in the folds of its stomach mucosa. This species is uncommon, but present in lagoon reef areas and seaward reefs where the water is not turbulent. It secludes itself under corals almost all of the time, and is rarely observed by the skin-diver. Doubtless it lies motionless under

corals watching for fish or invertebrates to pass by closely enough so that it may lunge out to seize them.

Species: *Plectropomus truncatus* (grouper)
Number examined: Eniwetok, 3 specimens: 2 empty
Sex: Undeveloped
Standard length: 295-600 mm
Digestive tract: Similar to *E. merra*, but with enlarged canines.

The one specimen containing food had a squirrel fish, *Holocentrus* sp., in its stomach. This species is common on reefs having an abundance of living coral from 4-20 ft in depth. It is more active and less demersal than other groupers, characteristically hovering in mid-water. It is shy and difficult for a swimmer to approach. It especially hovers in surge channels of the seaward reefs, or just over the reef front 6-20 ft below the surface. Although only one of the three specimens examined contained a fish as food, it is rather certain that fish are the principal food items taken.

Family Summary

Although all the members of this family are voracious carnivores ubiquitous on Marshallese coral reefs, there are great differences in habits between the smaller and larger species, and among the larger species certain pertinent differences occur. Most of the smaller species are demersal and conceal themselves in crevices or holes in corals, or under ledges and rocks in coral rubble. Their characteristic habit is to lie motionless on the bottom, mostly concealed by the coral except for the head always directed outward, where they lie in wait for unwary small fish or invertebrates to come within their reach. A rapid lunge of a few inches to a few feet is made to catch their prey. Some of the larger species can always be found lying motionless on sandy or rubble bottoms just a few feet from coral mounds. They appear to pay little attention to swimmers at the surface, but little by little they move further outward to deep water.

Certain of the larger species, notably *V. louti*, characteristically hover in mid-water near the coral caverns in which they seclude themselves. Still others, *Plectropomus truncatus* and *P. leopardus*, hover in mid-water over open areas in surge channels, just over the seaward reef edge, or near coral mounds and patches in deeper water on the lagoon reefs.

Groupers are not notoriously rapid swimmers; hence, even those larger forms which hover in open water, or those which are demersal and lie motionless on the bottom, probably subsist to a great extent on crustaceans and coral-dwelling fish which venture too closely to them. It is doubtful that they could catch other mid-water fishes.

Family Pseudochromidae

Species: *Plesiops melas*
Number examined: Arno, 15; Eniwetok, 1 specimen: 1 empty
Sex: Males and females
Standard length: 36-58 mm
Digestive tract: Mouth large, teeth in villiform bands on both jaws; intestine short.

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	33
Hermit crab fragments	13
Xanthid crab fragments	6
Shrimp fragments	6
<i>Alpheus</i> sp. fragments	6
Fish	
Unid. fragments	20
<i>Eviota</i> sp.	13
Gastropoda	
Unid. gastropod fragments	20
Sand	6

This species, common at Arno, was rather uncommon at Eniwetok. It lives on the interisland reef and seaward reefs where the wave action is rather strong. The species is demersal and hides in and under living coral. It characteristically remains motionless while lying in wait for its prey which comprises members of the benthonic fauna.

Species: *Plesiops nigricans*
Number examined: Arno, 6 specimens
Sex: Males and females
Standard length: 74-119 mm
Digestive tract: Similar to *P. melas*

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	50
<i>Portunus longispinosus bidens</i>	17
Xanthid crab fragments	17
<i>Coenobita</i> sp.	17
Hermit crab fragments	17
<i>Galathea</i> sp.	17
Copepods	17
Fish	
Unid. fragments	34
<i>Abudefduf glaucus</i>	17
<i>Apogon novemfasciatus</i>	17

This species was especially common at Arno Atoll on the seaward reef shallows. It is mainly an intertidal species and is commonly found stranded in small tide pools containing loose boulders, or even under rocks completely exposed at low tide. It is a voracious carnivore which apparently darts out from its hiding place to seize its prey which consists of benthonic intertidal crustaceans and small fish associated with corals in shallow water, or tide pool inhabitants.

Species: *Pseudogramma polyacantha*
Number examined: Arno, 13; Bikini, 3 specimens: 5 empty
Sex: Males and females
Standard length: 28-65 mm
Digestive tract: Similar to *P. melas*

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	54
Crab fragments	27
Xanthid crab fragments	9
Fish	
Unid. fragments	9

This species was uncommon at Eniwetok, but rather abundant at Arno Atoll, on both the lagoon and seaward reef shallows near living coral. It habitually hides in and under living coral and has a demersal nature. Like others of this family it lies in wait for prey to come sufficiently close to capture, and thus feeds mostly on benthonic crustaceans and small fish associated with living coral.

Species: *Pseudochromis tapeinosoma*
Number examined: Arno, 2 specimens
Sex: Males
Standard length: 29-37 mm
Digestive tract: As in *P. melas*, except that jaws contain teeth in villiform bands and strong canines

Both specimens examined had taken small crustaceans, and contained crab fragments, isopods, and copepods. This very small species, uncommon at Eniwetok, was common both at Bikini and at Arno in living coral both on the lagoon and seaward reefs. It is demersal, and doubtless feeds by lying in wait for small crustaceans to come close to it.

Family Summary

All species of this family live under ledges and rocks and in interstices of living corals, rather similar in

habits to the demersal groupers. Only *P. nigricans* is found in the intertidal zone where it is a characteristic carnivore in tide pools. All are voracious carnivores, although small in size, feeding predominantly on crustaceans, but taking any prey the proper size. Their characteristic feeding method is to lie in wait for prey species to come near enough for capture, which is then accomplished by a rapid lunge.

Family Pempheridae

Species: *Pempheris oualensis* (sweeper)
Number examined: Bikini, 11; Eniwetok, 5 specimens: 1 empty
Sex: Males and females
Standard length: 75-180 mm
Digestive tract: Mouth moderate in size, teeth in villiform bands on the jaws; intestine short

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	26
Alpheid shrimps	6
Xanthid crab fragments	26
<i>Trapezia</i> sp.	20
Crab megalopa	20
Stomatopod fragments	13
<i>Odontodactylus</i> sp.	6
Copepods	6
Polychaeta	
Unid. pelagic polychaetes	20
Polynoid polychaetes	6
Cephalopoda	
<i>Octopus cyanea</i>	6
Fish	
Juvenile wrasses	6

Sweepers are abundant locally at all three atolls, most commonly in seaward reef surge channels or under overhanging reef ledges at the seaward edge where they are subjected to severe wave action. Frequently large numbers school at the head of surge channels. They also occur commonly on the lagoon reef around large coral mounds in water 10-20 ft in depth. They appear to be voracious carnivores usually having the stomachs crammed with food, mainly crustaceans.

Family Lutjanidae

Species: *Lutjanus monostigmus* (snapper)
Number examined: Eniwetok, 3 specimens: 2 empty
Sex: Female
Standard length: 345-365 mm
Digestive tract: Mouth large, canines well developed on sides of jaws; stomach thick-walled; intestine short, one loop

The single specimen containing food had eaten several goat fish (Mullidae). This species does not wander about, but remains in small schools in the deeper waters of the lagoon reef. Frequently, it may be seen in large caverns in the coral mounds. The young swim in larger schools on the seaward reef shallows and interisland reef shallows.

Species: *Lutjanus bohar* (snapper)
Number examined: Bikini, 2 specimens: 1 empty
Sex: Males
Standard length: 470-550 mm
Digestive tract: Similar to *L. monostigmus*

The one specimen containing food had unidentified fish fragments in its stomach. This large snapper was never seen in the shallow reef areas, but was seen occasionally in deeper water down the lagoon reef slope or off the seaward reef edge. It is a hovering, mid-water carnivore.

Species: *Lutjanus vitta* (snapper)
Numbers examined: Arno, 2; Eniwetok, 24 specimens: 8 empty
Sex: Males and females
Standard length: 161-255 mm
Digestive tract: As in *L. monostigmus*

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	38
Portunid crabs	27
Crab fragments	27
Stomatopod fragments	5
Fish	
Unid. fragments	11
<i>Spratelloides delicatulus</i>	11
Polychaeta	
Unid. fragments	5
Chordata	
<i>Ptychodera</i> sp.	5

This snapper is very abundant in the Marshall Islands, and was observed commonly in schools, comprised, frequently, of both *L. vitta* and *L. gibbus*, along rocky ledges bordering sandy patches. It was also observed frequently in large holes 6-8 ft deep in the interisland reefs at Eniwetok. Apparently, it feeds from the surface to the bottom, as the food items range from surface swimming round herring, *S. delicatulus*, to fossorial balanoglossids, *Ptychodera* sp.

Species: *Lutjanus vaigiensis* (snapper)
 Number examined: Arno, 6 specimens
 Sex: Undeveloped
 Standard length: 33-58 mm
 Digestive tract: Similar to *L. monostigmus*

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	50
Amphipods	33
Shrimp fragments	17
Stomatopod fragments	17
Fish	
Unid. fragments	50

The specimens examined were all juveniles taken from a large school on the lagoon reef at Arno in water about 5 ft deep. At this age they apparently feed mostly on the benthonic fauna in shallow water. The adults reach about 18 inches in length, and probably have different habits than those indicated here for the juveniles. However, Randall (1955) reported on the food of two larger *vaigiensis* from the Gilbert Islands and listed a small crab for one and a small holothurian for the other, both benthonic forms.

Species: *Lutjanus gibbus* (snapper)
 Number examined: Arno, 1; Eniwetok, 32 specimens: 10 empty
 Sex: Males and females
 Standard length: 175-260 mm
 Digestive tract: Similar to *L. monostigmus*

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crab fragments	60
Portunid crab fragments	17
<i>Kraussia rugulosus</i>	8
Parthenopid crabs	4
Hermit crabs (<i>Calcinus</i> sp.)	4
Alpheid shrimp	4
<i>Alpheus ventrosus</i>	4
Shrimp fragments	4
Amphineura	
Solenogastroid (<i>Neomenius</i> sp.)	13
Cephalopoda	
<i>Octopus</i> sp.	4
Gastropoda	
<i>Natica</i> sp.	4
Chordata	
<i>Ptychodera</i> sp.	4
Echinodermata	
Small unid. holothurians	4
Polychaeta	
Unid. polychaetes	4
Sipunculoidea	
Unid. fragments	4
Fish	
<i>Apogon erythrinus</i>	4

This snapper is one of the most abundant in the Marshall Islands. It is seen commonly on all reefs, particularly in the interisland reefs where coral growth is luxuriant and the water is at least 6-8 ft deep. At Arno huge schools moved back and forth just beyond the seaward reef edge. It feeds just about everywhere on the reefs, taking species commonly associated with living, branching corals, and benthonic fauna characteristic of sandy bottoms, some of which are fossorial species. It depends primarily upon crustaceans, the bulk of which are sandy-bottom dwellers.

Species: *Scolopsis cancellatus* (snapper)
 Number examined: Arno, 3 specimens: 1 empty
 Sex: Males and females
 Standard length: 40-137 mm.
 Digestive tract: Similar to *L. monostigmus*

One specimen contained crab fragments and the other had only gurry. This species lives near branching corals, especially at the protected seaward reef edge and the lagoon reef edge. Because of its structure and habits it is probably predacious on crustaceans and small fish.

Species: *Gymnocranius griseus* (snapper)
 Number examined: Arno, 1; Eniwetok, 1 specimen
 Sex: Female
 Standard length: 298-375 mm
 Digestive tract: Mouth moderate in size, teeth short, canines near symphyses of jaws, rounded and molariform on sides of jaws; stomach heavy-walled; intestine moderately short with slight looping

In the two specimens examined the following food items were found: Crustacea—*Thalamita* sp., Xanthid crab fragments; Echinodermata—*Holothuria* sp. (entire specimen), *Maretia* sp. (heart urchin); Pelecypoda—Unid. clam.

This species has rather different food habits than other lutjanids examined, as would be expected from its highly modified dentition. It is strictly a feeder on the benthonic fauna, and more particularly on the fossorial types, many of which are hard shelled and must be crushed before being digested. It has been observed in the process of foraging on sandy bottoms where it "blows" the sand away from buried prey. *G. griseus* is a rather slow-swimming "solemn" appearing fish. It is often seen in groups of two or three individuals hovering around large coral mounds adjacent to open sandy areas. They slowly circle these coral mounds keeping an eye on skin divers.

Species: *Lethrinus microdon* (snapper)
 Number examined: Eniwetok, 2 specimens
 Sex: Male and female
 Standard length: 270-340 mm
 Digestive tract: Similar to *L. monostigmus*

The two specimens examined had eaten the following: Crustacea—Maid crab; Portunid crab; Crab fragments; Fish—Unid. fragments.

This species is solitary and occurs only in the deeper water over the lagoon reef slope. None were seen in water shallower than 15 ft. According to the food items eaten, the species must swim close to the bottom where it feeds on benthonic crustaceans primarily. Al-Hussaini (1947) reports that two species of this genus in the Red Sea also prefer benthonic crustaceans, but take a wide variety of prey, including echinoderms and molluscs.

Species: *Aprion virescens* (streaker)
 Number examined: Eniwetok, 3 specimens: all empty
 Sex: Males and females

Standard length: 540-760 mm

Digestive tract: Mouth very large, teeth strongly developed, heavy canines; intestine moderately short

The specimens examined had been eating garbage, but this species is a large, solitary, voracious carnivore which hovers in mid-water over the lagoon reef slope from 10-40 ft in depth. It will cruise quite slowly up to the shallows in search of prey, but when disturbed it moves back into deeper water, where it swims along the bottom. At no time have we seen this fish feeding, except during rotenone poisoning stations, but there is no doubt about its niche being that of a voracious, roving carnivore on the lagoon reefs.

Species: *Gnathodentex aureolineatus*

Number examined: Bikini, 4 specimens

Sex: Males and females

Standard length: 160-180 mm

Digestive tract: Both jaws with outer row of conical canines, three pairs of which are enlarged at front of jaws; intestine moderately short

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crabs	100
Gastropoda	
<i>Cerithium</i> sp.	75
Polychaeta	
Unid. fragments	25
Fish	
<i>Stenatherina temminckii</i>	25
Unid. fragments	25

This species frequents the relatively deep water over the lagoon reefs and the surge channels along the seaward reef margin. It is apparently a solitary carnivore which takes both food at the surface or in mid-water (silversides) and benthonic fauna (xanthid crabs, polychaetes, and gastropods).

Family Summary

Snappers are all carnivorous fish, with one possible exception, *Macolor niger*, which will be discussed below. They vary in size from small fish a few inches in length to some of the largest of the reef-dwelling species, exceeding 3 ft. Several species school (*Lutjanus kaimira*, *gibbus*, *vitta*), but most are solitary or occur as loosely organized aggregations. The largest species, i.e., *L. bohar*, and *A. virescens*, are solitary. All have large mouths and strong dentition. By and large they seem to be predominantly benthonic feeders and swim just above the bottom. A few, of which *A. virescens* is a good example, are mid-water forms. At least three species, *L. vitta*, *L. gibbus*, and *Gymnocranius griseus*, take fossorial forms, with the latter species having developed the proper dentition and habits to feed almost exclusively on hard shelled clams, heart urchins, and gastropods. Except for *G. griseus* very little specificity is shown in types of prey taken; most capture any type of fish or invertebrate which they contact and can handle. Randall (1955) examined a few lutjanids in the Gilbert Islands and found similar feeding habits to those described here.

One species, *Macolor niger*, was taken by hook and line from the Eniwetok pier, so was not included in the food study. However, its great divergence in food habits and structural features from the usual snapper make it worthwhile to mention here. This species has the gill rakers modified for sieving plankton and they project well forward into the buccal cavity. However, the fact that it was caught on a baited hook indicates that it is by no means restricted to a planktonic diet. Species of the genus *Caesio* are full-fledged plankton

feeders, but none were collected for our study. Randall (1955) reports the food of *C. xanthonotus* in the Gilbert Islands to consist of pelagic copepods, mollusc larvae, shrimp nauplii, and fish eggs.

Thus, the family Lutjanidae comprises a heterogeneous group of fishes as regards their food and feeding habits and associated structural modifications. This heterogeneity is reflected in the many taxonomic changes made by successive authors in evaluating the parameters of this family.

Family Leiognathidae

Species: *Gerres argyreus* (silver perch)

Number examined: Arno, 2 specimens

Sex: Female

Standard length: 133-186 mm

Digestive tract: Rather long, highly protrusible snout, small teeth in villiform bands on both jaws; stomach thin-walled; intestine long, coiled.

The following food items were found in the two specimens examined: Crustacea—Isopods, Ostracods; Polychaeta—Unid. polychaetes; Foraminifera; Algae—Algal scrapings, little sand; Algal filaments, little sand.

Silver perch are solitary individuals distributed usually over sandy bottoms in quiet lagoon reef waters from 6-30 ft. deep. They work busily at stirring up the surface layers of the bottom with their protrusible snouts, taking anything edible. They are clearly omnivorous in habits, a fact reflected by the long, coiled intestine and thin-walled stomach. Al-Hussaini (1947) found *G. oyena* in the Red Sea to prefer polychaetes, but to take also such items as small crustaceans, fish, and other organisms.

Family Sparidae

Species: *Monotaxis grandoculis*

Number examined: Arno, 3; Eniwetok, 5 specimens: 1 empty

Sex: Males and females

Standard length: 195-250 mm

Digestive tract: Mouth moderately large, both jaws with a single row of molar teeth, the posterior few very broad and heavy, strong canines at front of both jaws; stomach heavy-walled; intestine of medium length.

Food item	Percentage of fish containing the item
Gastropoda	
Crushed <i>Atys</i> sp. and <i>Cerithium</i> sp.	100
Pelecypoda	
Crushed sand-dwelling clams, few whole	71
Crustacea	
Crushed crab fragments	42
Portunid crabs	28
Parthenopid crabs	14
Hermit crabs (crushed gastropod shells)	28
Echinodermata	
Small spatangids, crushed	14
Polychaeta	
Unid. polychaetes	14

This species is always found alongside coral mounds, swimming slowly or hovering over sandy patches. It is most often solitary, but does form loose aggregations of two or three individuals at times. Its food habits and dental structure designate it as a feeder on fossorial forms, taking hard-bodied species which are crushed with the massive grinding-, crushing-type molariform teeth. When feeding this fish virtually stands on its head and "blows" away the sand surrounding its prey. Randall (1955) found specimens in the Gilbert Islands to feed as reported here.

This genus is frequently included with the family Lutjanidae (Schultz *et al.* 1953). However, we believe that it is sufficiently distinct, structurally and behavioristically, to merit its taxonomic segregation.

Family Mullidae

Species: *Mulloidichthys samoensis* (goatfish)

Number examined: Arno, 19; Bikini, 7; Eniwetok, 8 specimens: 11 empty

Sex: Males and females

Standard length: 81-250 mm

Digestive tract: Chin with barbels, mouth medium, teeth minute; stomach V-shaped; intestine medium-long

Food item	Percentage of fish containing the item
Fish	
Gurry	42
Unid. fragments	28
Polychaeta	
Unid. polychaetes	14
Sabellids	4
Crustacea	
Shrimp fragments	14
Crab fragments	9
Hermit crab fragments	9
Cyclopoid copepods	9
Pelecypoda	
<i>Semelangulus</i> sp.	14
Gastropoda	
Crushed gastropods	9
Echinodermata	
Spatangid fragments	9
Chordata	
<i>Ptychodera</i> sp.	4
Sand, including foraminiferans	14

This species was found in large schools of 25-100 individuals swimming over and probing sandy bottoms with their barbels. They are especially abundant on shallow lagoon shores and on seaward reef flats when the tide is high. As its food items indicate, it consumes fossorial as well as surface benthonic fauna. At Eniwetok the specimens examined had been feeding heavily on the small clam, *Semelangulus* sp.

Species: *Parupeneus trifasciatus* (goatfish)

Number examined: Arno, 27 specimens: 3 empty

Sex: Males and undeveloped

Standard length: 46-150 mm

Digestive tract: Similar to *M. samoensis*

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crab fragments	17
Maid crab fragments	12
Shrimp fragments	33
Unid. shrimps	17
<i>Alpheus</i> sp.	17
Cyclopoid copepods	12
Calanoid copepods	8
Copepod metanauplii	4
Ostracods	8
Tanaid isopods	8
Amphipods	4
<i>Galathea</i> sp.	4
Fish	
Unid. fragments	20
Gastropods	
<i>Oliva</i> sp.	12
Polychaeta	
Unid. polychaetes	4
Foraminifera	
<i>Calcarina</i> sp.	8

P. trifasciatus is a small goatfish which occurs in groups of two or three on virtually all reefs from 3-10 ft deep. Frequently it is seen probing the sand with its barbels around the base of coral heads. It forages in typical goatfish fashion, but takes mostly smaller crustaceans, other invertebrates, and small benthonic fish. In the Gilbert Islands, Randall (1955) reported this fish to have consumed amphipods, copepods, and other small crustaceans.

Species: *Parupeneus barberinus* (goatfish)

Number examined: Arno, 9; Eniwetok, 3 specimens

Sex: Males

Standard length: 60-390 mm

Digestive tract: Similar to *M. samoensis*

Food item	Percentage of fish containing the item
Polychaeta	
Unid. polychaetes	58
Crustacea	
Shrimp fragments	41
Ostracods	25
Isopods	25
<i>Thalamita</i> sp.	17
<i>Tetralia globerrima</i>	8
Xanthid crabs	8
Amphipods	8
Copepods	8
Nebalaceans	8
Foraminifera	
<i>Calcarina</i> sp.	8
Sand grains	8

This species is common in groups of two or three over sandy-bottom areas on all reefs in water 2-30 ft deep. It reaches a large size. Its foraging habits are similar to other goatfish, consequently, polychaetes and benthonic crustaceans predominate in its diet.

Species: *Parupeneus cyclostomus* (goatfish)

Number examined: Bikini, 1; Eniwetok, 5 specimens: 2 empty

Sex: Males and females

Standard length: 130-285 mm

Digestive tract: Similar to *M. samoensis*

Food item	Percentage of fish containing the item
Crustacea	
<i>Thalamita</i> sp.	75
Xanthid crabs	25
<i>Odontodactylus</i> sp.	50
Shrimp larvae	25
Alpheid shrimps	25
Amphipods	25
<i>Galathea</i> sp.	25
Fish	
Unid. fragments	50
Wrasse, small	25
<i>Calymnichthys goramensis</i>	25
<i>Eriota</i> sp.	25
<i>Gnatholepis anjerensis</i>	25

This comparatively large goatfish is usually found solitary, although loose aggregations of two or three are commonly seen on all reefs with open sandy areas in water from 1-20 ft deep. It probes the bottom actively, now and then stirring up the sand to capture crustaceans hidden there. It is an active feeder on small, benthonic fish species also. Frequently rather extensive bottom areas are left "rooted" up as the result of the foraging habits of this species.

Species: *Upeneus arge* (goatfish)

Number examined: Eniwetok, 2 specimens

Sex: Male and female

Standard length: 260-270 mm

Digestive tract: Similar to *M. samoensis*

The two specimens contained the following food items in their stomachs: Crustacea—*Thalamita* sp., *Callappa* sp., *Callianassa* sp., Unid. shrimp. This rather large species schools in groups numbering five to about 50 individuals, and frequents sandy-bottom areas on the lagoon reef in water 4-15 ft deep and on the seaward reef flat. It does not probe the sand with its barbels as do other goatfish, but rather seeks out those benthonic crustaceans living exposed on the sandy bottoms. Perhaps because it does not probe, it seems much swifter than other goatfish. Suyehiro (1942) reports that *U. bensasi* feeds rather similarly in Japan, having found alpheid shrimps, amphipods, crawling shrimps (*Crago* sp.) and sand worms (*Nereis* sp.) in their stomachs.

Family Summary

Goatfish are small to medium-sized fish, some solitary, others schooling, which frequent the sandy bottom areas

of all reefs and the seaward reef flats when sufficiently covered by the rising tide. Except for the rapidly swimming *U. arge*, most busily probe the sand, moving very slowly, giving it a thorough searching for prey. Both surface benthonic forms and fossorial species are captured. In general they avoid hard-bodied fossorial forms such as clams and echinoderms because they have no crushing dentition. The teeth are mostly small and weak, restricting them to crustaceans and soft-bodied invertebrates.

Family Cirrhitidae

Species: *Amblycirrhitus arcatus* (hawkfish)

Number examined: Arno, 18; Bikini, 1; Eniwetok, 1 specimen;
3 empty

Sex: Males and females

Standard length: 46-72 mm

Digestive tract: Mouth large, teeth not strongly developed;
intestine short straight.

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	47
<i>Stenatherina temmincki</i>	5
Paraperoid	5
Crustacea	
<i>Galathea</i> sp.	17
Xanthid crab fragments	11
<i>Thalamita</i> sp.	5
Maid crab fragments	5
<i>Trapezia</i> sp.	5
Hippolytid shrimps	5
<i>Leander</i> sp.	5
<i>Alpheus</i> sp.	5
Isopods	5

This solitary species is ubiquitous in reef areas containing large, living coral heads. It habitually lies motionless on the upper surface of living coral heads waiting for crustaceans and small fishes to come within range of its rapid thrust to capture them. It does not move much even if disturbed. Its food items are those very closely associated with living coral, hence it need not venture far away from its home base.

Species: *Paracirrhites forsteri* (hawkfish)

Number examined: Arno, 7; Bikini, 1 specimen

Sex: Females

Standard length: 50-137 mm

Digestive tract: Similar to *A. arcatus*

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	62
Wrasses, young	25
<i>Chromis caeruleus</i>	12
<i>Istiblennius</i> sp.	12
Fish eggs	12

This species has very similar habits to those of *A. arcatus*, and occupies the same general areas of the reef. Its food habits seem to run to fish rather more than to crustacea as contrasted with *A. arcatus*, but this may be the result of the larger size of *P. forsteri*. Randall (1955) reports that one of this species examined in the Gilbert Islands contained a shrimp.

Species: *Cirrhitichthys aprinus* (hawkfish)

Number examined: Arno, 3 specimens

Sex: Females

Standard length: 42-48 mm

Digestive tract: Similar to *A. arcatus*

The following food items were found in the stomachs of the three fish examined: Crustacea—Isopods, Amphipods, Crab fragments; Fish—Unid. fragments, Fish eggs; Polychaeta. This small hawkfish remains under ledges and in branching coral near the outer reef edges on both lagoon and seaward reefs, and does not lie in

exposed areas as do the two species previously mentioned. It has not been observed in the act of feeding, but apparently it takes any small forms which approach it closely enough for capture.

Species: *Cirrhitus pinnulatus* (hawkfish)

Number examined: Bikini, 1 specimen

Sex: Female

Standard length: 140 mm

Digestive tract: Similar to *A. arcatus*

The one specimen examined contained a small coral crab, *Trapezia* sp. This species resides commonly at the outer edge of the seaward reef where it lies in holes in living coral and feeds in the interstices. Similar habits for this species were mentioned by Randall (1955) for a specimen from the Gilbert Islands.

Family Siganidae

Hawkfish are small, solitary, demersal carnivores which lie in wait for their prey which consists mostly of crustaceans and small fish closely associated with living corals. The larger members of the family usually lie motionless on the tops and sloping sides of living coral heads, rather than partially concealed as do the small groupers. Those that lie in exposed situations are brilliantly colored and very easily seen on the coral. None are protectively or obliteratively colored, but rather appear to possess warning colors. They are sluggish when molested, moving only a few inches or a few feet. *C. pinnulatus*, however, is actually camouflaged comparable to the patterns exhibited by a scorpaenid.

Family Siganidae

Species: *Siganus rostratus* (rabbitfish)

Number examined: Arno, 2; Bikini, 3; Eniwetok, 10 specimens

Sex: Males and females

Standard length: 167-310 mm

Digestive tract: Mouth small, numerous small, conical teeth in each jaw, pharyngeal teeth well developed; stomach rather thick-walled; intestine broad, extremely long, coiled, and thick-walled

Food item	Percentage of fish containing the item
Algae	
Scraped algal filaments with calcareous powder	60
Fronds bitten off, no sand	40
Foraminifera	
<i>Calcarina</i> sp. (probably taken with scraped algae)	20

Rabbitfish are abundant on Marshallese reefs, particularly on interisland reefs and seaward reef flats during high tide, where they occur in dense schools of from 20-500 individuals. They are busy feeders, browsing head down on algal covered rocky bottoms, moving slowly along. Little attention is paid to skin-divers in the vicinity of these schools. The species is herbivorous, and may be classed as a typical browser. It, like a number of other naturally herbivorous species (Family Acanthuridae), becomes an habitu   of garbage dumps where it consumes waste meat scraps. This indicates that it is not an obligatory herbivore and that both its feeding and digestive apparatus can convert to a fleshy diet on occasion.

Suyehiro (1942), in mentioning the earlier studies of Uchida on this genus, stated that this worker had found the smaller individuals (140 mm) feeding chiefly on copepods and those from 180 to 200 mm on diatoms and seaweeds, i.e., as they grew older they turned more and more to an herbivorous diet. Suyehiro, in his own investigation, failed to find any evidence for ascribing a carnivorous diet to the young and classed them as

herbivorous, even though some animal food was admixed with the prodigious quantities of algae eaten. Our results agree perfectly with his findings.

Family Kyphosidae

Species: *Kyphosus cinerascens* (pilot fish, rudder fish)
Number examined: Arno, 1; Eniwetok, 3 specimens: 1 contained garbage only
Sex: Males and females
Standard length: 230-345 mm
Digestive tract: Mouth small, protrusible, both jaws with a uniserial outer row of obtusely lanceolate incisors, with minute villiform teeth behind; stomach a two part gizzard; intestine very long, coiled

The specimens examined contained fronds and filaments of algae bitten off and scraped, but with no sand or calcareous powder.

This kyphosid occurred in small schools, usually swimming rapidly in mid-water or near the surface on both lagoon and seaward reefs at depths of 6-20 ft. It was especially abundant just beyond the reef edge of the seaward reefs. It is a strictly herbivorous species which may be classed as a browser.

Family Chaetodontidae

Species: *Chaetodon lunula* (butterfly fish)
Number examined: Eniwetok, 1 specimen
Sex: Female
Standard length: 135 mm
Digestive tract: Mouth very small, snout somewhat produced, teeth long, slender, straight, bent at tip where they taper to a point; stomach Y-shaped, thick-walled; intestine long, coiled

The specimen examined contained many browsed tips of coral polyps. This chaetodontid was frequently observed swimming close to isolated coral heads surrounded by patches of sand. The adults were seen most commonly in the lagoon to depths of 10 feet, while the young were most abundant on the seaward reef shallows. It is a rather shy species, always turning the edge of the body to a skin-diver, so as to make it virtually impossible to spear. In confinement this species will take occasional scraps of meat, and frequently browses on algae growing on the walls of the tank.

Species: *Chaetodon citrinellus* (butterfly fish)
Number examined: Arno, 4; Bikini, 2; Eniwetok, 10 specimens
Sex: Males and females
Standard length: 39-95 mm
Digestive tract: Similar to *C. lunula*

Food item	Percentage of fish containing the item
Coelenterata	
Coral polyps, no skeletal material	61
Coral polyps, some skeletal material	33
Algae	
Algal scrapings, no calcareous powder	11
Algal scrapings, with calcareous powder	5
Polychaeta	
Unid. polychaetes	5

This butterfly fish is abundant in and around coral heads at depths of 2-20 ft in the lagoon, interisland reefs, and the seaward reef. Frequently it can be seen browsing on the surface of live coral heads, particularly *Aeropora* and *Porites*, where it nibbles off the small coral polyps extending from the corallites. Living coral heads placed in confinement with this chaetodontid were browsed in the same manner while under careful observation by us. The species is not restricted to a diet of polyps, however, as it is also capable of scraping fine filaments of algae off rocks and dead bases of coral

heads, as well as taking polychaetes from interstices of living coral heads.

Species: *Chaetodon ephippium* (butterfly fish)
Number examined: Arno, 4; Eniwetok 6 specimens
Sex: Males and females
Standard length: 123-160 mm
Digestive tract: Similar to *C. lunula*

Food item	Percentage of fish containing the item
Coelenterata	
Coral polyps, with skeletal particles	60
Algae	
Fine filaments, no calcareous material	50
Crustacea	
Shrimp fragments	10
Polychaeta	
Unid. polychaetes	10

This species is very common around living coral on all reefs in water 2-25 ft deep. Unlike most butterfly fish, it is also commonly seen in sandy regions containing but few coral heads. Its feeding habits are similar to the chaetodontids described above.

Species: *Chaetodon vagabundus* (butterfly fish)
Number examined: Arno, 4 specimens
Sex: Males
Standard length: 58-85 mm
Digestive tract: Similar to *C. lunula*

Food item	Percentage of fish containing the item
Coelenterata	
Coral polyps, with skeletal particles	75
Algae	
Fine scrapings, with calcareous powder	25
Filaments, without calcareous powder	25

This species was common only at Arno Atoll, and apparently does not occur at all, or is extremely rare, in the northern Marshall Islands. It swims about living coral on both the lagoon, and seaward reefs, and doubtless does likewise on the interisland reefs. Its food and feeding habits are similar to the chaetodontids described above.

Species: *Chaetodon reticulatus* (butterfly fish)
Number examined: Bikini, 1 specimen
Sex: Male
Standard length: 110 mm
Digestive tract: Similar to *C. lunula*, except that the teeth are very fine, numerous, flexible and brush-like

The one specimen examined contained only fine filamentous algae. This species is common on the seaward reef flats, particularly on the outer half, and in quiet waters of the lagoon rich in living coral. It habitually remains in hiding in crevices and holes in the coral. It has been observed to graze on the fine algal filaments which cover the seaward reef shallows, and apparently does not take coral polyps, at least to any great extent.

Species: *Chaetodon auriga* (butterfly fish)
Number examined: Arno, 15; Bikini, 1; Eniwetok, 13 specimens: 1 empty
Sex: Males and females
Standard length: 43-165 mm
Digestive tract: Similar to *C. lunula*

Food item	Percentage of fish containing the item
Polychaeta	
Unid. polychaetes	46
Coelenterata	
Coral polyps, no skeletal material	28

Algae	
Fine filaments, no calcareous powder	25
Fine filaments, with calcareous powder	3
Crustacea	
Shrimp fragments	10
<i>Alpheus</i> sp.	3
<i>Tetralia</i> sp.	3
Ostracods	3
Gastropoda	
Egg masses	7
Vermetid fragment	3
Nemertinea	10
Foraminifera	
<i>Calcarina</i> sp.	3

This is a common butterfly fish on all reefs visited in water 2-25 ft in depth. It frequently is seen swimming over sandy areas near coral rubble, rather far removed from beds of living coral. Its food is more heterogeneous than other chaetodontids, although it is still classed as omnivorous. The predilection for polychaete worms noted for this species is not shared to the same extent by other members of the family. In confinement with living coral, it busily nibbles off the polyps. Its feeding habits are extremely facultative, which probably accounts for its food forays over sandy areas and in coral rubble not closely adjacent to living corals.

Species: *Megaprotodon strigangulus* (butterfly fish)
Number examined: Eniwetok, 11 specimens: 2 empty
Sex: Males and females
Standard length: 60-110 mm
Digestive tract: Similar to *C. lunula*, except that the teeth are massed toward front of jaws and protrude

All specimens with food in their stomachs contained only coral polyps with no skeletal material admixed. This species is very common on all reefs visited where living coral is abundant. It stays very close to living corals, never venturing more than a few feet away from cover. It is the only chaetodontid which seems to feed exclusively on coral polyps in nature, and its dentition is especially suited to this feeding habit. However, in confinement it will graze on encrusting algal filaments and take meat scraps.

Species: *Centropyge flavissimus* (angel fish)
Number examined: Arno, 8; Bikini, 2; Eniwetok, 2 specimens
Sex: Male and female
Standard length: 45-75 mm
Digestive tract: Snout not produced, mouth small, teeth setiform, long, flattened, tricuspid, the middle lobe much larger than the lateral lobes; intestine very long, coiled, rectum huge

These specimens had taken algae exclusively, with 88% of them biting off algal fronds which had no calcareous powder admixed, and 12% had scraped fine filaments of algae in which some calcareous powder was mixed. This angel fish is common around living coral, usually hiding in crevices or holes, on all reefs in quiet water 4-15 ft deep. It is entirely herbivorous, mostly a browser, but occasionally a grazer.

Family Summary

The chaetodontids are brilliantly colored, laterally highly compressed, deep-bodied fish as typical of coral reefs as the corals themselves. They occur singly or in pairs on both lagoon, seaward, and interisland reefs wherever coral growth is luxuriant.

Considerable heterogeneity is evident as regards the food and feeding habits of the several members of this family examined. Some appear to be rather strict herbivores, grazing or browsing short algal filaments on reef rock or on the dead bases of coral heads (*C. reticulatus* and *Centropyge flavissimus*). Others seem

to have a strong predilection for browsing and grazing off polyps of coral as well as algal filaments, and thus are omnivores (*C. citrinellus*, *C. ephippium*, *C. vagabundus*). Yet others are strictly browsers on coral polyps, and thus are carnivores (*C. lunula*, *Megaprotodon strigangulus*). Only one, *C. auriga*, is an habitual non-selective omnivore, although polychaetes comprise the bulk of its diet.

It is of interest to note, from the standpoint of feeding methods and related structural modification of the dentition, that the less specific omnivorous species which take coral polyps as part of their diet, along with algae, always contain a considerable amount of calcareous skeletal particles admixed with the food; whereas, those which are selective and consume only coral polyps do not have this admixture of calcareous skeletal material. These observations suggest that the latter species have attained a higher degree of adeptness in nibbling off the polyps. It is apparent that the omnivorous species must scrape the fine algal filaments off rocks and dead coral bases, so when taking coral polyps they probably also scrape the surface, rather than neatly biting off the polyp without touching the corallite.

To add evidence to stomach analyses and field observations on the role of chaetodontids in subsisting, in part, on living coral, several fish, *C. auriga* and *C. citrinellus*, were placed in aquaria along with living coral heads of *Acropora* sp. The fish quickly nosed down to the surface of the corallum, examined it very carefully, and then neatly nibbled off the polyps. On *Acropora* the terminal polyps on the branches were consumed first, and in a few days a great many of the polyps had been nipped off, leaving white patches on the corallum.

It was also observed that the tubular snouts of these fish were thrust into crevices and interstices in the coral possibly to secure polychaetes or small crustaceans secluded there.

Suyehiro (1942) was rather perplexed about the food and feeding habits of *Chaetodon modestus* from Japan, and concluded that the usual food was hermit crabs and algae. No coral is available to this species, so feeding habits comparable to the Marshallese specimens would not be expected, but the omnivorous nature of *C. modestus* certainly agrees in general with our findings.

Family Acanthuridae

Species: *Acanthurus mata* (surgeon fish, tang)
Number examined: Eniwetok, 1 specimen
Sex: Undeveloped
Standard length: 390 mm
Digestive tract: Mouth small, teeth immovable, close-set, compressed, denticulate; stomach a heavy-walled gizzard; intestine thin-walled, long, coiled

This specimen had taken the following food: Algae—bitten and scraped filamentous algae from a sandy bottom, admixed with a great amount of sand and associated organisms; Foraminifera—several foraminiferans taken were probably picked up along with the sand grains while scraping algae; Gastropoda—minute gastropods, probably also taken incidental to feeding on algae growing on the sand; Detritus. This surgeon fish was commonly seen on the lagoon reef at Eniwetok in 8-10 ft of water over sandy bottoms adjacent to coral mounds. It takes immediate refuge under the coral when approached closely by a swimmer. Its feeding position is head down on compacted sandy bottoms covered with fine, filamentous algae. In the process of scraping off the algae it takes inadvertently numerous minute animals among

the benthos. *A. mata* is strictly a grazing herbivore on algal-covered, sandy bottoms.

Species: *Acanthurus xanthopterus* (surgeon fish, tang)
Number examined: Eniwetok, 4 specimens; 2 empty
Sex: Male and female
Standard length: 310-470 mm
Digestive tract: Similar to *A. mata*

The two specimens containing food in their stomachs had the followings items: Algae—short, bitten off filaments with much sand; Coelenterata—Hydroid hydrocaulus; wood splinters. This species is uncommon in the Marshall Islands, but a few were observed at Eniwetok hovering over compacted sandy bottoms on the lagoon reef at depths of 4-50 ft. Its habits are very similar to *A. mata*, feeding frequently in the same area in the same manner.

Species: *Acanthurus gahhm* (surgeon fish, tang)
Number examined: Arno, 1; Eniwetok, 8 specimens
Sex: Males and females
Standard length: 170-215 mm
Digestive tract: Similar to *A. mata*

Food item	Percentage of fish containing the item
Algae	
Short, bitten off algal bases with much fine sand	100
Foraminifera	
<i>Calcarina</i> sp., probably taken incidentally to algal browsing on sand	11
Detritus, probably taken incidentally to algal browsing on sand	11

This species is abundant on all reefs with comparatively quiet water 4-40 ft deep. Large schools frequently browse over sandy bottoms, feeding on the fine, short algae growing on the compacted sand. Randall (1956) noted it to behave similarly in the Gilbert Islands.

Species: *Acanthurus olivaceus* (surgeon fish, tang)
Number examined: Arno, 7; Bikini, 1 specimen
Sex: Males and females
Standard length: 57-181 mm
Digestive tract: Similar to *A. mata*

Food item	Percentage of fish containing the item
Algae	
Fronds bitten off, with calcareous powder	100
Algal scrapings, with calcareous powder	100
Coralline algae	25
Gastropoda	
Crushed small gastropods	12
Foraminifera	
<i>Calcarina</i> sp.	12

This species is common on the lagoon reefs and leeward ocean reefs in 8-25 ft of water where it swims about coral heads and coral rubble adjacent to compacted, sandy bottoms. Similar habits for this species in the Gilbert Islands were noted by Randall (1956).

During foraging periods this species may feed on the short algal cover on compacted sandy bottoms by swimming head down, or it may scrape algae from coral rubble or the dead bases of coral heads. The gastropods and foraminiferans in the stomach probably are taken inadvertently.

Species: *Acanthurus triostegus triostegus* (convict tang, manini)
Number examined: Arno, 17; Bikini, 1 specimen
Sex: Males and females
Standard length: 42-136 mm
Digestive tract: Similar to *A. mata* except that there is no gizzard, but rather a thick-walled pyloric portion of the stomach.

Food item	Percentage of fish containing the item
Algae	
Filaments bitten off, no sand or calcareous dust	100
Scraped filaments, with calcareous dust	5
Foraminifera	
<i>Calcarina</i> sp.	11
Coelenterata	
Scraped coral polyps and skeletal particles	5
Crustacea	
Copepods	5

An ubiquitous, exceedingly abundant surgeon fish on all reefs; sometimes occurring in schools of several hundred busily foraging on the algae of the reef surface. The convict tang is predominantly a browser on algal filaments growing on the reef rock or on bases of dead coral. It apparently grazes only incidentally. The animal constituents of the food probably are inadvertently taken, as this species is strictly herbivorous. Doty & Morrison (1954) report that this species characteristically fed on non-calcareous algae covering dead coral heads (*Pocillopora* sp.) with a brown coating on the reefs of Raroia Atoll, Tuamotus.

The vast numbers of this species on coral reefs provide dynamic evidence of the greater efficiency in energetics for building protoplasm at the lower trophic levels of the food chain.

Species: *Acanthurus achilles* (achilles tang)
Number examined: Bikini, 1; Eniwetok, 2 specimens
Sex: Males and females
Standard length: 130-175 mm
Digestive tract: Similar to *A. t. triostegus*

All three specimens examined contained scraped filamentous algae which was not cropped closely as very little calcareous powder was present. This species is common at the outer edge of the seaward reefs where the surf is strong, and is particularly common in the surge channels. It apparently bites off algal filaments very close to the rocky base; some even appear to be scraped, but the very little calcareous powder found indicates that it is a browser rather than a grazer.

Species: *Acanthurus aliala* (surgeon fish, tang)
Number examined: Arno, 13 specimens
Sex: Males and females
Standard length: 107-162 mm
Digestive tract: Entire digestive tract thin-walled, long, coiled

All specimens examined had consumed algal fronds and filaments which were bitten off, with no sand or calcareous powder admixed. This species is uncommon and rather restricted ecologically to the outer edge of the seaward reef and to surge channels where wave action is moderate to severe. It browses on seaweeds growing in areas of luxuriant coral growth.

Species: *Acanthurus nigroris* (surgeon fish, tang)
Number examined: Arno, 21; Eniwetok, 6 specimens
Sex: Males and females
Standard length: 42-175 mm
Digestive tract: Similar to *A. mata*

Food item	Percentage of fish containing the item
Algae	
Fronds and filaments bitten off	96
Algal scrapings, with calcareous powder	11
Algal filaments, admixed with sand grains	3

This small surgeon fish is exceedingly abundant on the lagoon and interisland reefs, as well as in quiet water on the seaward reefs in depths from 2-20 feet. Schultz

et al. (1953) list this species as *elongatus*, and state that in the northern Marshall Islands it is apparently the most abundant surgeon fish on the reefs; it occurred in almost every type of habitat investigated by them. This species browses on small seaweeds primarily, but does some grazing of short filaments growing both on reef rock and on sandy bottoms. It is more characteristic of coral patches, however, than of reef flats or sandy bottoms.

Species: *Acanthurus guttatus* (surgeon fish, tang)
Number examined: Bikini, 2; Eniwetok, 3 specimens
Sex: Males and females
Standard length: 100-155 mm
Digestive tract: Stomach heavy-walled, not gizzard-like; intestine long, coiled

These specimens contained both fronds and filaments of algae which had been browsed, together with scraped algal filaments admixed with calcareous powder. Consequently, these surgeon fish both browse and graze. Randall (1955) examined several specimens and found them to contain many types of fine algae, *Jania* sp. predominating. The presence of the blue-green alga, *Calothrix*, suggested that they probably crop the algae close to the substrate. The species is abundant on the ocean reef margin, particularly in surge channels, where the current is strong and the water frequently white with bubbles. It frequently ranges up onto the seaward reef flats to forage as the tide rises.

Species: *Acanthurus lineatus* (surgeon fish, tang)
Number examined: Arno, 14 specimens
Sex: Males and females
Standard length: 142-168 mm
Digestive tract: Similar to *A. mata*

These specimens fed predominantly on algal filaments which they browsed, taking little or no calcareous material or sand. The species is, therefore, a browser, with only incidental grazing done. In the Gilbert Islands it was found to subsist mostly on finely divided red algae (Randall 1955). This surgeon fish is rare in the northern Marshall Islands, but locally abundant at Arno Atoll, where it occurred in large schools on the seaward reef flats as the tide arose. Randall (1956) reported it also abundant in the Gilbert Islands. When the seaward reef flats are largely exposed during low tide, schools of this species swim back and forth just beyond the outer reef margin.

Species: *Otenochaetys striatus* (surgeon fish, tang)
Number examined: Arno, 12; Bikini, 2; Eniwetok, 1 specimen
Sex: Males and females
Standard length: 118-170 mm
Digestive tract: Similar to *A. mata* except for the teeth which are long, slender, moveable and expanded at the tip

Food item	Percentage of fish containing the item
Algae	
Algal scrapings, mixed with calcareous powder	80
Algal filaments, mixed with calcareous powder	40
Algal fronds browsed, no sand or calcareous powder	6

This species was common at Arno and at Bikini Atolls, but uncommon at Eniwetok. It occurs on both the lagoon and seaward reefs in shallow water from 6-20 ft deep. It characteristically grazes by scraping dead bases of coral heads and the reef rock, but occasionally forages on the algae growing on the compacted sand adjacent to coral mounds.

Species: *Naso lituratus* (unicorn fish, surgeon fish)
Number examined: Arno, 3; Eniwetok, 6 specimens
Sex: Males and undeveloped

Standard length: 76-390 mm
Digestive tract: Mouth small, teeth bluntly rounded and close-set; stomach thin-walled; intestine long, coiled

Food item	Percentage of fish containing the item
Algae	
Fronds and filaments bitten off (mostly <i>Dictyota</i> sp.), no sand	67
Fronds and filaments bitten off, admixed with sand	33

This common species of unicorn fish frequents both quiet and turbulent water on the lagoon and seaward reefs 4-30 ft deep. It travels in small schools which browse on the larger seaweeds growing on the rocky substrate, and occasionally on the larger seaweeds growing on compacted sandy bottoms.

Species: *Naso unicornis* (unicorn fish, tang)
Number examined: Arno, 1; Eniwetok, 5 specimens
Sex: Males and females
Standard length: 298-440 mm
Digestive tract: Similar to *N. lituratus*

Food item	Percentage of fish containing the item
Algae	
Fronds bitten off, no sand (<i>Dictyota</i> sp. and <i>Padina</i> sp.)	83
Fronds (<i>Dictyota</i> sp.), mixed with calcareous powder	17

This unicorn fish was common in water 3-30 ft in depth on all reefs visited. It usually occurs in small schools which swim about coral heads, especially in the deep, rocky pools on the seaward reefs. This species, like *N. lituratus*, is strictly a browser on the larger seaweeds growing on the rocky flats and coral mounds.

Species: *Zebrasoma veliferum* (surgeon fish, tang)
Number examined: Arno, 1; Eniwetok, 7 specimens
Sex: Males and females
Standard length: 140-260 mm
Digestive tract: Stomach thin-walled, no gizzard; intestine long, coiled

Food item	Percentage of fish containing the item
Algae	
Filaments bitten off and scraped, with small amount of calcareous powder	63
Fronds and filaments bitten off, no sand or calcareous powder	37

This species is especially common on the seaward reef in the surf zone, but also occurs on the interisland reefs and the quiet lagoon reefs around living coral patches. It has been observed in water 3-20 ft deep. These fish cruise slowly around coral mounds, now and then nibbling at the algal tufts growing on the bases of coral heads. Frequently, they form large schools and move onto the seaward reef flats as the tide rises. Oftentimes their dorsal fins extend out of water as they crowd each other in their foraging activities in the shallow flats. They are strictly browsers which crop seaweed rather close to its base.

Family Summary

Surgeon fishes, all herbivorous, can be segregated into three feeding types. All species have a long, coiled intestine, and a few species have a heavy-walled, muscular gizzard. The dentition is especially well suited to browsing and grazing algae.

One group, those having a well-developed gizzard (*A. mata*, *A. olivaceus*, *A. gahhm*, and *A. xanthopterus*) are habitues of compacted sandy bottoms on which grows a carpet of short algal filaments. Each species characteristically assumes a position with its head downward and

caudal fin upward as it grazes the algal mat. Considerable sand is ingested along with the algal filaments, making the gizzard a very effective triturating organ because much of the sand is concentrated there. It is of interest to note that, although apparently distinct species, two of these gizzard-bearing surgeon fish, *A. olivaceus* and *A. gahhm*, have similar color patterns, morphology, and behavior, and the other two species, *A. xanthopterus* and *A. mata*, are also exceeding similar morphologically and behavioristically. Taxonomically *A. olivaceus* and *A. gahhm* have been confused, and *A. xanthopterus* and *A. mata* are rather difficult to distinguish (Randall 1956).

A second group, having no gizzard, but with essentially similar dentition, browses primarily algal fronds and filaments, with some actually grazing the rock surface for fine algal filaments. The latter group nearly always contains a small amount of calcareous powder scraped from the rock surface mixed in with the algae. Among this group, the following species are strictly browsers and rarely, if ever, have any admixed calcareous powder with the algae: *A. t. triostegus*, *A. achilles*, *A. aliala*, *Naso unicornis*, and *Zebrazoma veliferum*. The following species of this group frequently do have calcareous powder admixed with the fine algal filaments, but always have much more browsed algae than that scraped while grazing: *A. lineatus*, *A. guttatus*, *A. nigroris*, and *Naso lituratus*.

The third category contains a single species, *Ctenochaetus striatus*, among the acanthurids examined. This species is strictly a grazer on very short and fine algal filaments matted on rocky surfaces. It usually always contains a large proportion of admixed calcareous powder with the algae eaten. The dentition of this species is strikingly different from other genera of surgeon fishes. The teeth which are long, movable, bristle-like, and expanded at the tips, are apparently better adapted for scraping or grazing than for biting or browsing the filaments and fronds.

There is little question that, among the fish fauna on coral reefs in the Marshall Islands, the surgeon fishes are the most important group in converting primary productivity into animal tissue. Their great abundance is ascribable only to the fact that they have more to work with than fish of higher trophic levels in regard to available potential energy, and, whether or not they attain a high percentage of efficiency in the energy transfer, they are able to convert a substantial amount of abundant plant material into fish protoplasm.

Family Scorpaenidae

Species: *Scorpaenodes parvipinnis* (scorpion fish)

Number examined: Bikini, 1 specimen

Sex: Female

Standard length: 60 mm

Digestive tract: Mouth large, teeth minute; stomach thick-walled; intestine medium-long, coiled

The single specimen examined contained an alpheid shrimp in its stomach. These voracious, small carnivores are found in coral mounds almost everywhere on the reefs. They apparently conceal themselves under ledges or in the interstices of coral, lying in wait for small prey to venture close enough to be captured.

Species: *Scorpaenodes* sp. (scorpion fish)

Number examined: Bikini, 2 specimens: 1 empty

Sex: Undeveloped

Standard length: 40-75 mm

Digestive tract: Similar to *S. parvipinnis*

The single specimen containing food in its stomach had eaten several shrimps, the fragments of which remained. The habitat and behavior of this scorpion fish are similar to those described for *S. parvipinnis*.

Species: *Scorpaenopsis gibbosa* (scorpion fish)

Number examined: Arno, 2; Bikini, 1; Eniwetok, 4 specimens: 2 empty

Sex: Males and females

Standard length: 85-150 mm

Digestive tract: Similar to *S. parvipinnis*

Three of the five fish containing food had unidentified fish fragments in their stomachs, another had eaten a small wrasse, and the fifth one had consumed a small parrot fish, *Scarus* sp. This scorpion fish is a sluggish, medium-sized carnivore which lurks beneath coral heads and ledges on both interisland reef shallows and the seaward reef. It lies motionless in wait for small coral fishes and invertebrates to venture closely enough to capture. It is camouflaged as are many other fishes of a sluggish nature, but in addition bears brilliantly colored patches beneath the pectoral fins, suggestive of warning coloration. It reaches a length of about one foot, and has large, pungent dorsal spines which are probably venomous.

Species: *Pterois radiata* (turkey fish, lion fish)

Number examined: Eniwetok, 6 specimens

Sex: Males and females

Standard length: 60-100 mm

Digestive tract: Rather similar to *S. parvipinnis*

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crab fragments	50
<i>Stenopus hispidus</i>	16
Alpheid shrimp	16
Shrimp fragments	16

Turkey fish are strikingly-colored, bizarrely-shaped scorpaenids whose sluggish habits and attractive appearance mask one of the most venomous of coral reef fishes in the Marshall Islands. They lurk beneath ledges and in crevices in luxuriant coral beds 3-15 ft deep on all reefs, and are locally very common in some areas. Their extremely poor swimming ability, the result of the highly over-developed impedimenta of the fins, would suggest that the crustaceans taken by them must venture very closely in order that capture can be made. It is not unlikely that the highly colored, greatly elongate and threadlike rays of the fins prove attractive to prey species which are captured when they come close to investigate. The turkey fish seems "aware" of its protective ability since it stands its ground when molested.

Species: *Pterois volitans* (turkey fish, lion fish)

Number examined: Eniwetok, 1 specimen

Sex: Undeveloped

Standard length: 230 mm

Digestive tract: Same as *S. parvipinnis*

The single specimen examined had eaten a bandana prawn, *Stenopus hispidus*. The habitat and behavior of this species are essentially similar to those described for *P. radiata*. However, this species is less common, and seems more aggressive or pugnacious than *P. radiata*.

Species: *Synanceja verrucosa* (stonefish)

Number examined: Arno, 2 specimens

Sex: Males

Standard length: 110-176 mm

Digestive tract: Head broad and depressed, mouth superior, cavernous; stomach thick-walled; intestine moderately short

Both specimens examined had consumed fish which were in a late stage of digestion. This species, fortunately uncommon, is found on all reef areas where the

water is quiet. It inhabits rocky bottoms where it lies perfectly dormant for long periods of time. It is completely camouflaged because its external morphology, coloring, and shape is stonelike. Stonefish engulf small fish when they venture closely enough by a lightning-fast lunge upward while opening the cavernous mouth to draw them in. The dorsal spines are associated with poison glands and the venom, if not lethal, causes excruciating pain and serious secondary effects.

Family Summary

All scorpion fish, except *Pterois*, have essentially similar habits and feeding methods. In all cases they are sluggish, voracious carnivores, occurring solitarily under ledges or in holes where they await their prey. Except for *Pterois* and *S. gibbosa* they are well camouflaged by color and body sculpture. *S. verrucosa* attains the greatest success in this regard because it habitually lies dormant on rocky bottom and looks exactly like an algal covered rock. *P. radiata* and *P. volitans* appear to be highly colored and morphologically constructed to attract potential prey species. Their venomous spines doubtless serve them well as protection against potential enemies, as their "insolent" behavior suggests.

Family Caracanthidae

Species: *Caracanthus unipinnus*

Specimens examined: Bikini, 1 specimen

Sex: Undeveloped

Standard length: 20 mm

Digestive tract: Mouth moderate in size, teeth minute; stomach large, heavy-walled; intestine short, straight

The specimen examined had eaten an alpheid shrimp. This very small species lives in the interstices of the branches of living coral, particularly *Pocillopora* spp. and *Acropora* spp., on virtually all reefs. It never ventures outside the confines of the coral head where it swims between the branches foraging for other coral-dwelling types. Alpheid shrimps would be particularly common in their diet because they also inhabit the interstices of living corals in great numbers. This caracanthid protects itself from predaceous types by bracing itself between the branches of coral with its exceedingly heavy pectorals.

Family Platycephalidae

Species: *Thysanophrys* sp. (flathead)

Number examined: Bikini, 4; Eniwetok, 8 specimens: 5 empty

Sex: Males and females

Standard length: 82-145 mm

Digestive tract: Head depressed, mouth large, teeth villiform on jaws, canines on palatines, pharyngeal teeth large; stomach thick-walled; intestine moderately short

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	28
Xanthid crab	14
Portunid crab	14
<i>Stenopus hispidus</i>	14
Shrimp fragments	14
Fish	
Unid. fragments	14

This commonly occurring, dorso-ventrally very flattened fish lies on sandy bottoms on all reef areas where it is very well camouflaged. It is a voracious carnivore which lies in wait on exposed, sandy bottoms for small crustaceans and fish to venture closely enough for capture. A rapid lunge with the enormous mouth open is sufficient to capture its comparatively slow-moving prey. In Japan the flathead, *Platycephalus indicus*, feeds ex-

clusively on benthonic fauna including small fish, crabs, polychaetes, and ophiuroids (Suyehiro 1942).

Family Pomacentridae

Species: *Abudefduf sordidus* (damselfish)

Number examined: Arno, 9; Bikini, 2; Eniwetok, 8 specimens: 1 empty

Sex: Males and females

Standard length: 34-160 mm

Digestive tract: Mouth small, teeth incisiform, uniserial; stomach thick-walled; intestine moderately long, coiled

Food item	Percentage of fish containing the item
Algae	
Algal scrapings, with calcareous powder	38
Filaments bitten off, with sand	27
Filaments bitten off, without sand	27
Algal covered pebbles	16
Crustacea	
Crab fragments	16
Shrimp fragments	5
Isopods	5
Amphipods	5
Fish	
Unid. fragments	22
Polychaeta	
Unid. polychaetes	16
Foraminifera	
<i>Calcarina</i> sp.	16
Arachnida	
Mites	5
Coelenterata	
Hydroid fragments	5
Pelecypoda	
Small clam shell fragments	5
Detritus and sand	5

This damselfish was abundant on all reefs visited, particularly in the shallower portions in depths up to 6 ft. It is especially abundant in large tidepools left by the receding tide on seaward reef flats. The species is gregarious but does not form dense schools.

Its omnivorous habits are obvious from the list of food items consumed, although it is clear that algae form its principal food supply. This damselfish apparently captures all small benthonic animals encountered while foraging on the algal-covered rocks. It is primarily a grazing species as regards its herbivorous habits. Randall (1955) reports that the one specimen examined in the Gilbert Islands had consumed green algae.

Species: *Abudefduf septemfasciatus* (damselfish)

Number examined: Bikini, 1 specimen

Sex: Male

Standard length: 135 mm

Digestive tract: Similar to *A. sordidus*

This specimen examined contained the following food items in its stomach: Algae—Fronds bitten off, no calcareous powder; Crustacea—Palaemonid shrimp larva, Copepods; Fish—Unid. fragments.

This solitary damselfish has habits and occupies a habitat similar to those described for *A. sordidus*. It is likewise omnivorous, although algae formed the bulk of the food in the digestive tract. Two specimens examined by Randall (1955) in the Gilbert Islands had taken only algae, primarily the fine coralline red alga, *Jania* sp.

Species: *Abudefduf leucopomus* (damselfish)

Number examined: Bikini, 6 specimens

Sex: Males and females

Standard length: 40-55 mm

Digestive tract: Similar to *A. sordidus*

Food item	Percentage of fish containing the item
Algae	
Scraped filaments, with much sand and calcareous powder	33
Crustacea	
Copepods, calanoid	33
Mysids	17

Fish	
Unid. fragments	33
Wrasses	17
Gastropoda	
Pteropods	17

This bright yellow damsel fish usually lives solitarily, or in groups of two or three, under rubble on reefs having a rather strong current. It appears to be a true omnivore, taking not only fine algal filaments scraped from the rubble, but also feeding in mid-water on small planktonic crustaceans, pteropods, and smaller fish.

Species: *Abudefduf saratilis* (sergeant-major)
 Number examined: Arno, 1 specimen
 Sex: Female
 Standard length: 88 mm
 Digestive tract: Similar to *A. sordidus*

The single specimen examined contained the following items in its stomach: Algae—Filaments and fronds bitten off, no sand or calcareous powder (intestine nearly filled with algae); Crustacea—Calanoid copepods (numerous), Amphipods (numerous), Isopods (few), Ostracods (few). This species, uncommon in the Marshall Islands, usually occurs solitarily or in small aggregations at the outer edge of the sea reef and in surge channels. It feeds primarily as a browsing herbivore, but the large number of small epiphytic crustaceans leads us to suspect that these are taken more by design than by inadvertence along with the algae.

Species: *Abudefduf dicki* (damsel fish)
 Number examined: Arno, 10 specimens: 1 empty
 Sex: Males and females
 Standard length: 60-72 mm
 Digestive tract: Similar to *A. sordidus*

Food item	Percentage of fish containing the item
Algae	
Filaments bitten off	55
Filaments scraped off	55
Fish	
Unid. fragments	22
Detritus and sand	22

This solitary damsel fish is found on all reefs with quiet water where it is associated with living corals, particularly the broad, pedestal colonies of *Acropora reticulata* and the staghorn corals representing several species of *Acropora*. It is not at all demersal and swims mostly in mid-water or near the surface. The browsing herbivorous habits of this species predominate, but it is an opportunistic species which will take smaller fish and doubtless swimming invertebrates which venture near it.

Species: *Abudefduf biocellatus* (damsel fish)
 Number examined: Arno, 21; Eniwetok, 1 specimen
 Sex: Males and females
 Standard length: 47-68 mm
 Digestive tract: Similar to *A. sordidus*

Food item	Percentage of fish containing the item
Algae	
Fronds bitten off, no calcareous powder	33
Filaments scraped off, much calcareous powder	33
Fronds bitten off, admixed with sand	28
Crustacea	
Isopods	9
Cyclopoid copepods	4
Fish	
Unid. fragments	9
Fish eggs	4
Polychaeta	9
Foraminifera	
<i>Calcarina</i> sp.	4

According to some authors (Schultz 1943, Strasburg 1953, Randall 1955) the specimens included under *biocellatus* in this report probably represent a complex of two species, *biocellatus* and *zonatus*. However, it is also possible that *zonatus* may be just a color variant. It is of interest to note that the form considered *biocellatus* abounds in shallow water in depths up to 6 ft on all reefs where rubble is predominant. It prefers hard, conglomerate bottoms, taking refuge under reef rubble when disturbed, and is rarely if ever seen over sandy bottoms. On the other hand, the form referred to as *zonatus* is usually found over sandy bottoms and nowhere else. Because of these different habits Randall (1955) separated the species in his report on fishes of the Gilbert Islands, although he found *biocellatus* only in outer reef areas where coral was abundant. Regardless of the ultimate taxonomic disposition of these species, the food and feeding habits reported here will serve for one or both species. These damsel fish are usually solitary, but sometimes form loose aggregations of two or three individuals. They are primarily herbivores which both browse and graze algae growing on rubble or compacted sand. The cyclopoid copepods, fish fragments, and polychaetes in their diet indicate that they are facultative omnivores as well.

Species: *Abudefduf amabilis* (damsel fish)
 Number examined: Arno, 13; Bikini, 5 specimens
 Sex: Males and females
 Digestive tract: Similar to *A. sordidus*

Food item	Percentage of fish containing the item
Algae	
Filaments scraped off, much calcareous powder	38
Fronds bitten off, no sand or calcareous powder	33
Filaments admixed with sand grains	22
Coralline algae	5
Foraminifera	
<i>Calcarina</i> sp.	16
Fish	
Unid. fragments	5
Polychaeta	
Unid. fragments	5

This species occurs in groups of 2-3 individuals primarily on the seaward reef flats in 1-3 ft of water. It is also common on interisland reefs. It prefers areas where the water is in motion, particularly in the area of waves of translation coming across the seaward reef flats on an incoming tide. It will take refuge under pieces of reef rubble. *A. amabilis* may be designated a grazing herbivore primarily on fine algae covering reef rock, although it does browse at times. Like many other damsel fish it is a facultative omnivore.

Species: *Abudefduf glaucus* (damsel fish)
 Number examined: Arno, 26; Bikini, 6 specimens
 Sex: Males and females
 Standard length: 46-75 mm
 Digestive tract: Similar to *A. sordidus*

Food item	Percentage of fish containing the item
Algae	
Fine filaments, admixed with sand grains	78
Fine filaments, without sand grains	3
Scraped filaments, with calcareous powder	6
Crustacea	
Shrimp fragments	28
<i>Tetralia globerrima</i>	6
Isopods	3
Amphipods	3

Fish	
Unid. fragments	12
Eggs of <i>Istiblennius</i> sp.	6
Unid. goby	3
Polychaeta	
Unid. polychaetes	3
Gastropoda	
<i>Cerithium</i> sp.	3
Insect	
Winged ant	3

This common grey or blue damselfish occurs solitary or in groups of 2-3 individuals on almost all shallow areas of the reefs where the water is about 3-4 ft deep. It is most prevalent over hard rocky bottoms, and often seeks refuge below large reef rocks. Although it is primarily a grazing herbivore scraping off fine filaments of algae growing on rock surfaces, it very readily becomes a facultative carnivore taking small crustaceans and benthonic forms. The presence of trapezoid crabs and shrimps in about one-half of the specimens examined indicates that they actively seek these forms from the interstices of living heads of branching *Acropora* sp.

Species: *Abudefduf lacrymatus* (damselfish)
Number examined: Arno, 10; Eniwetok, 4 specimens
Sex: Males and females
Standard length: 39-67 mm
Digestive tract: Similar to *A. sordidus*

Food item	Percentage of fish containing the item
Algae	
Fine filaments, with few sand grains	57
Fine filaments, with no sand grains	42
Foraminifera	
<i>Calcarina</i> sp.	14
Unid. species	7
Crustacea	
Copepods	14
Gastropoda	
Crushed small gastropods	7
Fish	
Fish eggs	7

This solitary damselfish is shy and seen only occasionally despite the fact that it is one of the commonest in shallow reef areas in and around living coral where the water is from 3-12 ft deep. It forages as a browsing herbivore predominantly, with copepods and foraminifera, and possibly even fish eggs and small gastropods, being picked up inadvertently with algae. The crushed gastropods are difficult to explain because the species possesses no dental armature capable of crushing action. Since they are primarily thin-shelled, epiphytic types, it is probable that they were bitten while the fish browsed on the algae.

Species: *Chromis atripectoralis* (coral fish)
Number examined: Eniwetok, 24 specimens: 2 empty
Sex: Males and females
Standard length: 50-68 mm

Digestive tract: Mouth small, teeth with outer row of short canines with two enlarged near symphysis of lower jaw, inner row of teeth villiform; stomach very large, thin-walled; intestine short, straight

Food item	Percentage of fish containing the item
Crustacea	
Copepods	85
Shrimp nauplii	61
Small shrimps	33
Mysids	61
Crab zoeae	33
Fish	
Larval fish	4
Polychaeta	
Polychaeta larvae	4
Algae	
Fronds bitten off	4

These brilliant blue coral fish form dense schools about larger branching coral heads, particularly *Pocillopora* sp. and branching *Acropora* sp., in quiet water of the lagoon and leeward ocean reefs. They venture from the coral heads about 3-6 ft, frequently forming a "cloud" of fish about them.

Observations of these schools show the fish to be exceedingly busy capturing small plankters which swarm in the quiet waters of the reefs. The food analysis indicates that copepods, mysids, and shrimp nauplii are most commonly taken, and these can be observed to be the most abundant planktonic food available to them. Although they consume zooplankton, they are not plankton feeders in the sense that they possess structural features which enable them to sieve plankton from the water, but rather represent a carnivorous type which selects particular kinds of plankters which it catches one at a time through visual contact.

Species: *Chromis caeruleus* (coral fish)
Number examined: Arno, 11 specimens: 1 empty
Sex: Males and females
Standard length: 32-49 mm
Digestive tract: Similar to *C. atripectoralis*

Food item	Percentage of fish containing the item
Fish	
<i>C. caeruleus</i> eggs	60
Crustacea	
Calanoid copepods	50
Cyclopoid copepods	30
Metanauplii	20
Ostracods	20
Crab zoeae	10
Isopods	10
Sand grains	10

This species, like *C. atripectoralis*, occurs in comparatively large schools in and about interstices of branching corals, particularly *Acropora* sp., in the case of *C. caeruleus*. They are found wherever such corals occur in the quiet waters of the lagoon, interisland, and seaward reefs. Food habits and feeding methods for this species are rather similar to those of *C. atripectoralis*, in that they are a small, mid-water carnivore which feeds primarily on the crustacean elements of the zooplankton in and near the branching corals. It is of interest to note that over one-half of the specimens examined had eaten eggs spawned just previously. All females were gravid and spawning was in full swing. It is not unusual for fish to eat the eggs they have just spawned, and here is a good example of this phenomenon.

Species: *Dascyllus aruanus* (coral fish)
Number examined: Arno, 22 specimens
Sex: Males and females
Standard length: 32-51 mm
Digestive tract: Mouth small, teeth similar to *C. atripectoralis*; stomach thick-walled; intestine medium long, coiled

Food item	Percentage of fish containing the item
Crustacea	
Calanoid copepods	72
Copepod metanauplii	36
Cyclopoid copepods	27
Isopods	36
Crab zoeae	22
Shrimp fragments	9
Ostracods	9
Fish	
Fish eggs	45
Unid. fragments	22
Gobies	4
Polychaeta	
Unid. fragments	18
Algae	
Filaments bitten off	59
Filaments scraped, some calcareous powder	4

Frequently large numbers of this species aggregate in branching corals, particularly in *Pocillopora* sp. and *Stylophora* sp. They occur on all reefs where the water is relatively quiet down to a depth of about 15-20 ft. As a swimmer approaches they sink down into the interstices of the coral, remaining there even if the coral head is torn loose and carried ashore. The species is omnivorous, favoring, perhaps, animal food over plant food, but taking a sufficient amount of each to be definitely classed as omnivorous. Its food items are taken both from the mid-water fauna and from the surface of the living coral head and its dead base. The fish eggs taken were spawned in the interstices of the coral, probably by this species itself, although other species place their eggs in such locations.

Species: *Pomacentrus pavo* (damselfish)

Number examined: Arno, 20 specimens

Sex: Males and females

Standard length: 32-63 mm

Digestive tract: Mouth small, teeth in one series, incisiform; stomach small, heavy-walled; intestine long, coiled

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	40
Fish eggs	40
<i>Apogon novemfasciatus</i>	5
Fish scales	5
Crustacea	
Copepods	35
Copepod nauplii	5
Shrimp fragments	15
Ostracods	10
Isopods	5
Crab exoskeleton	5
Algae	
Fine filaments, no sand or calcareous powder	10

This more or less solitary pomacentrid is closely associated with living coral mainly in the quiet waters of lagoons at depths of 4-25 ft. Only a few individuals are associated with any one coral head. Although other pomacentrids examined were almost entirely herbivorous, this species is just the reverse and is almost exclusively a carnivore preying upon small fish, crustaceans, and polychaete worms taken either from the mid-water zooplankton or from the interstices of the coral in which it lives. Its rather typical herbivorous-type digestive tract is an enigma.

Species: *Pomacentrus nigricans* (damselfish)

Number examined: Arno, 19 specimens

Sex: Males and females

Standard length: 52-79 mm

Digestive tract: Similar to *P. pavo*

Food item	Percentage of fish containing the item
Algae	
Fine filaments, with sand grains	63
Algal scrapings, with calcareous powder	31
Algal fronds bitten off, no sand or powder	31
Fish	
Unid. fragments	5

P. nigricans is a very abundant species in shallow water around living coral on almost all reefs, where it lives in crevices in the coral. It exhibits very strong territorial tendencies. This species is almost exclusively a grazing herbivore taking fine filaments from the compacted sand surface adjacent to coral patches. The fact that some specimens had fish fragments remaining in the stomach indicates that they can be omnivorous at times.

Species: *Pomacentrus jenkinsi* (damselfish)

Number examined: Arno, 21 specimens

Sex: Males and females

Standard length: 53-83 mm

Digestive tract: Similar to *P. pavo*

Food item	Percentage of fish containing the item
Algae	
Fronds bitten off, no sand grains	80
Fine filaments, with sand grains	14
Algal scrapings, with calcareous powder	9
Fish	
Unid. fragments	9
Fish eggs	4

This species is rather uncommon in the northern Marshall Islands, but common at Arno Atoll in the southern Marshalls. It frequents branching corals, either dead or alive, in quiet water of the lagoon and leeward ocean reef shallows to a depth of about 6 ft. It is predominantly a browser on fine algal growth, but grazes at times. It will take animal food as evidenced by its ingestion of both fish eggs and small fish. Its animal food habits are certainly comparatively insignificant.

Species: *Pomacentrus albofasciatus* (damselfish)

Number examined: Arno, 22 specimens

Sex: Males and females

Standard length: 48-70 mm

Digestive tract: Similar to *P. pavo*

Food item	Percentage of fish containing the item
Algae	
Fine filaments, with admixed sand grains	81
Algal scrapings, with calcareous powder	22
Fine filaments, with no sand grains or powder	4
Crustacea	
Shrimp fragments	4
Fish	
Fish eggs	4

This species, common at Arno Atoll, was uncommon in the northern Marshall Islands. It occurs solitarily or in small groups in reef shallows near coral patches where the water is quiet in depths from 3-12 ft. The great quantity of sand admixed with the algae in the digestive tract clearly indicates that this species is a grazer of fine algal filaments on compacted sandy bottoms where it apparently crops very closely, and gets large quantities of sand along with the algae. It also grazes on rocks and dead coral surfaces. Like other pomacentrids it can be a facultative omnivore and takes small crustaceans on occasion.

Species: *Pomacentrus vaiuli* (damselfish)

Number examined: Arno, 8; Eniwetok, 12 specimens

Sex: Males and females

Standard length: 34-61 mm

Digestive tract: Similar to *P. pavo*

Food item	Percentage of fish containing the item
Algae	
Fine filaments, no sand grains	75
Scraped filaments, with calcareous powder	15
Fish	
Unid. fragments	10
Fish eggs	10
Crustacea	
Copepods	10
Amphipods	5
Polychaeta	5

This solitary species lives in crevices and is abundant about living coral patches in water 4-15 ft deep on all reefs. Although it is primarily a browsing herbivore, it frequently behaves omnivorously, and takes small fish and invertebrates occurring in the branching coral heads where it lives.

Family Summary

The pomacentrids are ubiquitous, usually brilliantly colored, coral fishes characteristic of coral reefs in almost every environment found there. Many are solitary, some form small aggregations, while others occur in dense aggregations which have the cohesive and integrated characteristics of highly developed schools. Almost all of them, particularly the aggregating species, are closely associated with, even ecologically bound to, giant heads of branching corals.

The food habits within the family, and even the structural anatomy of the digestive tract, are quite variable, and it is difficult to segregate them into discrete groups of homogeneous habits as regards food and feeding proclivities. They range from almost exclusive herbivores to exclusive carnivores, with most of the species pursuing an omnivorous life to a greater or lesser degree.

Among those species which feed primarily on algae, both by browsing and grazing with approximately equal facility are *A. dicki*, *A. biocellatus*, *A. amabilis*, *A. glaucus*, *A. lacrymatus*, *P. vaiuli*, *P. albofasciatus*, *P. jenkinsi*, and *P. nigricans*. In every case these species consumed some animal types.

One species, *P. pavo*, is almost exclusively carnivorous, taking fish and crustaceans primarily. This is a solitary species which swims about small boulders and coral mounds on the lagoon reef.

Among the omnivores which take animal food both from mid-water and bottom are *A. septemfasciatus*, *A. leucopomus*, *A. saxatilis*, and *A. sordidus*. Of these, *A. sordidus* is the most completely omnivorous species, taking all types of food. It is abundant on the seaward reef flats and in intertidal pools, in aggregations which are not well enough integrated to qualify as schools.

The three species which feed on zooplankton (*C. caeruleus*, *C. atripectoralis*, and *D. aruanus*) are characteristic dwellers in large, branched coral heads. Often as many as 500-1000 fish of *caeruleus* and *atripectoralis* may aggregate in and about one of these giant, ramose heads. When disturbed, they swim down in amongst the branches of the coral, but normally the swarm of fish extends several feet outward from the head. *D. aruanus*, while exhibiting habits similar to *Chromis*, occurs in much smaller aggregations and in smaller ramose heads. The plankters taken by these species are not sieved out of the water by any special device, but rather are captured individually on sight. These plankters form swarms over the reef shallows in quiet water.

The dentition of the feeders on plankton is somewhat different from that of the herbivorous or omnivorous feeders. The teeth of the former types are conical and widely spaced, whereas the teeth of the fish belonging to the other genera, *Abudefduf* and *Pomacentrus*, are villiform or incisiform in bands. The latter are adapted for biting (browsing) or scraping (grazing), just as were the teeth of the herbivorous surgeon fishes.

Family Labridae

Species: *Epibulus insidiator* (wrasse)
Number examined: Bikini, 1; Eniwetok, 1 specimen
Sex: Undeveloped
Standard length: 125-130 mm
Digestive tract: Mouth not produced, but highly protractile, jaws extending backward beneath head; canines at symphyses of jaws; stomach thick-walled; intestine short

Both specimens examined had eaten alpheid shrimps. This species is not common and those taken were from

the seaward reef in channels containing living coral. It doubtless occurs elsewhere on the reefs, particularly in coral patches on interisland reefs. This wrasse habitually feeds in ramose corals by extending its exceedingly protractile snout into the interstices to capture small alpheid shrimps and xanthid crabs living there.

Species: *Gomphosus varius* (wrasse)
Number examined: Arno, 3; Bikini, 4; Eniwetok, 14 specimens:
1 empty
Sex: Females
Standard length: 58-120 mm
Digestive tract: Snout produced, tubular; canines at symphyses of jaws; stomach thick-walled; intestine short

Food item	Percentage of fish containing the item
Crustacea	
Alpheid shrimps	40
Shrimp fragments	20
Xanthid crab fragments	35
<i>Trapezia</i> sp.	5
Pelecypoda	
Unid. small clam	5
Gastropoda	
Unid. small gastropods	5
Fish	
Unid. fragments	5
Algae	
Fronds, bitten off	5

This species has recently been combined with *G. tricolor*, with the latter referred to synonymy (Strasburg & Hiatt 1957). Although we did not examine the food of the males of this species (formerly designated *G. tricolor*), it may be assumed that the food predilections are the same as for the females examined by us. Randall (1955) examined two males (= *G. tricolor*) in the Gilbert Islands and found them to contain stomatopods and alpheid shrimps, crustaceans characteristic of branching corals.

These wrasses are uncommon but widely distributed about all reefs with living coral in water up to a depth of about 35 ft. They are more common on lagoon reefs, than elsewhere, usually swimming solitarily with characteristic oar-like movements of the pectoral fins. Their long snout is an effective device for probing into interstices of ramose corals where their crustacean prey conceal themselves.

Species: *Pseudocheilinus hexataenia* (wrasse)
Number examined: Arno, 5; Eniwetok, 4 specimens
Sex: Males and females
Standard length: 38-57 mm
Digestive tract: Mouth small, canines on each side of symphyses, upper pair long, curved outward and backward; stomach heavy-walled; intestine medium long

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	22
Copepods	44
Ostracods	11
Isopods	11
Foraminifera	
<i>Calcarina</i> sp.	44
Unid. foraminiferans	11

This small wrasse is common in all living coral patches on all reefs in water 3-10 ft deep. It lives solitarily among the branches of ramose corals and feeds primarily on the benthonic fauna living on rubble and sandy bottoms adjacent to coral patches. The specimens examined at Arno contained only the foraminiferan, *Calcarina* sp., and the stomach and gut were crammed full. It was noted then that this species was probably a selective feeder on *Calcarina* sp., but none of these foraminiferans were found in the digestive tracts of specimens examined from Eniwetok. The latter fish had taken only small, benthonic crustaceans. Our data

indicate that this species is probably non-selective among the benthonic fauna, but feeds exclusively on certain abundant, easily available forms.

Species: *Labroides dimidiatus* (wrasse)

Number examined: Arno, 1; Eniwetok, 4 specimens

Sex: Females and undeveloped

Standard length: 54-68 mm

Digestive tract: Deep notch at middle of lower lip with fleshy horn extending forward on each side of lower jaw forming lips; pair of large canines at front of each jaw separated by small teeth at symphysis; stomach thin-walled, large; intestine short, nearly straight

Food item	Percentage of fish containing the item
Crustacea	
Calagoid copepods	80
Copepods, free-living	40
Mysids	20
Fish	
Fish scales	20

This solitary, agile, strikingly-colored fish is common on all reefs around living coral to depths of about 15 ft. Its peculiar habits which attract the attention of a skin-diver have been noted by several authors. Randall (1955) states, "It often exhibited an unusual mode of swimming by oscillating the posterior part of the body up and down as if to attract attention. It was seen to dance around other fishes in this manner and to pick at their bodies. The fishes receiving such attention often slowed their swimming or came to a stop. It was thought at the time that the *Labroides* were picking off external parasites from these fishes. The gut contents of two specimens from the Gilbert Islands and three from the Marshall Islands consisted of calagoid copepods and a few fish scales. The two remaining Gilbert Islands specimens had eaten tiny isopods along with several fish scales."

Our results fit closely with those obtained by Randall, indicating that the parasitic copepod "picking" from other fish is its predominant mode of feeding, but that it can also take other mid-water plankters. The role of the cleft lower jaw in feeding is not understood. Smith (1953) refers to this species in African waters as one which feeds on minute organisms on rocks, and has been observed to nibble over the mouthparts and gill-covers of large rock-cods.

Species: *Novaculichthys taeniourus* (wrasse)

Number examined: Eniwetok, 1 specimen

Sex: Female

Standard length: 102 mm

Digestive tract: Mouth moderately small, canines at symphysis of both jaws; stomach not well-defined; intestine short, almost straight

The single specimen examined contained on alpheid shrimp in its stomach. This is an uncommon species which occurs solitarily on almost all sandy-bottomed and rubble-strewn reefs at depths of 4-20 ft. It seldom ventures more than a few feet from bottom rubble which serves it as shelter, and is never seen around living coral.

Species: *Stethojulis axillaris* (wrasse)

Number examined: Arno, 17; Eniwetok, 4 specimens

Sex: Males and females

Standard length: 44-75 mm

Digestive tract: Mouth moderately small, no canine teeth, small incisiform teeth in sides of jaws, pharyngeal teeth strong, rounded; stomach not well-defined; intestine rather short

Food item	Percentage of fish containing the item
Polychaeta	
Unid. polychaetes	61
Crustacea	
Cyclopoid copepods	38
Calanoid copepods	19
Haracticoid copepods	9

Copepod metanauplii	14
Cypris larvae	14
Isopods	33
Shrimp fragments	33
Ostracods	19
Xanthid crab fragments	14
Foraminifera	
<i>Calcarina</i> sp.	23
Gastropoda	
Unid. small gastropods	4
Algae	
Fine filaments with sand grains	14
Sand grains	19

This extremely abundant labrid occurs solitarily in shallow water on nearly all reefs. It lives along the bases of coral mounds and patches adjacent to sandy bottoms. It is obviously a non-selective carnivore which forages mostly on the benthonic fauna of sandy areas. It does, however, take some planktonic copepods which it must capture in mid-water.

Species: *Stethojulis* sp. (wrasse)

Number examined: Eniwetok, 6; Arno, 5 specimens

Sex: males and undeveloped

Standard length: 70-95 mm

Digestive tract: Similar to *S. axillaris*

Food item	Percentage of fish containing the item
Crustacea	
Isopods	72
Copepods	54
Cypris larvae	9
Ostracods	45
Shrimp fragments	27
Crab zoeae	9
Gastropoda	
Crushed small gastropods	45
Polychaeta	
Unid. polychaetes	18
Foraminifera	
Unid. foraminiferans	18
Pelecypoda	
Crushed small clams	9
Algae	
Filaments scraped, with sand grains	18
Sand grains	81

This species is common on nearly all reefs where it lives, solitarily, around living coral patches adjacent to sandy and rubble-strewn bottoms. It forages for both benthonic and fossorial invertebrates on sandy bottoms, taking primarily crustaceans and polychaetes. The heavy molariform, pharyngeal dentition enables it to crush small hard-bodied species.

Species: *Halichoeres hoeveni* (wrasse)

Number examined: Arno, 1; Eniwetok, 3 specimens

Sex: Female

Standard length: 54-66 mm

Digestive tract: Snout rather pointed, mouth small; symphysis of lower jaw with 1 pair of canines, upper jaw with 2 pairs, pharyngeal teeth molar-like; stomach not well-defined; intestine short

Food item	Percentage of fish containing the item
Polychaeta	
Unid. polychaetes	75
Crustacea	
Copepods	50
Isopods	50
Foraminifera	
<i>Calcarina</i> sp.	25
Algae	
Fine filaments of green and coralline algae with much calcareous powder	50

This wrasse is uncommon and is found only in quiet water on the lagoon and leeward ocean reefs at depths of 6-20 ft. It darts about coral heads and usually stays close to the bases of large coral mounds in the lagoon. At Arno Atoll, the single individual examined contained only the foraminiferan, *Calcarina* sp., with which its gut

was crammed. However, at Eniwetok different food habits prevailed, with no *Calcarina* taken at all.

Species: *Halichoeres marginatus* (wrasse)
Number examined: Eniwetok, 5 specimens
Sex: Females
Standard length: 48-88 mm
Digestive tract: Similar to *H. hoeveni*

Food item	Percentage of fish containing the item
Crustacea	
Isopods	80
Copepods	60
Polychaeta	
Unid. polychaetes	60
Gastropoda	
Crushed gastropods	20
Foraminifera	
Large foraminiferans	20
Algae	
Fine filaments scraped, with sand grains	20

This solitary species is common among luxuriant coral patches in shallow areas on all reefs. It characteristically swims around the top sides of coral heads, only rarely taking refuge when molested. *H. marginatus* may be classed as a benthonic carnivore which usually forages on compacted sandy bottoms, taking mostly small crustaceans and polychaete worms. The algae may have been taken inadvertently during its foraging activities for benthonic fauna in the algal-covered substrate. Its molariform pharyngeals are responsible for crushing the shells of gastropods.

Species: *Halichoeres hortulanus* (wrasse)
Number examined: Arno, 5; Eniwetok, 1 specimen
Sex: Males and females
Standard length: 69-230 mm
Digestive tract: Similar to *H. hoeveni*

Food item	Percentage of fish containing the item
Gastropoda	
Crushed gastropods	100
Polychaeta	
Unid. polychaetes	33
Fish	
Unid. fragments	33
Crustacea	
Fragments	17
Hermit crabs, shells crushed	17
Pelecypoda	
Sand-dwelling clams, crushed	17
Algae	
Fine filaments	17

This species is solitary and uncommon, but occurs on all reefs with living coral heads or coral mounds in depths from 3-15 ft. It is a rapid swimmer, seldom taking cover. The food taken indicates that it forages for benthonic and fossorial species, especially hard-bodied forms which it crushes with its heavy pharyngeal teeth. Its primary food consists of small sand-dwelling gastropods, and, in the process of capturing these, it undoubtedly takes many hermit crabs occupying gastropod shells. The shell-crushing habits of this genus are also mentioned by Suyehiro (1942) in his account of *H. poecilopterus* in Japan which bites off barnacles and mussels and then crushes them with its pharyngeal teeth.

Species: *Halichoeres trimaculatus* (wrasse)
Number examined: Arno, 24; Bikini, 6; Eniwetok, 2 specimens
Sex: Males and females
Standard length: 42-120 mm
Digestive tract: Similar to *H. hoeveni*

Food item	Percentage of fish containing the item
Crustacea	
Hermit crab fragments, crushed	83
Shrimp fragments	25
Xanthid crab fragments	12

Stomatopod fragments	6
Amphipods	3
Copepods	3
Fish	
Unid. fragments	9
Fish eggs	9
<i>Apogon novemfasciatus</i>	3
Foraminifera	
<i>Calcarina</i> sp.	6
Polychaeta	
Unid. polychaetes	3
Pelecypoda	
Crushed clams	3
Amphineura	
Solenogastroid chiton	3
Algae	
Fine filaments, with sand grains	6

This is the most abundant wrasse on all reefs, particularly favoring sandy bottoms with scattered rubble for cover. It will actually burrow under the sand if molested. Like the other members of this genus, this species is carnivorous on benthonic and fossorial fauna. It has a predilection for hermit crabs which it secures by crushing their shells with the heavy pharyngeal molars. Virtually any prey occurring on sandy bottoms is taken by this fish.

Species: *Halichoeres margaritaceus* (wrasse)
Number examined: Arno, 15 specimens
Sex: Males and females
Standard length: 40-86 mm
Digestive tract: Similar to *H. hoeveni*

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	46
Tanaid isopods	20
Xanthid crab fragments	13
<i>Trapezia</i> sp.	6
Foraminifera	
<i>Calcarina</i> sp.	26
Polychaeta	
Unid. polychaetes	26
Mollusca	
Crushed gastropods	13
Chiton fragments	6
Fish	
Unid. fragments	6
Fish eggs	6

This wrasse is a very abundant, solitary species which occurs in shallow water on all reefs. It is especially abundant at the outer edge of the seaward reefs and in the surge channels. In the lagoon it is found commonly around coral patches 15-20 ft deep. This wrasse feeds less often on sandy bottoms than the other members of the genus examined, and more on and in ramose corals. However, it still is predominantly a feeder on benthonic fauna, but takes no fossorial species as other members of the genus do.

Species: *Macropharyngodon meleagris* (wrasse)
Number examined: Eniwetok, 1 specimen
Sex: Undeveloped
Standard length: 70 mm
Digestive tract: Mouth small, 2 pairs of canines at symphysis of upper and lower jaws, strong canines at corner of upper jaw, pharyngeal teeth molariform; stomach not well defined; intestine short

The single specimen examined had a crushed rock-dwelling gastropod in its stomach. This small wrasse swims rapidly about coral heads, taking refuge in ramose types in quiet waters of the lagoon and seaward reefs in depths to about 6 feet. It evidently forages on and in coral heads and rocks.

Species: *Macropharyngodon pardalis* (wrasse)
Number examined: Arno, 1; Eniwetok, 3 specimens
Sex: Males and undeveloped
Standard length: 43-57 mm
Digestive tract: Similar to *M. meleagris*

Food item	Percentage of fish containing the item
Gastropoda	
Crushed rock-dwelling gastropods	75
Foraminifera	
<i>Calcarina</i> sp.	25
Unid. foraminiferans	25
Sand grains	25

This small, solitary species is very common over living coral on leeward ocean reefs and lagoon reefs in water 3-5 ft deep. It secludes itself in crevices in coral. The Arno specimen had fed exclusively on foraminiferans characteristic of sandy bottoms; whereas, the Eniwetok specimens fed exclusively on rock-dwelling gastropods which were crushed by the heavy pharyngeal teeth. It would appear that this species forages either on sand or rock bottoms, taking hard-bodied species which it can crush.

Species: *Thalassoma umbrostygma* (wrasse)
 Number examined: Bikini, 2 specimens
 Sex: Male and female
 Standard length: 160 mm
 Digestive tract: Mouth small, 1 pair canines at symphyses of jaws, pharyngeals molariform; stomach large, thin-walled; intestine short, straight

One of the specimens examined contained an unidentified fish, the other a stomatopod, *Odontodactylus* sp. This solitary wrasse is most common at the seaward reef front and in the back-ridge trough. It also occurs in the interisland reef shallows about living coral. Randall (1955) reported that this species consumed small crabs in the Gilbert Islands.

Species: *Thalassoma quinquevittata* (wrasse)
 Number examined: Arno, 20; Eniwetok, 3 specimens
 Sex: Males and females
 Standard length: 49-184 mm
 Digestive tract: Similar to *T. umbrostygma*

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	52
Shrimp fragments	13
<i>Trapezia</i> sp.	4
Fish	
Unid. fragments	21
<i>Apogon novemfasciatus</i>	8
Gastropoda	
Crushed gastropods	4
Echinodermata	
Echinoid fragments	4
Coelenterata	
Tip of <i>Pocillopora damicornis</i> , partially digested	4
Algae	
Short clumps	4

This wrasse is very abundant on all reefs around living coral and rocky rubble to depths of about 15 ft. Like other wrasses, it is solitary. Its consumption of crustaceans which live in the interstices of living coral, a coral-dwelling cardinal fish, and the tip of a ramose coral indicates that coral heads and their bases are its primary foraging areas.

Species: *Thalassoma lucasanum marnae* (wrasse)
 Number examined: Eniwetok, 2 specimens
 Sex: Undeveloped
 Standard length: 44-50 mm
 Digestive tract: Similar to *T. umbrostygma*

The two specimens examined contained the following food items: Crustacea—Shrimp larvae, Mysids, Crab zoeae, Copepods. This small common species swims rapidly about large lagoon coral heads in quiet water 3-10 ft deep. It feeds mostly on the abundant plankters in the vicinity.

Species: *Thalassoma hardwickei* (wrasse)
 Number examined: Arno, 7; Eniwetok, 4 specimens
 Sex: Females
 Standard length: 35-100 mm
 Digestive tract: Similar to *T. umbrostygma*

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	36
Crab zoeae	18
Crab megalopa	9
Shrimp larvae	18
Hippolytid shrimp fragments	9
Copepods	18
Isopods	9
Fish	
Unid. fragments	27
Belonid	9
Foraminifera	
Several species of pelagic foraminiferans	9

This wrasse is common on all quiet reef areas near living coral where it swims solitarily and actively about the tops and sides of the coral heads. The food consumed suggests that it feeds in and about living corals, at times taking small plankters in mid-water. The small belonid fish among the food items indicates that it is a predacious carnivore.

Species: *Thalassoma lutescens* (wrasse)
 Number examined: Arno, 1; Eniwetok, 9 specimens
 Sex: Females and undeveloped
 Standard length: 57-105 mm
 Digestive tract: Similar to *T. umbrostygma*

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crabs	30
<i>Tetralia globerrima</i>	10
Shrimp fragments	30
Alpheid shrimp fragments	10
Gastropoda	
Unid. crushed gastropods	20
<i>Atys</i> sp., crushed	10
Polychaeta	
Unid. polychaetes	10
Pelecypoda	
<i>Arca</i> sp., crushed	10
Echinodermata	
Ophiuroid fragments	10
Echinoid fragments	10
Algae	
Fine filaments scraped off	30
Fine scrapings, with calcareous powder	10

This bright yellow, solitary wrasse is common on all shallow reefs areas near living coral. It is particularly common in the lagoon around living coral patches where it swims rapidly about the tops and sides of the coral heads. This species exhibits quite heterogeneous carnivorous activities, feeding sometimes in amongst the ramose corals for small coral-dwelling crustaceans, and at other times apparently taking benthonic species from the sandy bottom. The algae contained in the stomach may possibly be the inadvertent result of foraging for benthonic gastropods and polychaetes.

Species: *Cheilinus oxycephalus* (wrasse)
 Number examined: Eniwetok, 5 specimens
 Sex: Females and undeveloped
 Standard length: 65-75 mm

Digestive tract: Mouth small, 1 pair of canines at symphyses of upper and lower jaws, pharyngeal teeth heavy, molariform; stomach virtually absent; intestine short, nearly straight

Food item	Percentage of fish containing the item
Crustacea	
Alpheid shrimp fragments	75
Crab fragments	25
Amphipods	25
Gastropoda	
Small gastropods	50

This is an abundant, medium-sized, solitary wrasse which occurs on all reefs with quiet water. It hides under coral or rocks. It is carnivorous, taking crustaceans living in corals and gastropods frequenting corals and coral mounds.

Species: *Cheilinus chlorourus* (wrasse)
Number examined: Arno, 7 specimens: 1 empty
Sex: Males and females
Standard length: 44-98 mm
Digestive tract: Similar to *C. oxycephalus*

Food item	Percentage of fish containing the item
Gastropoda	
Whole or crushed gastropods	66
Crustacea	
Shrimp fragments	50
Polychaeta	
Unid. polychaetes	17
Insecta	
Beetles	17

This is a common, solitary wrasse which is found on all reefs about living coral or rubble. It is a slow swimmer compared to many other wrasses in the same habitat. *C. chlorourus* is carnivorous, subsisting primarily on small gastropods taken from coral heads or the rocky bottom nearby. Most specimens had the lower part of the intestine filled with a solid bolus of gastropod shell fragments.

Species: *Cheilinus trilobatus* (wrasse)
Number examined: Arno, 14; Eniwetok, 1 specimen
Sex: Males and females
Standard length: 74-270 mm
Digestive tract: Similar to *C. oxycephalus*

Food item	Percentage of fish containing the item
Fish	
Unid. fragments	59
<i>Aponogon novemfasciatus</i>	6
Crustacea	
Crab fragments	40
Hermit crabs	6
Shrimp fragments	26
Gastropoda	
Crushed shells, <i>Cerithium</i> sp.	13
Pelecypoda	
Crushed clams	6
Algae	
Small fragments of rock containing algal fronds and filaments	6

This solitary wrasse is common on all reef areas around living coral or rubble, under which it lives. It frequently is seen hovering over the sandy bottom near its shelter. This species is carnivorous, taking fish, crustaceans, and gastropods primarily. The single specimen from Eniwetok had fed predominantly on hermit crabs by crushing their shells with the heavy pharyngeal teeth. It apparently forages rather widely, over and in corals and on sandy and rubble bottoms.

Species: *Coris angulata* (wrasse)
Number examined: Eniwetok, 1 specimen
Sex: Undeveloped
Standard length 265 mm
Digestive tract: Mouth small, 1 pair of canines at symphysis of jaws, pharyngeal teeth heavy, molariform; stomach indistinct; intestine rather short

The alimentary tract of the single specimen examined was filled with crushed, sand-dwelling pelecypods and gastropods. This solitary wrasse is common around living coral on all reefs in water 4-20 ft deep. It feeds almost exclusively on sand-dwelling molluscs which it crushes with its heavy pharyngeal teeth.

Species: *Coris gaimardi* (wrasse)
Number examined: Eniwetok, 2 specimens
Sex: Undeveloped

Standard length: 150-250 mm
Digestive tract: Similar to *C. angulata*

Both specimens examined contained shrimps and small crushed clams and gastropods. The following items were found in addition in at least one of the specimens: isopods, foraminiferans, and polychaetes. This wrasse is uncommon in all areas visited, but is found on all types of reefs around coral patches to depths of 20 ft or more. Clams and gastropods form the bulk of its diet. It is a carnivore which forages on open sandy bottoms, although it stays near coral mounds or rock rubble.

Species: *Hemigymnus melapterus* (wrasse)
Number examined: Eniwetok, 3 specimens
Sex: Female and undeveloped
Standard length: 120-220 mm
Digestive tract: Mouth small, 1 pair of canines at symphysis of jaws, pharyngeal teeth heavy, molariform; stomach indistinct; intestine rather short

All of the specimens examined contained small crushed gastropods. The remaining food items found in lesser quantities were: Crustacea—Tanaid isopods, Shrimp fragments, Amphipods, Crab fragments, Copepods; Foraminifera—*Calcarina* sp., undet. spp.; Algae—small, green filaments and coralline algal filaments bitten and scraped with considerable calcareous powder. This solitary wrasse, common on all reefs in depths from 4-20 ft around coral heads, is comparatively large. Its food includes both inhabitants of living coral heads and the benthonic fauna on sandy bottoms adjacent to luxuriant coral patches. It is quite possible that the algae found in two of the three specimens had been taken inadvertently.

Family Summary

The wrasses are as typical of coral reefs as the corals themselves. While most species are comparatively small, some (*Cheilinus undulatus*) reach gigantic proportions and constitute some of the largest fish ever seen on reefs. They are mostly brilliantly colored in striking contrast to the luxuriant coral patches over and in which many live. Because of their great abundance and widespread distribution on all reef types, they constitute one of the most important groups of fishes in the food complex. Several species are more typical of reef rubble and compacted sandy bottoms than they are of living coral patches.

Most of the species feed on benthonic invertebrates, particularly those on compacted sandy and rubble bottoms. A generic segregation based on food and feeding habits is not feasible. All have well-developed pharyngeal teeth adapted for crushing action. They habitually take hard-bodied species of clams, gastropods, hermit crabs, brachyurous crabs, sea urchins, heart urchins, and brittlestars, all of which are crushed before entering the stomach.

Two species examined habitually probe living ramose coral heads (*Gomphosus varius* and *Epibulus insidiator*) for the small crustaceans and polychaetes secluded in the interstices. Both have structural modifications to facilitate this mode of foraging; *G. varius* has an elongate, tubular snout, and *E. insidiator* has a highly protractile, tubular buccal apparatus. Both species had eaten invertebrates which could only have been removed from the branching corals with some such mechanism.

The availability of particular types of food had a great influence on some species which were not particularly selective in food items consumed. At Arno Atoll *Pseudocheilinus hexataenia* and *Halichoeres hoeveni* had selectively fed on the foraminiferan, *Calcarina* sp., their

stomachs and guts being completely crammed with the partly digested protozoans. However, at Eniwetok where *Calcearina* sp. is not nearly so abundant, these species had consumed mostly crustaceans.

Two species examined appear to be rather selective in that they depart from the more usual mode of benthonic foraging among the wrasses and confine their food-getting to mid-water plankters such as mysids, shrimp zoeae, crab zoeae, copepods, etc., so abundant over the reefs in areas of quiet water. These species, *T. hardwickei* and *T. lucasanum marnae*, have no special plankton feeding mechanism, so must capture each plankter individually on sight.

One species, *L. dimidiatus*, has such a unique method of feeding by "tending" other larger fish and removing the parasitic Copepoda that a detailed account of the process was described under the species account. It is the only wrasse with a considerably modified feeding apparatus. Almost all of them conform to the role of small carnivore on invertebrates inhabiting living coral and the sandy bottoms of the reefs.

Family Scaridae

Species: *Cryptotomus spinidens* (parrot fish)

Number examined: Arno, 1 specimen

Sex: Undeveloped

Standard length: 85 mm

Digestive tract: Mouth moderate in size, teeth not fully united to form a smooth beak; no stomach; intestine long, thin-walled

The single specimen examined contained algal filaments which had been grazed along with a large amount of calcareous powder, and coral polyps admixed with coral skeletal fragments. This solitary parrot fish is rather uncommon on the reefs visited, but occurs around coral mounds and coral patches in quiet lagoon waters from 6-8 feet in depth. Its feeding habits are similar to other parrot fishes which scrape reef rock for algae and living coral heads for the polyps. In this particular case much more algae is consumed than are coral polyps, hence the species is designated a grazing herbivore.

Species: *Scarus bicolor* (parrot fish)

Number examined: Eniwetok, 1 specimen

Sex: Female

Standard length: 265 mm

Digestive tract: Similar to *C. spinidens* except that the teeth are fused into a smooth beak.

The single specimen examined contained both coral polyps and algae admixed with great amounts of calcareous powder and coral skeletal fragments. This is a large, solitary parrot fish commonly seen in the surge channels and just off the edge of the ocean reef front in leeward areas of the atolls. Its food seems to consist more of coral polyps than of algae, hence it is here designated as a grazing omnivore.

Species: *Scarus sordidus* (parrot fish)

Number examined: Arno, 16; Eniwetok, 2 specimens

Sex: Females

Standard length: 61-111 mm

Digestive tract: Similar to *S. bicolor*

Food item	Percentage of fish containing the item
Coelenterata	
Coral polyps, with much skeletal material admixed	83
Algae	
Fine filaments, admixed with calcareous powder	27

This very common parrot fish forms large schools on all reefs visited in 3-20 ft of water. It is always associated with living coral patches. Scraping living coral

heads seems to be its predominant mode of feeding, although it does take some algal material. It is here designated as a grazing omnivore.

Species: Seven unidentified species of *Scarus*

Specimens examined: Arno, 6; Bikini, 2; Eniwetok, 9 specimens

Sex: Males and females

Standard length: 43-325 mm

Digestive tract: Similar to *S. bicolor*

Eleven specimens of this group had consumed coral polyps admixed with a large amount of skeletal particles, and eight specimens contained in addition algal filaments admixed with a great amount of calcareous powder. These parrot fish may therefore be designated as omnivores, with coral polyp scraping practiced somewhat more frequently than rock scraping for algal filaments.

Family Summary

Unfortunately, the taxonomic treatment of the Scaridae of the Marshall Islands, now in process at the U. S. National Museum, has not appeared in print at this writing, and, except for a few easily recognized species, too much confusion in the literature extant prevents us from making unqualified identifications of the seven species lumped in this report. Our treatment of the group should not be construed to mean that all species are similar in habitat, behavior, or influence in the coral reef community.

All parrot fish examined had scraped coral polyps, mostly from the massive, glomerate corals, particularly members of the coral genera *Porites*, *Astreopora*, and *Montipora*. The beak marks on these heads, and on the rather smooth, algal covered reef rock, are very striking, and their quantity provides a rough measure of the carrying capacity of the particular reef area. Boulenger (1922) stated that parrot fishes fed mostly on vegetable matter, corals, and hard-shelled molluscs, crushing the latter with their unusual dentition. We have not found them taking molluscs in the Marshall Islands. In Japan, where suitable corals are absent, the parrot fish, *Leptoscarus japonicus*, takes only algae (Suyehiro 1942).

Parrot fish are very common inhabitants of all reef areas with living coral. Most species travel in small schools, although a few are solitary, and others are simply gregarious. Particularly common in the back ridge trough of the seaward reef are three large species which form schools of 10 to 50 individuals. These schools are spaced at rather even intervals of a few hundred feet along the seaward reefs. These schooling species are particularly common in surge channels where they go when the water over the seaward reef becomes shallow at ebb tides.

As swimmers approach large parrot fish they usually move off over sandy bottom patches between coral mounds where, at rather frequent intervals, they are observed to void as feces great masses of calcareous powder. There is little doubt that parrot fish contribute substantially to the formation of fine sand by scraping coral and rock surfaces, digesting the algae and coral polyps, and returning the pulverized rock and skeletal material to the bottom as fecal components.

Family Gobiidae

Species: *Gnatholepis anjerensis* (goby)

Number examined: Arno, 5 specimens

Sex: Males and females

Standard length: 32-40 mm

Digestive tract: Mouth small, inferior, villiform teeth on jaws, pharyngeal teeth heavy; stomach indistinct; intestine long, coiled

Food item	Percentage of fish containing the item
Crustacea	
Copepods	100
Copepod metanauplii	20
Ostracods	20
Crustacean fragments	20
Detritus, with admixed sand grains	60
Algae	
Fine filaments, admixed with sand grains	40
Gastropoda	
Crushed small gastropods	20

This small goby is ubiquitous on all quiet, compacted sandy bottoms 3-25 ft in depth on lagoon, interisland, and seaward reefs. It is strongly demersal, lives on the sandy bottoms, and retreats into burrows or under rocks when disturbed. This species is omnivorous, taking any food available to it among the benthos. It also makes use of detritus to a certain extent. The rather heavy pharyngeal teeth enable it to crush small, thin-shelled gastropods and crustaceans.

Species: *Gobius ornatus* (goby)
Number examined: Arno, 13 specimens
Sex: Males and females
Standard length: 31-65 mm
Digestive tract: Similar to *G. anjerensis*

Food item	Percentage of fish containing the item
Crustacea	
Copepods	84
Copepod metanauplii	7
Isopods	69
Ostracods	53
Amphipods	7
Polychaeta	
Unid. polychaetes	46
Foraminifera	
Several unid. species	23
Gastropoda	
<i>Atys</i> sp.	15
Algae	
Fine filaments, with sand grains	7
Sand grains	61

This species lives in burrows in compacted sand bottoms 3-25 ft deep wherever the water is quiet. It is carnivorous, feeding almost exclusively on small benthonic species which it catches in a rather selective way, favoring crustaceans and polychaete worms.

Species: *Bathygobius fuscus fuscus* (goby)
Number examined: Arno, 14 specimens: 1 empty
Sex: Males and females
Standard length: 32-66 mm
Digestive tract: Mouth terminal, large, teeth villiform, pharyngeal teeth not heavy; stomach large, thick-walled; intestine short, 1 loop

Food item	Percentage of fish containing the item
Crustacea	
Crab fragments	30
Shrimp fragments	23
Polychaeta	
Unid. polychaetes	23
Fish	
Unid. fragments	15
Wrasse	7
Goby	7
Insecta	
Ant	15
House fly	7
Algae	
Fine filaments, admixed with sand grains	7

This species is exceedingly abundant, particularly in the intertidal zone on all reefs. It is an ubiquitous inhabitant of the tide pools and shallow depressions. When pursued it leaps from pool to pool, apparently exhibiting a thorough "memory" of its immediate sur-

roundings, since the leaps from pool to pool are accurate and rapid. In addition, it has definite homing tendencies. The fused ventral fins make an effective sucking disc with which it can cling to rock surfaces as the waves surge over it. Its food and feeding characteristics, combined with its digestive morphology, label the species as a carnivore, feeding mostly on the benthonic fauna of tidal flats and the inhabitants of tide pools. Occasionally it will scrape off some algal filaments.

Species: *Gobiodon erythrospilus* (goby)
Number examined: Arno, 5 specimens: 1 empty
Sex: Males and females
Standard length: 28-31 mm
Digestive tract: Mouth terminal, small; teeth villiform with some canines on inner row of lower jaw, 2 pairs rather strong near the symphysis; stomach large, heavy-walled; intestine short

Two of the four specimens examined contained only fish eggs, one of the others contained only isopods, and the fourth had a polychaete worm. This goby lives exclusively in the interstices of living heads of ramose corals (*Pocillopora* sp., *Acropora* sp., *Stylophora* sp.), and thus is found commonly on all quiet reefs where these corals occur in shallow water. Each head seems to have 1-10 individuals within it. They will not leave the coral head, even after it has been taken from the water. The heavy diet of fish eggs resulted from our sampling during the time when several species of coral-inhabiting fish were spawning. Since several of these fish spawn in the interstices of living corals, it is not unusual for the eggs to be eaten by such carnivorous coral-dwelling inhabitants. They also take small crustaceans and polychaetes which inhabit living corals.

Species: *Gobiodon rivulatus* (goby)
Number examined: Arno, 11 specimens: 3 empty
Sex: Males and females
Standard length: 21-33 mm
Digestive tract: Similar to *G. erythrospilus*

Food item	Percentage of fish containing the item
Crustacea	
Copepods	50
Copepod metanauplii	25
Isopods	25
Polychaeta	
Unid. polychaetes	25
Detritus and fine sand grains	12

This species occupies the same habitat in the same reef areas as does *G. erythrospilus*. Frequently, a single coral head will contain both species. As a matter of fact, it is entirely possible that what we identified as *G. rivulatus* may be a mixture of two closely-related species, *G. rivulatus* and *G. quinquestrigatus* (Cuvier and Valenciennes). In any event, they appear to have very similar carnivorous food predilections, taking small inhabitants of the coral heads in which they live. The detritus and fine sand found in one specimen examined probably was taken in as the fish was succumbing to rotenone poisoning.

Species: *Paragobiodon echinocephalus* (goby)
Number examined: Arno, 8 specimens: 5 empty
Sex: Females
Standard length: 12-19 mm
Digestive tract: Similar to *G. erythrospilus* except that both jaws have well-developed canines, and gravid females appeared to have no intestine at all, although it may have been collapsed and enclosed by the distended ovaries.

One of the three specimens with food had shrimp fragments, the other two contained isopods. These minute, highly carnivorous ramose coral-dwelling gobies, occur on all reefs with quiet water and luxuriant coral

growth, each head containing 1-10 individuals. The habits of this species are essentially similar to *G. erythrospilus*. Here again there is a complex of very similar forms, other species found in identical habitats being *P. kerri* and *P. melanosomus*. Appearance, habitat, and behavior were very similar for all three forms. The gravid females examined contained no food, nor could we locate any digestive tract. It is possible that it could have been overlooked, should it have been entwined among the ovaries.

Family Summary

Usually solitary, sometimes in pairs, at other times in gregarious aggregations, gobies live in ramose corals, as commensals in burrows made by fossorial shrimps or other forms, or on bottoms of tidepools, tidal flats, or shallow lagoon sandy-bottomed areas. For the most part they are carnivorous, but some are actually omnivorous, taking a considerable amount of fine algal filaments and detritus along with small prey species.

From the standpoint of habitats occupied, and to a lesser extent the type of food items consumed, gobies can be segregated into two groups; those which live exclusively in living ramose coral heads, and those living elsewhere.

The most important tidepool and seaward reef flat inhabitant is *B. f. fuscus*, and in burrows on compacted sandy bottoms are found *G. ornatus* and *G. anjerensis*. The food of these species is predominantly small crustaceans and polychaetes, but *G. anjerensis* consumes far more algae and detritus than any of the others and can be designated an omnivore.

In living, ramose corals, particularly in *Pocillopora*, *Stylophora*, and *Aerophora* heads, are the minute carnivorous species *G. rivulatus*, *G. erythrospilus*, and *P. echinocephalus*. Their food consists of the neighboring small invertebrates occupying the same coral head.

Suyehiro (1942) reporting on the food and feeding habits of several gobies in Japan, also indicated heterogeneous feeding habits for the various species, accompanied by changes in the nature of the digestive tract. He also showed that the food habits of one species, *Chasmichthys gulosus*, changed markedly during growth, from microplankton as juveniles to copepods as they grew slightly larger, and, as adults, to eating each other mostly, but varying the diet with isopods, amphipods, and nereid worms. Other species were zooplankton feeders (*Pterogobius elapoides elapoides*), diatom feeders (*Boleophthalmus pectinirostris*), and scavengers (*Periophthalmus cantonensis*).

Family Eleotridae

Species: *Valenciennaea violifera* (sleeper)

Number examined: Arno, 13; Eniwetok, 5 specimens

Sex: Males and females

Standard length: 40-85 mm

Digestive tract: Mouth large, canine teeth strong in front of both upper and lower jaws, pharyngeal teeth weak; stomach indistinct; intestine long, coiled.

Food item	Percentage of fish containing the item
Crustacea	
Copepods	100
Cypris larvae	11
Ostracods	88
Isopods	83
Amphipods	16
Shrimp fragments	5
Gastropoda	
<i>Atys</i> sp.	33
Unid. small gastropods	5
Foraminifera, several species	27

Polychaeta	
Unid. polychaetes	16
Pelecypoda	
Small clams	5
Sand grains	72

This sleeper occurs in pairs which live in permanent burrows in compacted sandy bottoms usually beneath a rock. It plugs its burrow with a ball of algae. It is common on all compacted sandy bottoms in depths up to 15 ft on the lagoon, interisland, and seaward reefs where the water is quiet.

The very long intestine suggests that this species ought to subsist to a considerable extent on detritus, but our results indicate that it is, instead, a carnivorous species which subsists on benthonic invertebrates without being particularly selective among them. Crustaceans form the bulk of its diet, but they also comprise the most abundant benthonic group. The fish can be observed to take in a mouthful of the surface material, sift it, and reject the unwanted portion through the gills while swallowing the remainder.

Species: *Valenciennaea strigata* (sleeper)

Number examined: Arno, 9; Eniwetok, 11 specimens: 2 empty

Sex: Males and females

Standard length: 44-116 mm

Digestive tract: Similar to *V. violifera*

Food item	Percentage of fish containing the item
Crustacea	
Cyclopoid copepods	66
Harpacticoid copepods	11
Calanoid copepods	5
Copepod metanauplii	11
Ostracods	66
Unid. isopods	50
Tanaid isopods	5
Cypris larvae	33
Shrimps	5
Mollusca	
Small gastropods and veliger larvae	33
Pelecypoda	
Small clams	5
Echinodermata	
Small echinoids	11
Fish	
Unid. fragments	5
Fish eggs	5
Sand grains	50

The habitat and behavior of this common sleeper is essentially the same as that for *V. violifera*. Both species may be found in the same sandy area. Its food habits are exceedingly heterogeneous, and its diet appears to be those items met as the fish scans the benthos and sifts it for food.

Family Summary

Both species of sleepers examined appear to have virtually identical habits and distribution on the sandy-bottom reefs in quiet water. The sandy bottoms occupied are those in which some rocky rubble is present under which they construct their permanent burrows. In so doing they carry out the sand in their mouths and eject it at the entrance to the burrow. They are rather busy fish, and when not sifting the benthos for food, seem to be engaged in lengthening their burrows. When they retreat into the burrow they pull a ball of algal filaments into its opening to plug the hole. This activity was observed many times on the lagoon reef at Arno in water 2-30 ft deep.

They forage by taking in a mouthful of sand and benthos, apparently sift it, then eject the unwanted portion through the gills. They are certainly not selective feeders, but some species taken must be captured on

sight, rather than sifted from the benthonic surface layer. The items taken from sifted sand appear in about the same proportion as they occur naturally in the benthos.

Family Microdesmidae

Species: *Paragobiodes grandoculis*
Number examined: Eniwetok, 4 specimens: 2 empty
Sex: Females
Standard length: 88-90 mm
Digestive tract: Mouth large, canines well-developed in rows on both jaws; intestine short.

The two specimens examined had taken a small portunid crab and a larval shrimp. This unusual, elongate fish hovers solitarily over the light sand on lagoon reefs at depths of 6-20 ft or more, where it can be detected only by close inspection because of its slenderness and pale coloration. It remains just a few inches above the substrate, rather motionless, but when approached by a swimmer it dives into a borrow. Whether the burrows are self-constructed or are polychaete tubes was not determined. In laboratory aquaria the species readily entered "burrows" made from glass tubing. This microdesmid is a carnivore, taking small crustaceans from the benthos. The well-developed canines and large mouth provide it with an efficient mechanism for catching small prey species.

Family Echeineidae

Species: *Echeneis naucrates* (Pilot fish, shark-sucker)
Number examined: Eniwetok, 1 specimen: empty
Sex: Undeveloped
Standard length: 660 mm
Digestive tract: Mouth large, small, sharp teeth on jaws; stomach and intestine a single broad, straight tube.

The specimen examined contained garbage only, and was one of several remoras frequenting the garbage dump at Eniwetok. Several were observed attached by the elliptical sucker on the dorsal side of the head, to sharks (*Ginglymostoma*, *C. melanopterus* and *C. menisorrhah*) and to a large grouper, *Promicrops lanceolatus*. Frequently it has been suggested that these fish feed on fragments of food which the larger, host fishes drop while they themselves are feeding. Both Jordan (1907) and Boulenger (1922) state that these fish are carnivores, and Suyehiro (1942) examined three specimens, all of which were empty. Recently (Maul 1956) various echeineids have been shown to feed upon ectoparasites presumably removed from the skin of their hosts.

Family Paraperidae

Species: *Paraperis cephalopunctatus* (sand perch)
Number examined: Arno, 19; Bikini, 2; Eniwetok, 4 specimens: 1 empty
Sex: Males and females
Standard length: 70-121 mm
Digestive tract: Mouth moderate in size, jaws heavily armed with recurved canines; stomach large; intestine short, straight.

Food item	Percentage of fish containing the item
Crustacea	
Xanthid crabs	54
Maïd crabs	8
Portunid crab fragments	8
Shrimp fragments	25
Palaemonid shrimps	8
Stomatopod fragments	8
<i>Galathea</i> sp.	4
Fish	
Unid. fragments	25
<i>Apogon novemfasciatus</i>	4
Fish eggs	4

Paraperids are common on all reefs visited where they live solitarily under coral heads adjacent to sandy bottoms, or lie motionless on the sand which they closely resemble in pattern and color. This species is a voracious, demersal carnivore which lies in wait for its prey, then, when it is sufficiently close, makes a rapid dash of one or two feet along the bottom or into mid-water to make the capture. Both crustaceans and fish are taken as available.

Species: *Paraperis clathrata* (sand perch)
Number examined: Arno, 2 specimens
Sex: Females
Standard length: 122-126 mm
Digestive tract: Similar to *P. cephalopunctatus*

One of the specimens examined contained shrimp fragments; the other had consumed a portunid crab. This species is uncommon on the reefs visited, but it occupies the same habitat and has a behavior pattern similar to that described for *P. cephalopunctatus*.

Family Summary

Sand perch are solitary fish which lie on exposed sandy bottoms, on rocky surfaces, or just beneath coral heads. Their coloration obliterates them effectively as they lie motionless on the sandy substrate. Because of this feature they feed by lying in wait for crustaceans and small fish to come close to them. They seize their prey with a rapid dart of at most 2-3 ft. Their rather large mouths and recurved canines, together with their feeding methods, are much like those of lizard fish (Synodontidae), except that the dentition of sand perch is somewhat less-developed and they are more sluggish.

Family Blenniidae

Species: *Aspidontus taeniatus* (blenny)
Number examined: Arno, 3 specimens
Sex: Males and females
Standard length: 82-92 mm
Digestive tract: Mouth small, minute teeth on both jaws and 1 pair of enormous, recurved fangs on lower jaw; intestine short.

One of the fish examined contained shrimp fragments, another had consumed fish eggs, and the third contained only gurry in its stomach. The color and color pattern of this brilliantly hued blenny are exceedingly like that of the wrasse, *Labroides dimidiatus*, discussed earlier. It is uncommon, but seen occasionally on the seaward and interisland reefs about living coral patches in depths from 3-6 ft and on the lagoon reef around coral mounds down to a depth of about 20 ft. It frequently lives in pipes, tubes, etc., and usually occurs in pairs. It is one of the few fish which will bite severely if handled. This species is carnivorous, taking small crustaceans and fish, usually from living coral heads. Doty & Morrison (1954) apparently mistook this blenny for *L. dimidiatus* in their description of the blenny's behavior as regards its foraging for parasites on the bodies of parrot fish. The almost perfect mimicry, possibly on the part of this blenny (Randall 1955), would make such mistaken identity easily possible.

Species: *Istiblennius coronatus* (blenny)
Number examined: Bikini, 2; Eniwetok, 3 specimens
Sex: Males and females
Standard length: 73-85 mm
Digestive tract: Mouth large, jaws with numerous fine teeth; intestine very long, coiled.

All of the specimens examined had taken large amounts of detritus and fine sand with many algal filaments admixed. Two specimens also contained the fora-

miniferan, *Calcarina* sp. This blenny is abundant on the seaward reef flats in the intertidal zone. It occurs only on hard bottoms where it lies with just its head protruding from holes and crevices. It is extremely active and alert. During feeding it apparently scoops up the surface sediments on the hard substrate which consist of fine sand, detritus, fine algal filaments and the organic leptopel which covers the substrate in most reef and shore areas (Strasburg Ph.D. thesis).

Species: *Istiblennius paulus* (blenny)

Number examined: Arno, 19; Bikini, 3 specimens; 1 empty

Sex: Males and females

Standard length: 51-130 mm

Digestive tract: Similar to *I. coronatus*.

Food item	Percentage of fish containing the item
Detritus and fine sand grains	71
Algae	
Fine filaments, with fine sand	61
Scraped filaments, with fine sand	28
Diatoms	38
Foraminifera	
<i>Calcarina</i> sp.	38
Unid. species	33
Crustacea	
Ostracods	28
Copepods	28
Gastropoda	
Unid. minute gastropods	4

This very abundant species occurs on all hard-bottomed reef shallows. It lives on permanently submerged reef flats in depths of 1-2 ft, and not intertidally as does *I. coronatus*. It is an extremely agile and alert species. Like *I. coronatus*, *paulus* also lies on the bottom with just its head protruding from its hiding place. *I. paulus* is quite omnivorous, taking primarily detritus, leptopel, and benthonic algae and invertebrates by scraping off the thin, sedimentary layer on the reef rock or on compacted sand. It appears to ingest this benthos without exercising much selection between organisms.

Species: *Exallias brevis* (blenny)

Number examined: Bikini, 1 specimen

Sex: Female

Standard length: 80 mm

Digestive tract: Similar to *I. coronatus*

The single specimen examined contained fine, filamentous algae and detritus admixed. This uncommon species is found on both the lagoon and seaward reefs in depths from 4-15 ft near living coral. It hides below the living coral heads, the adults being very demersal; however, the young are pelagic. It is predominantly an herbivore scraping the fine algal filaments from the bases of coral heads and coral rock.

Species: *Cirripectus variolosus* (blenny)

Number examined: Bikini, 1 specimen

Sex: Female

Standard length: 70 mm

Digestive tract: Similar to *I. coronatus*

The single specimen examined had taken fine algal filaments with detritus admixed, but no sand grains. This common species occurs most abundantly on the seaward reef flat from about the middle to the outer edge, being more abundant in areas containing much living coral. Apparently it prefers regions having considerable water movement. It lives in small holes in the hard substrate, and frequently is seen swimming actively about living coral. Its food consists of fine algae and the precipitated detritus or leptopel which covers rocks in its living area.

Species: *Cirripectus sebae* (blenny)

Number examined: Arno, 9 specimens

Sex: Males and females

Standard length: 25-71 mm

Digestive tract: Similar to *I. coronatus*

Food item	Percentage of fish containing the item
Detritus	88
Algae	
Fine filaments, with fine sand grains admixed	77
Diatoms	22
Foraminifera	
<i>Calcarina</i> sp.	33
Ostracoda	22
Gastropoda	
Minute gastropods	11

This abundant species prefers regions of considerable water movement and is found most commonly at the outer reef edge and in surge channels on leeward ocean reefs 3-10 ft deep. There it lives in small holes in the substrate, and is often seen flitting about living coral. It has a tendency to move about the reefs rather than to remain secluded in one hole. This species, like *C. variolosus*, subsists on the organic materials on the surface of the hard substrate, particularly on precipitated detritus and fine algal filaments. In the process of scraping off this sediment, it takes minute animal forms (ostracods, foraminiferans) which occur in the benthos.

Family Summary

These active, small fish are found in most habitats on coral reefs, but most of them prefer the seaward reefs, either on the seaward reef flat, or in surge channels and the back ridge trough.

Most species are morphologically adapted to consume a diet heavy in detritus and fine filamentous algae. With this material, gotten by scraping the sediments and organic covering of rocks or hard bottoms, they secure some minute animal species such as foraminiferans, ostracods, copepods, etc., which comprise part of the benthos. There is little question, however, that their diet must be high in leptopel, and experimental holding of several species in captivity has verified this.

Within the family, however, there are some aberrant types which have very different food and foraging habits. One of these examined, *A. taeniatus*, is strictly carnivorous, taking both crustaceans and fish, and not at all morphologically suited to a diet of detritus and algae. Suyehiro (1942) reported on the feeding habits of three genera of blennies, one of which was entirely herbivorous, and two strictly carnivorous. He remarked about the heterogeneity in digestive morphology and food habits and questioned the taxonomic parameters of the family.

Family Brotulidae

Species: *Dinemachthys iluocoteoides* (brotulid)

Number examined: Arno, 12; Bikini, 4 specimens; 4 empty

Sex: Males and females

Standard length: 34-83 mm

Digestive tract: Mouth large, canines in jaws numerous and well-developed; stomach heavy-walled; intestine short.

Food item	Percentage of fish containing the item
Crustacea	
Shrimp fragments	33
Crab fragments	25
Isopods	8
Ostracods	8
Fish	
Unid. fragments	25
Gurry	8

This brotulid is uncommon, but occurs on all reefs visited. It is present at the leeward ocean reef edge and in the surge channels. In the lagoon it lives in coral

mounds in about 8-10 ft of water. It has very secretive habits, none ever having been seen alive by us, and apparently secludes itself in holes or crevices in coral. It is a voracious carnivore, taking mostly crustaceans and fish which venture close to its hiding place. From its appearance and seclusiveness we judge it to be very demersal, probably lying in wait for its prey which it dashes out to capture.

Family Balistidae

Species: *Rhinecanthus rectangulus* (trigger fish)
Number examined: Arno, 4; Bikini, 3; Eniwetok, 1 specimen
Sex: Males and females
Standard length: 50-160 mm
Digestive tract: Mouth small, teeth heavy, incisiform, almost fused, pharyngeal teeth not heavy; stomach heavy-walled; intestine long, coiled.

Food item	Percentage of fish containing the item
Algae	
Scrapings and filaments, with much calcareous powder	75
Filaments, without sand	12
Crustacea	
Isopods	37
<i>Thalamita</i> sp.	12
Copepods	12
<i>Gonodactylus</i> sp.	12
Polychaeta	
Unid. fragments	12
Foraminifera	
<i>Calcarina</i> sp.	12

This is a very common trigger fish on the seaward reef shallows and on the interisland reefs. It never strays far from its refuge hole or crevice in the hard bottom. It characteristically forages about the shallow reefs away from living coral. The species is omnivorous, taking algae and crustacea primarily. The crustaceans taken are common residents of the sandy and rubble bottoms.

Species: *Rhinecanthus aculeatus* (trigger fish)
Number examined: Arno, 7; Bikini, 1; Eniwetok, 7 specimens
Sex: Males and females
Standard length: 105-181 mm
Digestive tract: Similar to *R. rectangulus*

Food item	Percentage of fish containing the item
Algae	
Scrapings, mixed with minute rocky fragments	93
Algal fronds, bitten off	33
Coralline algal fragments	13
Gastropoda	
<i>Atys</i> sp.	40
Small, crushed gastropods	13
Foraminifera	
<i>Calcarina</i> sp.	40
Crustacea	
Isopods	33
Crab fragments	26
Shrimp fragments	20
Amphipods	6
Polychaeta	
Unid. fragments	20
Pelecypoda	
Crushed clams	6
Fish	
Unid. fragments	13
<i>Chromis caeruleus</i>	6
Coelenterata	
<i>Acropora</i> sp., tips broken off	6

This trigger fish is common on the lagoon and interisland reef shallows, and on the seaward reef only in areas of quiet water. It prefers a compacted sandy bottom or one with rubble near coral mounds. Such a heterogeneous feeder can only be omnivorous with no particular predilections noted. It apparently takes anything organic, whether it be soft or hard-bodied.

Those containing *Acropora* tips had consumed great numbers of them, and the intestine was crammed with the sharp skeletal fragments.

Species: *Balistapus undulatus* (trigger fish)
Number examined: Arno, 12; Eniwetok, 8 specimens
Sex: Males and females
Standard length: 115-205 mm
Digestive tract: Similar to *R. rectangulus* except that teeth in front are much heavier and stronger

Food item	Percentage of fish containing the item
Coelenterata	
<i>Acropora</i> sp., living tips of branches	65
Scraped polyps, with much skeletal powder	10
<i>Pavona varians</i> , fragments of living corallum	5
<i>Stylocystis sanguineus</i> , fragments	5
Fish	
Unid. fragments	55
<i>Abudefduf biocellatus</i>	5
Crustacea	
Crab fragments	45
Xanthid crab fragments	30
Unid. hermit crab	5
Shrimp fragments	20
Gastropoda	
Crushed shells	45
Crushed vermetid tubes	10
<i>Cypraea carneola</i> , crushed	5
Algae	
Fronds, bitten off	45
Fine filaments and scrapings, with much calcareous powder	35
Coralline algal fragments	15
Echinodermata	
<i>Echinometra mathaei</i> , crushed	15
Eucidarid urchin, crushed	10
Spatangid heart urchin, crushed	5
Tunicata	
Unid. fragments	10
Pelecypoda	
Clam fragments	10
<i>Arca</i> sp., crushed	5
<i>Chama</i> sp., crushed	5

This common trigger fish frequents all deep, quiet reefs with considerable living coral, in depths from 4-20 ft. Its omnivorous habits of a completely heterogeneous nature are evident from the table of food items consumed. Although unselective, specimens were encountered frequently which had consumed a meal entirely of one or two items. This was especially true of those that had broken off living tips of ramose corals, and those that had taken tunicates. The strong teeth are used to break off corals, and to crush gastropods, echinoderms, etc. Even coralline algae had been broken off and consumed. Eight specimens examined by Randall (1955) in the Gilbert Islands had similar food habits, even to tunicate fragments, sea urchins, and *Acropora* sp. tips.

Species: *Balistoides viridescens* (trigger fish)
Number examined: Eniwetok, 2 specimens
Sex: Males
Standard length: 490-515 mm
Digestive tract: Similar to *B. undulatus*

One specimen had consumed mostly the living tips of *Pocillopora damicornis*, but also contained crushed shells of cake urchins (*Clypeaster* sp.) and sea urchins (*Eucidaris metularia*), and crushed boring clams, *Lithophaga* sp. The other specimen had eaten solely starfish of an unidentified genus. This solitary species, though uncommon, is large and striking in shape and coloration. It occurs on lagoon reefs around living coral mounds or over sandy bottoms near living coral patches, and on the seaward reef it is found in sheltered areas near coral mounds. *B. viridescens* is strictly a carnivore, subsisting mostly on living coral and echinoderms.

Species: *Pseudobalistes flavimarginatus* (trigger fish)
 Number examined: Arno, 1; Eniwetok, 1 specimen
 Sex: Female and undeveloped
 Standard length: 190-460 mm
 Digestive tract: Similar to *B. undulatus*

The food items consumed by the two specimens examined included: Crustacea—*Lydia annulipes*, Isopods; Gastropoda—crushed *Oliva* sp., crushed unid. gastropods; Foraminifera—*Calcarina* sp.; Tunicata—colonial tunicate fragments. This uncommon, solitary trigger fish grows to about 2 ft in length. It was found on the lagoon and interisland reefs where the water was quiet and 10-30 ft deep. It appears to be entirely carnivorous and not particularly selective about its food items. Although these specimens had eaten no coral tips, it is likely that they do take them on occasion.

Species: *Pseudobalistes fuscus* (trigger fish)
 Number examined: Arno, 1 specimen
 Sex: Not noted
 Standard length: 310 mm
 Digestive tract: Similar to *B. undulatus*

This specimen contained the following food items: Echinodermata—Heart urchin fragments; Foraminifera—*Calcarina* sp., *Marginopora* sp., unid. foraminiferans; Gastropoda—Vermetid fragments; Pelecypoda—Protoconchs. This large, solitary trigger fish is uncommon, and is found swimming over sandy bottoms in water 10-20 ft in depth. It swims near the bottom, and takes refuge when molested in piles of coralline rubble or under rocks. This species appears to be entirely carnivorous, taking hard-bodied fossorial echinoderms, and breaking off vermetid tubes from their attachment to rocks.

Species: *Melichthys vidua* (trigger fish)
 Number examined: Eniwetok, 1 specimen
 Sex: Female
 Standard length: 140 mm
 Digestive tract: Similar to *B. undulatus*

The single specimen of this species contained the following food items: Algae—bitten and scraped filaments and fronds, with many sand grains and much calcareous powder; Crustacea—Xanthid crab fragments, Copepods; Pelecypoda—Small clams; Gastropoda—Small gastropods. This uncommon, solitary species is found on leeward ocean reef shallows with abundant living coral. There it hovers around living coral heads, and hides under the coral when molested. This trigger fish feeds mostly on algae, with the other animal food items being only incidental from a quantitative standpoint. It may be designated as a grazing herbivore and facultative omnivore.

Family Summary

Trigger fish, in general, adhere to a rather heterogeneous and omnivorous diet. Only the genera *Pseudobalistes* and *Balistoides* were found to be completely carnivorous, and this finding may only be the result of too few being examined. Both *P. flavimarginatus* and *P. fuscus* forage mostly on sandy bottoms taking both benthonic and fossorial forms such as echinoderms, foraminiferans, molluscs, and crustaceans which they crush with their exceedingly strong teeth. *B. viridescens* varies this type of diet with meals of the living tips of ramose and cespitose corals such as *Acropora* and *Pocillopora*.

The other trigger fish examined fed on a great variety of items. One species, *B. undulatus*, apparently takes almost anything organic, soft or hard. In all these species algae comprise a prominent part of the diet,

and the intestine is very long in compensation. Admixed with the large amounts of grazed algae are fragments of the living tips of branching corals, crustaceans, fish, and molluscs. Almost all of the hard-bodied organisms had been crushed into small pieces, illustrating the versatility of these fish in making a living on a coral reef.

Especially noteworthy is the fact that these trigger fish make good use of the abundant coral and even the echinoderms, the latter a group of ubiquitous organisms avoided by most predaceous animals, and for a time, thought likely to be rather well removed from the more intricate composition of the food web in coral reef communities.

Family Monacanthidae

Species: *Amanes carolae* (file fish)
 Number examined: Arno, 2 specimens
 Sex: Male and undeveloped
 Standard length: 131-151 mm
 Digestive tract: Mouth small, teeth long, heavy, incisiform; intestine long, coiled

One of the two specimens examined had the stomach and gut crammed solely with living tips of *Acropora* sp. which were partly digested. The remaining specimen had mostly fragments of a sponge (Calcispongiae), along with algal filaments and fronds bitten off, coralline algal fragments, and scraped coral polyps admixed with much skeletal material. These uncommon file fish occur on quiet, leeward ocean reefs near the outer edge, where they swim slowly about the luxuriant growth of corals and hide under them when molested. This species is omnivorous, but apparently makes a complete meal of a single item if available in sufficient quantity.

Species: *Oxymonacanthus longirostris* (file fish)
 Number examined: Eniwetok, 2 specimens
 Sex: Male and female
 Standard length: 75 mm.
 Digestive tract: Snout very long, pointed, mouth terminal, teeth protrude well beyond lips as long cupped incisors; intestine long, coiled.

Both specimens examined contained only coral polyps bitten off, with no skeletal material admixed. This small file fish is common on the lagoon, interisland, and seaward reefs where luxuriant coral growth occurs. It has been observed to have a very close association with living coral, and large numbers of them have been seen head down in living coral heads. Apparently they are engaged in nibbling off the coral polyps, a feeding method for which their dentition is well adapted. This species can be classed as strictly a carnivore.

Species: *Monacanthus* sp. (file fish)
 Number examined: Bikini, 1 specimen
 Sex: Male
 Standard length: 290 mm
 Digestive tract: Similar to *A. carolae*, but with incisors even more strongly developed.

This specimen had the entire digestive tract crammed full of the living tips of ramose and cespitose corals (*Acropora*, *Pocillopora*). Some coralline algal fragments were admixed. The fragments of coral were large, some over 1 inch in length. The intestine, being very thin-walled, protruded outward in all directions as a result of the long coral fragments contained within it. This species is probably exclusively a carnivore, although on occasion some algae may be taken.

Family Summary

All file fish examined fed almost exclusively on coral, although their feeding methods varied considerably. *O. longirostris*, for example, nibbles off the tips of expanded

polyps without touching the corallite. On the other hand, the large file fish, *Amanes carolae*, and *Monacanthus* sp., break off the ends of the branches of such ramose and cespitose species as *Acropora*, *Pocillopora*, and *Stylophora*, and fill the entire gut with these large, sharp fragments so that the organic material may be digested. Many fragments an inch or more in length were removed from intestines having a diameter of only half that. *A. carolae* varies its diet by taking sponges and algae in addition to coral. There is little question that file fishes derive the bulk of their nutriment from living corals, and thus are important in helping to bring into circulation within the food web the abundant corals which serve comparatively few predators in relation to the vast bulk of protoplasm they represent.

Family Ostracionidae

Species: *Ostracion cubicus* (trunk fish)
Number examined: Eniwetok, 6 specimens
Sex: Males and females
Standard length: 125-260 mm
Digestive tract: Mouth small, teeth moderate, slightly incisiform; intestine very long, coiled.

Food item	Percentage of fish containing the item
Algae	
Fine algal scrapings, with calcareous powder	50
Filaments, bitten off	16
Polychaeta	
Unid. polychaetes (sand-dwelling)	50
Gastropods	
<i>Atys</i> sp.	33
Pelecypoda	
Crushed clams	16
Fish	
Unid. fragments	16
Crustacea	
Isopods	16
Xanthid crab fragments	16
Sand grains and foraminiferans	67

Trunk fish commonly inhabit all reefs where the water is relatively quiet at depths of 3-20 ft. They are very weak swimmers, cruising slowly around coral heads, hiding in caves, crevices, etc. They are completely omnivorous, taking what food items they can get, mostly from the sandy bottoms around coral mounds. Except for the algae which was probably growing on the coral mound or rocks, all food items are benthonic. The polychaetes taken are exceedingly abundant in the sandy bottoms of the lagoon just below the surface. As would be expected from its structural design and small mouth, trunk fish food getting proclivities are restricted to sedentary or slow-moving invertebrates.

Family Tetraodontidae

Species: *Arothron mappa* (puffer, balloon fish)
Number examined: Arno, 2 specimens
Sex: Male and female
Standard length: 405-540 mm
Digestive tract: Mouth moderately small, teeth 2 large plates in each jaw forming a beak; intestine very long, coiled.

Both specimens examined had the entire digestive tract distended with large fragments of a sponge. In addition a few other food items listed below had been taken: Tunicata fragments; Gastropoda—Crushed shells; Crustacea—Xanthid crab fragments; Algae—Coralline algal fragments, *Halimeda* branches, *Valonia* sp. This large, reticulated puffer is uncommon, occurring in our collections only from the lagoon reef shallows of Arno Atoll. It apparently stays near the lagoon reef edge in 5-10 ft of water. Its noteworthy feeding on sponges is significant in bringing another, little preyed upon organism into the food web.

Species: *Arothron hispidus* (puffer, balloon fish)
Number examined: Arno, 1 specimen
Sex: Male
Standard length: 300 mm
Digestive tract: Similar to *A. mappa*

The single specimen examined contained the following items in its stomach: Pelecypoda—*Pinctada martensi* (crushed), *Codakia punctata* (crushed), *Valisella auriculata* (crushed), *Isognomon costellatum* (crushed); Coelenterata—fine tips of *Pocillopora damicornis*; Porifera fragments; Tunicata fragments; Crustacea—Xanthid crab fragments; Algae—Coralline algal fragments, *Halimeda* fragments. This puffer is uncommon in the Marshall Islands and occurs mostly in the quiet water of the lagoon near living coral at depths of 4-20 ft. It usually secludes itself under a ledge or in a hole in the coral. This species is omnivorous, though primarily a carnivore. The heterogeneity of food habits indicates that it is an opportunist, taking whatever animal food it can get at the time. Its heavy teeth are well adapted for crushing hard-bodied forms and breaking off branches of living coral.

Species: *Arothron meleagris* (puffer, balloon fish)
Number examined: Arno, 3 specimens
Sex: Female
Standard length: 158-176 mm
Digestive tract: Similar to *A. mappa*

In the Marshall Islands this species is almost exclusively a feeder on live coral. All specimens examined contained many living tips of *Acropora* sp., and the following species of corals were taken by at least one of the specimens examined: *Porites lobata* fragments, *Porites superfusa* fragments, *Goniastrea parvistella* fragments, *Pavona varians* fragments, *Montipora* sp. fragments, Alcyonarian tips. The entire gut in all three specimens was choked with the stony fragments of several species of living coral. This puffer is uncommon in the Marshall Islands, and in our collections was taken only at Arno Atoll. There it frequents lagoon reefs wherever luxuriant growths of coral occur. It secludes itself in holes or crevices, or under the living coral heads.

Species: *Arothron nigropunctatus* (puffer, balloon fish)
Number examined: Arno, 1; Eniwetok, 4 specimens
Sex: Females and undeveloped
Standard length: 120-158 mm
Digestive tract: Similar to *A. mappa*

Except for crab fragments in one specimen and unidentified crushed clams in another, these puffers had eaten only living tips of *Acropora* sp. The stomach and intestine of each specimen were completely crammed with the stony branches, those in the stomach just beginning to undergo digestion, while those in the lower intestine were white and cleaned of the fleshy polyps. This puffer is the most common one in the Marshall Islands where it occurs on all reefs having living coral from 2-20 ft deep. Although it is predominantly a carnivore taking living coral as food, it can and does, on occasion, take other organisms such as crustaceans and molluscs. Randall (1955) examined two specimens in the Gilbert Islands and found them both to contain nothing but bite-sized pieces of living coral.

Species: *Arothron* sp. (puffer, balloon fish)
Number examined: Eniwetok, 4 specimens: 3 empty
Sex: Males and females
Standard length: 420-600 mm
Digestive tract: Similar to *A. mappa*, but with more highly developed upper pharyngeal teeth

The single specimen with food contained nothing but ossicles of the recently digested sea star, *Linckia guildingi*. This puffer, taken off the pier at Eniwetok, was not seen elsewhere by us. It is a very large species, attaining a length of over 2 ft.

Family Summary

The puffers, like the trigger fish, have interesting food habits because they incorporate into the food web so many kinds of food organisms which would not otherwise contribute to higher trophic levels because they are usually avoided as food items by other predators. In our experience no two specimens of the same species of puffer had eaten exactly the same food items, or in the same proportionate quantities. They appear to feed predominantly as opportunists, and virtually nothing alive on the reefs is beyond their capacity for utilization.

Perhaps the most consistently taken food item was living tips of ramose and cespitose corals, and even fragments of glomerate and foliaceous types which require considerable strength to break off from the remaining corallum. One specimen had eaten seven different species of corals. However, living tips of the rather delicate *Acropora* sp. heads seem to be preferred. This genus is the most abundant of the corals, and probably the easiest to break off from the main corallum. Various molluscs, particularly pelecypods growing attached to rocks and dead coral bases, are broken away from their attachment and crushed by the heavy dental armature.

Two specimens examined are especially noteworthy for having fed so extensively on unusual items. In one case, the two specimens of *A. mappa* examined from Arno Atoll, the entire gut was greatly distended, literally bloated with large chunks of sponge. Obviously, this was not a case of the chance taking of an unusual food item by them, because the two puffers were caught on different days on different parts of the reef. In another species of puffer from Eniwetok, yet unnamed, the entire gut was choked with small specimens of the ubiquitous sea star of rocky reefs and coral bases, *Linckia guildingi*.

Family Canthigasteridae

Species: *Canthigaster solandri* (sharp-backed puffer)
Number examined: Bikini, 5; Eniwetok, 11 specimens
Sex: Males and females
Standard length: 38-160 mm
Digestive tract: Mouth small, snout somewhat produced, teeth 2 large plates in each jaw forming a powerful beak; intestine long, coiled.

Food item	Percentage of fish containing the item
Algae	
Fronds and scraped filaments, with much calcareous powder	81
Crustacea	
Unid. fragments	12
Isopods	6
Tunicata fragments	12
Fish	
Unid. fragments	6
Polychaeta	
Serpulid polychaete	6
Unid. fragments	6
Foraminifera	
<i>Calcarina</i> sp.	6
Coelenterata	
Bitten off and scraped living tips of <i>Acropora</i> sp.	6
Bitten off lobes of alcyonarian coral	6

This sharp-backed puffer is very common, and locally abundant, on Marshallese reefs in all areas around living coral. It is common on the seaward reef shallows in all protected areas. The predominant food taken by these specimens was algae, but the animal composition is sufficient to designate the species as an omnivore. The dentition is especially fitted for scraping algal filaments off rocks and dead coral bases.

Family Diodontidae

Species: *Diodon hystrix* (spiny puffer)
Number examined: Arno, 1 specimen
Sex: Undeveloped
Standard length: 320 mm
Digestive tract: Mouth small, teeth in each jaw fused into 1 unit forming a powerful beak; intestine medium long.

The single specimen examined contained the following items: Gastropoda—Crushed shells; Crustacea—Xanthid crab fragments; Foraminifera—*Calcarina* sp.; coarse sand grains. The spiny puffer is rather uncommon on all reefs in the Marshall Islands and occurs where the water is relatively quiet in depths of about 8 ft. It feeds primarily on hard-shelled molluscs and crustaceans which it crushes easily with its heavy teeth and strong jaws. It is strictly a carnivore.

ANALYSIS OF FEEDING HABITS BY FORAGING METHODS

ALGAL FEEDERS

Of evolutionary significance is the fact that the herbivorous feeding habit and associated morphological and physiological changes do not appear in the more primitive fishes considered here, but make their entry with the percomorphs in the Family Mugilidae. This is not surprising, of course, because of the rise of modern bony fishes from highly carnivorous predecessors. Although our evolutionary time scales are somewhat unreliable in dating the rise of the several orders of the Osteichthyes, it is certain that these fishes were prevented from direct utilization of the tremendous plant food resources of the sea for a very long time.

The algal feeders can best be segregated into four categories, depending upon the nature of their algal foraging habits. First, there are a few which subsist to a very large extent, at least, on unicellular algal types. The mullets (Mugilidae) and some blennies (Blenniidae) are significant in this regard. Second, there are grazers on algae which crop very closely to the substrate, taking, more often than not, some of the substrate along with the algae. Here, of course, some of the surgeon fishes (Acanthuridae), damsel fishes (Pomacentridae), gobies (Gobiidae), blennies (Blenniidae), and trigger fish (Balistidae), are important. Third there are browsers which have cutting teeth for biting off bits of fronds or filaments above the substrate. In this category are placed some surgeon fishes (Acanthuridae), damsel fishes (Pomacentridae), and trigger fish (Balistidae). The fourth category includes those fishes which take algal food incidental to other food types which predominate in the diet. Some of the more important members of this group are the butterfly fish (Chaetodontidae), wrasses (Labridae), parrot fish (Scaridae), gobies (Gobiidae), and puffers (Tetraodontidae).

In the following lists the more important species in each category of algal feeding type are indicated:

Unicellular Algae

Family Mugilidae (mullet)—*N. chaptali*, *C. crenilabis*; Family Blenniidae—*I. paulus*.

Grazers

Family Leiognathidae (silver perch)—*G. argyreus*; Family Siganidae (rabbit fish)—*S. rostratus*; Family Acanthuridae (surgeon fish)—*C. striatus*, *A. olivaceus*, *A. gahhm*, *A. guttatus*, *A. nigroris*, *A. xanthopterus*, *A. mata*, *Z. veliferum*, *N. lituratus*; Family Pomacentridae (damselfish)—*P. nigricans*, *P. jenkinsi*, *P. albofasciatus*, *A. sordidus*, *A. glaucus*, *A. dicki*, *A. biocellatus*, *A. amabilis*; Family Labridae (wrasse)—*H. hoeveri*; Family Gobiidae (goby)—*G. anjerensis*; Family Blenniidae (blenny)—*E. brevis*, *I. coronatus*, *C. sebae*, *I. paulus*, *C. variolosus*; Family Balistidae (trigger fish)—*B. undulatus*, *R. rectangulus*, *R. aculeatus*, *M. vidua*; Family Monacanthidae (file fish)—*A. carolae*; Family Ostracionidae (trunk fish)—*O. cubicus*; Family Canthigasteridae (sharp-backed puffer)—*C. solandri*.

Browsers

Family Siganidae (rabbit fish)—*S. rostratus*; Family Kyphosidae (pilot fish)—*K. cinerascens*; Family Chaetodontidae (butterfly fish)—*C. ephippium*, *C. auriga*, *C. reticulatus*, *C. flavissimus*; Family Acanthuridae (surgeon fish)—*A. t. triostegus*, *A. achilles*, *A. guttatus*, *A. lineatus*, *A. aliala*, *A. nigroris*, *Z. veliferum*, *N. unicornis*, *N. lituratus*; Family Pomacentridae (damselfish)—*D. aruanus*, *P. vaiuli*, *P. jenkinsi*, *A. saxatilis*, *A. lacrymatus*, *A. dicki*, *A. biocellatus*, *A. amabilis*, *A. septemfasciatus*; Family Balistidae (trigger fish)—*B. undulatus*, *R. aculeatus*; Family Tetraodontidae (puffers)—*A. hispidus*.

Incidental

Family Chaetodontidae (butterfly fish)—*C. vagabundus*, *C. citrinellus*; Family Pomacentridae (damselfish)—*A. leucopomus*; Family Labridae (wrasse)—*H. melapterus*, *T. lutescens*, *H. hortulanus*, *H. marginatus*, *Stethojulis* sp., *S. axillaris*; Family Scaridae (parrot fish)—*C. spinidens*, *S. bicolor*, *S. sordidus*, Scarids (7 unid. species); Family Gobiidae (goby)—*B. f. fuscus*, *G. ornatus*; Family Tetraodontidae (puffer)—*A. mappa*.

DETRITUS FEEDERS

Comparatively few species among fishes are detritus feeders. It is apparent that on coral reefs benthonic invertebrates are the chief organisms for converting the particulate and colloidal organic material in the benthonic deposits to animal protoplasm. This food source, in turn, reaches the fishes through the multitude of species which prey upon these benthonic and fossorial invertebrate forms. The following fish species depend to a very large extent upon detritus in its several physical forms for their subsistence: Family Mugilidae (mullet)—*N. chaptali*, *C. crenilabis*; Family Gobiidae (goby)—*G. anjerensis*; Family Blenniidae (blenny)—*E. brevis*, *I. coronatus*, *C. sebae*, *I. paulus*, *C. variolosus*.

SCAVENGERS

Only one species in our collections seems to fit the category of a natural scavenger, *Ginglymostoma ferrugineum*, the nurse shark.

PLANKTON FEEDERS

No fish examined consumed phytoplankton, but several fed upon zooplankton, and of these only a very few have structural adaptations to facilitate sieving the minute plankters out of the water. The manta ray, *M. alfredi*, is perhaps the most highly adapted plankton feeder of the species encountered, but this species is

not actually part of the reef fauna, although it does come into the lagoons and even into comparatively shallow water on the reefs. It is believed that the cephalic fins serve to push plankters toward the wide open mouth in which peculiar organs, known as praebranchial appendages, together with the branchial apparatus, serve as straining devices as do gill rakers in other plankton-feeding fishes.

Among the more abundant small plankton feeders on the reefs are the round herring, *S. delicatulus*, the half-beaks, *H. affinis*, *H. laticeps*, and the silversides, *A. ovalaua* and *P. pinguis*. All of these species possess rather long, fine gill rakers for sieving out small crustacean and other plankters. One species of silversides examined, *S. temmincki*, has gill rakers only of medium length, and this species was found to feed to a great extent on the benthonic fauna rather than on mid-water plankters.

Several species of pomacentrids and two species of labrids were also found to consume plankters, but did not have special filtering devices. Rather, they selected the plankters eaten by visual means.

The following species examined subsist on zooplankton: Family Mobulidae (manta ray)—*M. alfredi*; Family Dussumieridae (round herring)—*S. delicatulus*; Family Hemiramphidae (half-beaks)—*H. affinis*, *H. laticeps*; Family Atherinidae (silversides)—*A. ovalaua*, *P. pinguis*, *S. temmincki*; Family Pomacentridae (damselfish)—*D. aruanus*, *C. caeruleus*, *C. atripectoralis*, *P. pavo*; Family Labridae (wrasse)—*T. hardwickei*, *T. lucasanum marnae*.

CARNIVORES

Coral reefs of the Marshall Islands are replete with carnivores of all sizes, and with a great variety of prey. The carnivores are segregated below into groups which predominantly, or to a great extent at least, seek their prey among the fossorial fauna, benthonic fauna, or mid-water fauna. Lastly the larger, roving carnivores are segregated into those characteristically dwelling on the reefs, and those deep or open water forms which forage over the reefs at regular or irregular intervals. In some cases carnivorous species forage rather widely and are classed in more than one of the groupings listed.

Carnivores on Fossorial Fauna

Family Ophichthidae (snake eels)—*L. semicinctus*, *B. sauropsis*; Family Moringuidae (whip eels)—*M. macrochir*; Family Holocentridae (squirrel fish)—*M. microphthalmus*, *H. diadema*; Family Polynemidae (thread fins)—*P. sexfilis*; Family Lutjanidae (snappers)—*L. gibbus*, *G. griseus*; Family Sparidae (snapper)—*M. grandoculis*; Family Mullidae (goat fish)—*M. samoensis*, *P. barberinus*; Family Labridae (wrasse)—*C. gaimardi*, *C. angulata*, *C. trilobatus*, *H. trimaculatus*, *H. hortulanus*, *H. marginatus*, *Stethojulis* sp., *S. axillaris*; Family Balistidae (trigger fish)—*B. undulatus*, *P. fuscus*; Family Ostracionidae (trunk fish)—*O. cubicus*.

Carnivores on Benthonic Fauna

Family Orectolobidae (carpet sharks)—*G. ferrugineum*; Family Clupeidae (sardines)—*H. kunzei*; Family Muraenidae (moray eels)—*E. zebra*, *E. leucotaenia*, *E. polyzona*, *G. pictus*, *G. petelli*, *G. javanicus*, *G. flavimarginatus*; Family Congridae (conger eels)—*C. noordzieki*; Family Synodontidae (lizard fish)—*S. variegatus*, *S. gracilis*; Family Bothidae (flounders)—*B. mancus*; Family Holocentridae (squirrel fish)—*M.*

berndti, *M. microphthalmus*, *H. sammara*, *H. lacteoguttatus*, *H. microstomus*, *H. laevis*, *H. diadema*, *H. spinifer*; Family Syngnathidae (pipe fish)—*C. i. waitei*, *C. f. conspicillatus*; Family Atherinidae (silversides)—*S. temmincki*; Family Polynemidae (thread fins)—*P. seafilis*; Family Carangidae (jacks)—*T. crumenophthalmus*; Family Apogonidae (cardinal fish)—*P. quinquefasciata*, *C. macrodon*; Family Serranidae (groupers)—*E. merra*, *E. fuscoguttatus*, *E. kohleri*, *E. hexagonatus*, *E. macrospilos*, *E. spilatus*, *V. louti*, *C. argus*, *C. urodelus*, *A. leucogrammicus*, *P. truncatus*; Family Pseudochromidae—*P. melas*, *P. nigricans*; Family Leiognathidae (silver perch)—*G. argyreus*; Family Pempheridae (sweepers)—*P. oualensis*; Family Lutjanidae (snappers)—*L. monostigmus*, *L. bohar*, *L. vitta*, *L. vaigiensis*, *L. gibbus*, *G. griseus*, *L. microdon*, *G. aureolineatus*; Family Sparidae (snappers)—*M. grandoculis*; Family Mullidae (goat fish)—*M. samoensis*, *P. trifasciatus*, *P. barberinus*, *P. cyclostomus*, *U. arge*; Family Cirrhitidae (hawkfish)—*C. aprinus*; Family Chaetodontidae (butterfly fish)—*C. auriga*; Family Scorpaenidae (scorpion fish)—*S. parvipinnis*, *S. gibbosa*, *S. verrucosa*; Family Platycephalidae (flatheads)—*Thysanophrys* sp.; Family Pomacentridae (damselfishes)—*P. pavo*, *P. vaiuli*, *A. sordidus*, *A. saxatilis*, *A. laerymatus*, *A. glaucus*, *A. leucopomus*; Family Labridae (wrasses)—*H. melapterus*, *C. gaimardi*, *C. trilobatus*, *C. chlorourus*, *P. hexataenia*, *T. lutescens*, *T. quinquevittata*, *T. umbrostigma*, *M. pardalis*, *M. meleagris*, *H. margaritaceus*, *H. trimaculatus*, *H. hoeveni*, *H. hortulanus*, *H. marginatus*, *Stethojulis* sp., *S. axillaris*; Family Gobiidae (gobies)—*B. f. fuscus*, *G. ornatus*, *G. anjerensis*; Family Eleotridae (sleepers)—*V. violifera*, *V. strigata*; Family Microdesmidae—*P. grandoculis*; Family Parapercidae (sand perch)—*P. cephalopunctatus*, *P. clathrata*; Family Blenniidae (blennies)—*A. taeniatus*, *C. sebae*, *I. paulus*; Family Brotulidae—*D. ihuocoeteoides*; Family Balistidae (trigger fish)—*B. viridescens*, *B. undulatus*, *P. fuscus*, *B. rectangulus*, *R. aculeatus*, *P. flavimarginatus*; Family Monacanthidae (file fish)—*A. carolae*; Family Ostracionidae (trunk fish)—*O. cubicus*; Family Tetraodontidae (puffers)—*A. hispidus*, *A. mappa*, *Arothron* sp.; Family Canthigasteridae (sharp-backed puffer)—*C. solandri*; Family Diodontidae (spiny puffer)—*D. hystrix*.

Carnivores on Mid-water Fauna

Family Carcharhinidae (gray sharks)—*C. melanopterus*, *C. menisorrhah*; Family Triakidae (smooth dogfishes)—*T. obesus*; Family Belonidae (needle fish)—*S. incisa*, *S. gigantea*; Family Holocentridae (squirrel fish)—*M. berndti*, *M. microphthalmus*; Family Aulostomidae (trumpet fish)—*A. chinensis*; Family Fistulariidae (cornet fish)—*F. petimba*; Family Atherinidae (silversides)—*S. temmincki*; Family Carangidae (jacks)—*T. bailloni*, *C. f. jordani*, *C. melampygus*, *E. bipinnulatus*, *S. sanctipetri*; Family Serranidae (groupers)—*V. louti*, *P. leopardus*, *P. truncatus*; Family Lutjanidae (snappers)—*Lethrinus miniatus*, *Lutjanus monostigmus*, *Lut. bohar*, *Lut. vitta*, *A. virescens*; Family Blenniidae (blennies)—*A. taeniatus*; Family Scombridae (tunas)—*G. nuda*, *K. pelamis*, *E. a. yaito*; Family Sphyraenidae (barraudas)—*S. genie*.

Resident Roving Carnivores

Family Carcharhinidae (gray sharks)—*C. melanopterus*, *C. menisorrhah*; Family Triakidae (smooth dogfish)—*T. obesus*; Family Carangidae (jacks)—*C. f. jordani*,

C. melampygus; Family Serranidae (groupers)—*P. truncatus*, *P. leopardus*.

Transient Roving Carnivores

Family Carcharhinidae (gray sharks)—*C. melanopterus*, *C. menisorrhah*; Family Triakidae (smooth dogfish)—*T. obesus*; Family Carangidae (jacks)—*C. melampygus*, *E. bipinnulatus*; Family Serranidae (groupers)—*P. leopardus*; Family Lutjanidae (snappers)—*L. bohar*, *A. virescens*; Family Sphyraenidae (barraudas)—*S. genie*; Family Scombridae (tunas)—*G. nuda*, *K. pelamis*, *E. a. yaito*.

CORAL POLYP FEEDERS

Coelenterates, perhaps because of their nematocysts, do not enter into the food web as intermediate forms in most marine communities, and are rarely mentioned as an influential group of organisms in the complex of ecological affairs. However, in tropical coral reefs where luxuriant coral growth not only dominates the scene as regards providing the physical habitat of countless reef species, but also comprises a substantial portion of the total animal protoplasm present (Odum & Odum, 1955), it would be strange indeed if some provision were not made within the many niches to provide for direct utilization of this food resource.

Three distinct evolutionary trends in dentition among a few families of fish have adapted them for accepting a live coral diet. For example, some butterfly fish (Chaetodontidae) and the filefish, *Orymonacanthus*, have developed pointed, produced snouts with very small terminal mouths containing fine, incisiform, protruding teeth for biting off individual polyps above the level of the corallite. Other butterfly fish crop the polyps so closely that they scrape off the tips of the individual corallites, and parrot fish (Scaridae) have developed a strong, protruding beak of fused teeth with which they heavily scrape glomerate heads of coral, taking not only the polyps but biting deeply into the calcareous corallum as well. Other groups, particularly the trigger fish (Balistidae) and the puffers (Tetraodontidae) have developed very strong, heavy, protruding teeth (trigger fish) or have them fused into a beak as in the puffers with which the ends of ramose and cespitose coral heads (*Acropora*, *Pocillopora*, *Stylophora*) are broken off and ingested. The comparatively small amount of animal tissue in relation to the mass of skeletal material requires that such fish keep the gut well crammed with these broken tips nearly all the time.

The most important members characteristic of these three types of coral feeders are listed below:

Browsers on Coral Polyps

Family Chaetodontidae (butterfly fish)—*C. citrinellus*, *C. auriga*, *C. lunula*, *M. strigangulus*; Family Monacanthidae (file fish)—*O. longirostris*.

Grazers on Living Coral Heads

Family Chaetodontidae (butterfly fish)—*C. vagabundus*, *C. ehippium*, *C. citrinellus*; Family Scaridae (parrot fish)—*C. spinidens*, *S. sordidus*, *S. bicolor*; Unidentified scarids (?); Family Balistidae (trigger fish)—*B. undulatus*; Family Monacanthidae (file fish)—*A. carolae*.

Feeders on Branching Coral Tips

Family Balistidae (trigger fish)—*B. viridescens*, *B. undulatus*, *R. aculeatus*; Family Monacanthidae (file fish)—*A. carolae*; Family Tetraodontidae (puffers)—

A. nigropunctatus, *A. meleagris*, *A. hispidus*; Family *Canthigasteridae* (sharp-backed puffers)—*C. solandri*.

OMNIVORES

A large number of fish on Marshallese reefs have omnivorous habits, some of which are facultative omnivores and usually contain both plant and animal tissue in their digestive tracts, but do also, on occasion, take full meals of either plants or animals, whichever appears to be the most available. Another group are those fish which are primarily herbivores or primarily carnivores, but which incidentally delve into the opposite food realm, either by inadvertence through their foraging habits, or by design.

Among the facultative group, the damsel fishes (Pomacentridae), gobies (Gobiidae), trigger fish (Balistidae), and the puffers (Tetraodontidae) are the most important. Within the more incidental group the damsel fishes and parrot fishes appear to be the most important.

The lists below indicate the species examined which most clearly fall into the two categories:

Facultative Omnivores

Family Leiognathidae (silver perch)—*G. argyreus*; Family Chaetodontidae (butterfly fish)—*C. ephippium*, *C. auriga*; Family Pomacentridae (damsel fish)—*D. aruanus*, *A. sordidus*, *A. glaucus*, *A. leucopomus*; Family Labridae (wrasses)—*H. hoeveni*; Family Gobiidae (gobies)—*G. anjerensis*; Family Blenniidae (blennies)—*I. paulus*, *C. sebae*; Family Balistidae (trigger fish)—*B. undulatus*, *R. rectangulus*, *R. aculeatus*; Family Monacanthidae (file fish)—*A. carolae*; Family Ostracionidae (trunk fish)—*O. cubicus*; Family Tetraodontidae (puffers)—*A. hispidus*; Family Canthigasteridae (sharp-backed puffers)—*C. solandri*.

Incidental Omnivores

Family Chaetodontidae (butterfly fishes)—*C. citrinellus*; Family Pomacentridae (damsel fishes)—*P. vaiuli*, *A. saxatilis*, *A. lacrymatus*, *A. dicki*, *A. biocellatus*, *A. amabilis*; Family Scaridae (parrot fishes)—*C. spinidens*, *S. sordidus*, *S. bicolor*, Unid. *Scarus* sp.; Family Tetraodontidae (puffers)—*A. mappa*.

HABITAT GROUPS ON MARSHALLESE CORAL REEFS

Anyone visiting coral reefs in the Marshall Islands will at once recognize certain characteristic associations of fishes ecologically tied to particular habitats. To analyze these natural associations we have undertaken to depict by descriptions and illustrations their essential physical and biological features.

TIDEPOOL FAUNA

For purposes of describing tidepool life on Marshallese coral reefs we have divided our account into communities living in supratidal pools, above the mean high water mark, and intertidal pools in between the mean high water mark and the mean low water mark. The supratidal pools are only found on the boulder rampart fringing the windward and semi-windward shores where the waves at high tide splash water into pools in the consolidated beach rock. The intertidal pools are found abundantly on the inner half of the seaward reef flat on the windward and semi-windward shores of the atoll.

The physical conditions in both types of tidepools are far more varied than in habitats continually sub-

merged, as tidepools are exposed not only to very high insolation from the tropical sun, but subject also to frequent periods of intense rainfall during low tides when the water in the pools becomes greatly diluted. For example, three small tidepools sufficiently within the intertidal stratum to contain small fish at Arno Atoll were checked for temperature maxima during sunny periods as the tide receded. The uppermost pool examined was awash only during the highest reaches of the incoming tide, the pool examined midway within the intertidal zone was isolated as the tide receded about half way, whereas the lowermost pool examined was awash only during strong surges at extreme low tide. On one afternoon when the air temperature was 87°F, water in the highest pool was 106°F, in the middle pool 105°F, and in the lower pool 99°F. The lower pool had received two or three tidal washes just prior to taking the temperatures. Fish in the two higher pools (*Istiblennius edentulus*, *Bathygobius f. fuscus*) were still swimming about, but in the lower pool two convict surgeon fishes (*Acanthurus t. triostegus*) and one blenny (*I. edentulus*) had died.

On a second afternoon with an air temperature of 82°F the three pools had water temperatures of 106°F, 103°F, and 106°F. No fish were dead. On a third afternoon when the air temperature was 88°F the three pools had water temperatures of 102°F, 101°F, and 101°F. The considerable variation of water temperatures in relation to air temperatures appears to result directly from the amount of cloud cover in the period just preceding the observations. The fish species inhabiting the supratidal pools are: Family Muraenidae (moray eels)—*G. pictus*; Family Acanthuridae (surgeon fishes)—*A. t. triostegus*, juveniles; Family Pomacentridae (damsel fishes)—*A. sordidus*, *A. glaucus*; Family Gobiidae (gobies)—*B. f. fuscus*; Family Blenniidae (blennies)—*Istiblennius edentulus*, *I. lineatus*. These species are shown in characteristic locations and activities in Fig. 2.

Fish species characteristically inhabiting an intertidal pool are: Family Muraenidae (moray eels)—*G. pictus*; Family Pseudochromidae—*P. nigricans*; Family Acanthuridae (surgeon fish)—*A. t. triostegus*, half-grown; Family Pomacentridae (damsel fishes)—*A. sordidus*, *A. glaucus*; Family Gobiidae (gobies)—*B. f. fuscus*; Family Blenniidae (blennies)—*I. paulus*, *I. lineatus*, *I. edentulus*, *Rhabdoblennius snowi*. Fish species inhabiting intertidal pools are shown in Fig. 2 in characteristic locations and activities.

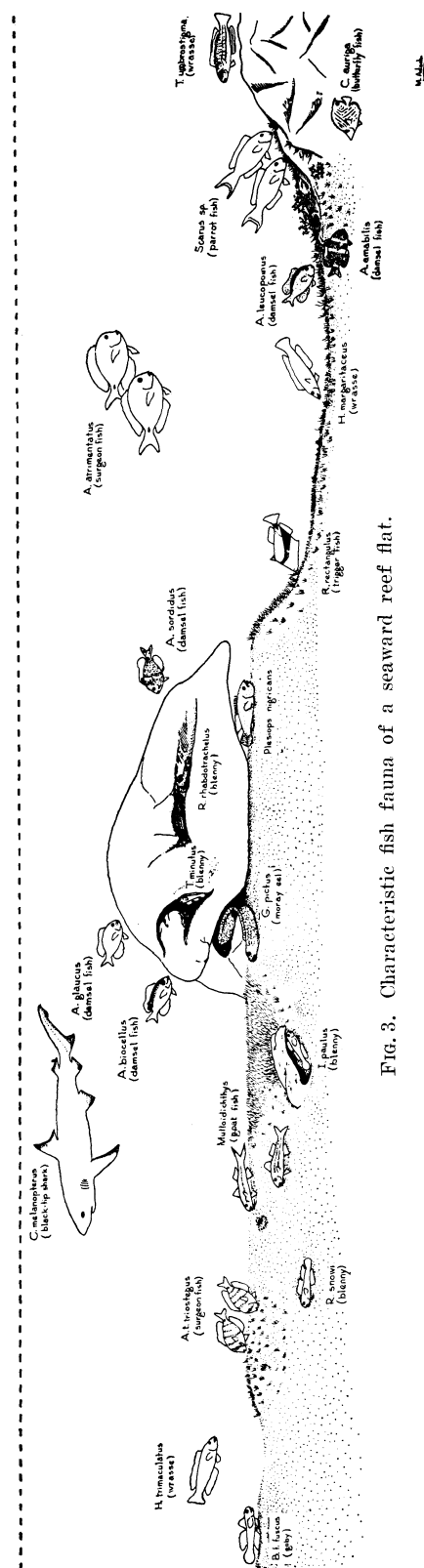
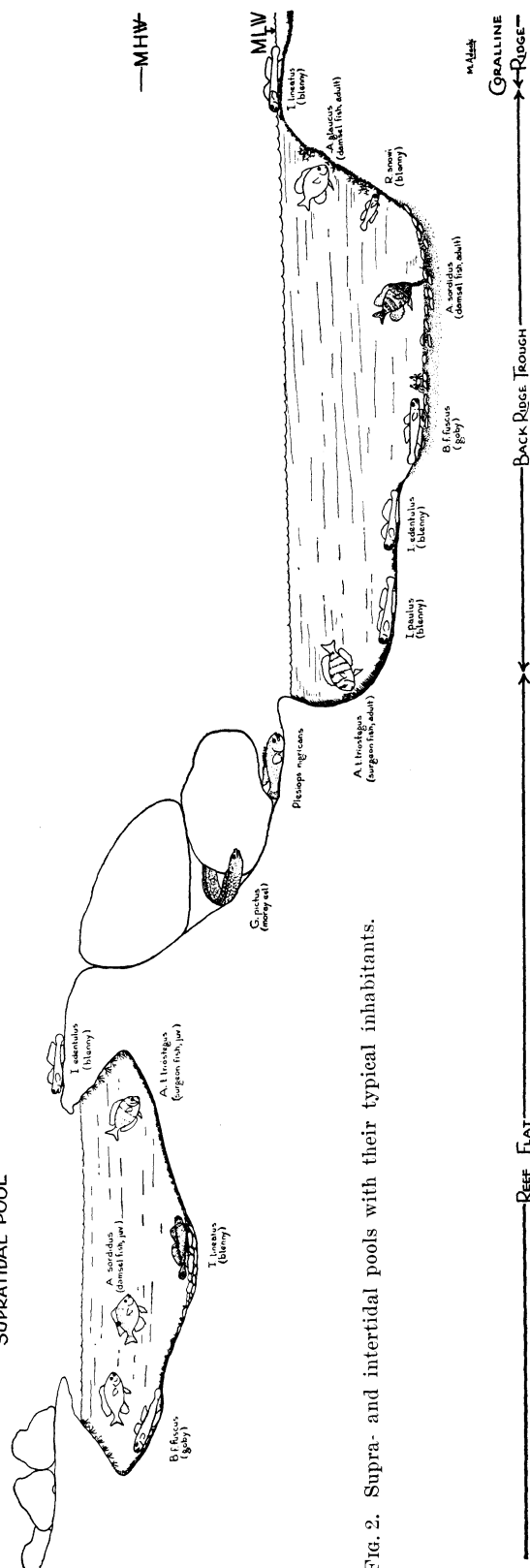
In all types of tidepools on Marshallese reefs the substrate contains a heavy layer of particulate matter intermixed with short algal filaments and precipitated detritus. Because of the abundance of food of these types, herbivores and detritus feeders predominate. In each instance, however, a few carnivores occur; the tide-flat moray, *G. pictus*, and the voracious pseudochromid, *P. nigricans*, being the most important. Supratidal pools frequently serve as comparatively safe rearing ponds for species such as the convict surgeon fish, *A. t. triostegus*. However, a considerable mortality occurs in this species when water temperatures range over 100°F.

SEAWARD REEF FLAT FAUNA

The outer half of the seaward reef flat slopes just perceptibly downward to the back ridge trough which is a slightly depressed area always covered with water. Immediately seaward of the back ridge trough is the elevated coralline ridge. A vertical section showing the elevations of the seaward reef flat at Arno Atoll in

INTERTIDAL POOL

SUPRATIDAL POOL



relation to mean sea level has been worked out and submitted for publication (Hiatt, in press).

The outer half of the seaward reef flat is always covered at mean sea level, and is exposed only on certain spring lows, and then only for a few minutes. Ordinarily, the sea swell is adequate to send waves of translation over it even when the tide is exceedingly low. The variations in salinity and temperature are far less than those characteristic for the inshore half of the reef flat.

During low water very little activity, except for the smaller organisms, is evident in this area of the reef. However, as soon as the tide rises sufficiently this region is actually inundated by a horde of larger fish, among them large schools of parrot fish, surgeon fish, goat fish, and small, widely ranging sharks. This intense activity ensues until the water recedes, and these roving types then move out and over the coralline ridge to await along the reef front for the next tidal rise.

The characteristic fishes of this habitat are shown in Fig. 3, and listed below: Family Carcharhinidae (gray sharks)—*C. melanopterus*; Family Muraenidae (moray eels)—*G. pictus*; Family Pseudochromidae—*P. nigricans*; Family Mullidae (goat fishes)—*M. samoensis*, *U. arge*; Family Chaetodontidae (butterfly fishes)—*C. auriga*; Family Acanthuridae (surgeon fishes)—*A. nigrofasciatus*, *A. t. triostegus*; Family Pomacentridae (damsel fishes)—*A. sordidus*, *A. glaucus*, *A. biocellatus*, *A. amabilis*, *A. leucopomus*; Family Labridae (wrasses)—*T. umbrostigma*, *H. margaritaceus*, *H. trimaculatus*; Family Scaridae (parrot fish)—Several unidentified species of *Scarus*; Family Gobiidae (gobies)—*B. f. fuscus*; Family Blenniidae (blennies)—*I. paulus*, *Rhabdoblennius rhabdotrachelus*; Family Tripterygiidae—*Tripterygion minutus*.

FAUNA OF THE SURF ZONE AND SURGE CHANNELS

The fish fauna of the outer reef edge and the surge channels, especially on leeward ocean reefs is so varied and complex that it defies adequate description and characterization. A view into one of these surge channels and out over the steep seaward slope is truly one of the most spectacular to be experienced by man. The reef edge and slope are almost solidly covered by over one hundred species of corals of all shapes and hues, and the density and diversity of the fish fauna is exceedingly great. We have made a very feeble attempt at depicting such a scene in Fig. 4.

Because it is manifestly impractical to try to list the fish fauna of this zone, we have selected for presentation only those types most influential in this community. Their characteristic positions and activity are shown in the accompanying figure. Two species are so characteristic of the breaker zone, the sweeper, *Pempheris oualensis*, and the surgeon fish, *Acanthurus guttatus*, that they are here given special notation. *A. guttatus* particularly can be seen in large, fast-swimming schools in the white water of the breaking waves. The sweepers usually occupy positions near the head of shallow channels or just below the white water. The most important species in this habitat are listed below: Family Carcharhinidae (gray sharks)—*C. melanopterus*, *C. menisorrh*; Family Triakidae (smooth dogfishes)—*T. obesus*; Family Muraenidae (moray eels)—*G. javanicus*; Family Cirrhitidae (hawkfish)—*A. arcatus*, *P. forsteri*; Family Serranidae (groupers)—*E. merra*, *P. leopardus*, *P. truncatus*; Family Pseudochromidae—*P. tapeinosoma*; Family Lutjanidae (snappers)—*L. gibbus*; Family Sparidae

(snappers)—*M. grandoculis*; Family Acanthuridae (surgeon fishes)—*A. achilles*, *A. aliala*, *A. nigrofasciatus*, *A. lineatus*, *N. lituratus*, *N. unicornis*, *Z. veliferum*; Family Pomacentridae (damsel fishes)—*A. lacrymatus*; Family Labridae (wrasses)—*H. margaritaceus*; Family Scaridae (parrot fishes)—*Scarus* sp. (several); Family Blenniidae (blennies)—*C. sebae*, *C. variolosus*; Family Balistidae (trigger fish)—*R. rectangulus*.

FISH FAUNA ASSOCIATED WITH ALGAE

Earlier in this report the algal feeders were considered from the standpoint of their actual foraging methods. In this section we shall consider the herbivores as regards their associations with different types of algae growing on both rocky and compacted sandy substrates. The important herbivores in this reef association are shown in their characteristic localities and activities in Fig. 5.

Among the algal feeders are a few which scoop up the surface benthos, sift it to remove the unicellular algae with some admixed detritus for ingestion, and reject the remainder either through the mouth or gill opening. The mullets, *N. chaptali* and *C. crenilabis*, feed entirely in this manner, and can be seen in schools sucking up and sifting the fine benthos on the sandy bottoms.

A rather large group of surgeon fish feeds exclusively on the short filaments of algae growing on the compacted sand. To do this schools of them literally stand on their heads and busily graze on the bottom. Species such as *A. mata*, *A. xanthopterus*, *A. gahhm*, and *A. olivaceus* forage in this manner.

Most herbivores browse or graze algae growing on rocky surfaces. Some browse only the larger seaweeds, while many browse and graze the shorter filaments. Among the most important browsers which bite off fronds and filaments from algae growing on rocky surfaces are: rabbit fish (Siganidae), pilot fish (Kyphosidae), butterfly fish (Chaetodontidae), surgeon fish (Acanthuridae), damsel fish (Pomacentridae), and trigger fish (Balistidae). The kinds of algae taken are shown diagrammatically in Fig. 5 and the species are listed in detail under the section on algal feeders considered earlier in this paper.

FISH FAUNA ASSOCIATED WITH LEDGES AND CAVERNS

A swimmer approaching a coral bed is immediately aware of, and greatly impressed by, the large number and variety of fish he sees. However, only a small part of the fish fauna is then in evidence, because most are concealed under rocks or ledges, or are hiding in holes and caverns in the coral itself. It is only after intense searching that some of these species become evident, and only after the area has been poisoned with rotenone that the full impact of the concealed species is felt. No special figure was prepared to show only these species as many of them are visible in our illustrations of other reef situations.

A very large group which remains concealed in coral patches and in rubble is the moray eels. These are primarily ledge and hole dwellers. Another important segment of the fish fauna which inhabits caverns is the squirrel fishes (Holocentridae) which never venture far from their caverns, and usually are seen only in them. They are curious about swimmers, however, and if one watches the opening of a cavern he will see them come up, usually one at a time, take a good look at the swimmer and then disappear again. Also living



FIG. 4. The fish fauna of a surge channel and the surf zone.

in holes in the coral and in small caverns are many species of cardinal fish (Apogonidae) which frequently hover inside caverns in exceedingly large schools, only venturing out if there is no danger foreseen.

Under ledges and pedestal coral colonies live solitary demersal groupers (Serranidae) of many species, but with similar lying-in-wait foraging techniques, having only the head extended from beneath cover. Although several species of snappers (Lutjanidae) characteristically hide under large coral heads or in ledges, they are not demersal and do not lie in wait for prey. Instead, they forage just a short distance away from their refuge.

A number of the butterfly fishes (Chaetodontidae) also frequent caverns or stay below large coral heads a good deal of the time. Two species holding great attraction for, as well as commanding great respect from, reef biologists are the turkey or lion fish, *Pterois volitans* and *P. radiata*. These venomous species, having greatly elaborated fins and striking coloration, seclude themselves under ledges or corals and have never been seen by us in an exposed situation.

Observations made on the reefs, coupled with a check on the proportion of empty stomachs in fishes caught during the day, indicate that certain of these ledge and cavern dwellers probably have nocturnal foraging proclivities. These species are: Family Muraenidae (moray eels)—*G. pictus*, *G. flavimarginatus*, *G. undulatus*, *G. fimbriatus*; Family Holocentridae (squirrel fishes)—*M. berndti*, *M. microphthalmus*, *H. sammara*, *H. lacteoguttatus*, *H. microstomus*, *H. laevis*, *H. diadema*, *H. spinifer*.

Ledge and cavern dwellers known to be day foragers are: Family Muraenidae (moray eels)—*E. zebra*, *E. leucotaenia*, *E. polyzona*, *U. xanthopterus*, *R. marshallensis*, *G. javanicus*, *G. buroensis*, *G. margaritophorus*; Family Congridae (conger eels)—*C. noordzieki*; Family Apogonidae (cardinal fishes)—*A. novemfasciatus*, *A. snyderi*, *A. exostigma*, *A. nigrofasciatus*, *A. novaeguineae*, *A. erythrinus*, *P. quinquelineata*; Family Priacanthidae (big eyes)—*P. cruentatus*; Family Serranidae (groupers)—*E. merra*, *E. fuscoquittatus*, *E. kohleri*, *E. hexagonatus*, *E. macrospilus*, *E. spilatus*, *V. louti*, *C. argus*, *C. urodolus*, *A. leucogrammicus*, *P. truncatus*; Family Pempheridae (sweepers)—*P. ovalensis*; Family Lutjanidae (snappers)—*L. monostigmus*, *L. vitta*, *L. vaigiensis*, *L. gibbus*; Family Chaetodontidae (butterfly fish)—*C. vagabundus*, *C. ephippium*, *C. auriga*, *C. lunula*, *C. flavissimus*, *M. strigangulus*; Family Acanthuridae (surgeon fishes)—*C. striatus*, *A. mata*; Family Scorpaenidae (scorpion fishes)—*P. radiata*, *P. volitans*; Family Bratulidae—*D. iluocoeteoides*.

FISH FAUNA ASSOCIATED WITH MID-WATER AND SURFACE COMMUNITIES

Surface and mid-water communities are comparatively distinct, although some larger carnivores range rather widely and enter both areas on occasion. Surface communities are composed primarily of minute zooplankton, larger zooplankton, small plankton-feeding fish, (the round herring, *S. delicatulus*, and silversides, *A. ovalaua* and *P. pinguis*), larger macroplankton feeding fish such as the half-beaks (Hemiramphidae), trumpet fish (Aulostomidae), cornet fish (Fistulariidae), and fish-eating carnivores such as needle fish (Belonidae), tunas (Scombridae), barracuda (Sphyraenidae), and rainbow runner (Carangidae).

In mid-water a number of large, hovering groupers (Serranidae) and snappers (Lutjanidae) occur just above the bottom, and several species of more rapidly swimming roving carnivores such as sharks (Carcharhinidae and Triakidae), jacks (Carangidae), and snappers (Lutjanidae) are usually always present in quiet waters on all reefs. Fig. 6 depicts the important species engaging in their usual activities in the characteristic habitat.

The important species in the surface community are listed below: Family Mobulidae (manta rays)—*M. alfredi*; Family Dussumieridae (round herrings)—*S. delicatulus*; Family Belonidae (needle fishes)—*S. incisa*, *S. gigantea*; Family Hemiramphidae (half-beaks)—*H. affinis*, *H. laticeps*; Family Atherinidae (silversides)—*A. ovalaua*, *P. pinguis*; Family Scombridae (tunas)—*G. nuda*, *K. pelamis*, *E. a. yaito*; Family Sphyraenidae (barracuda)—*S. genie*; Family Carangidae—*S. sanctipetri*.

The important species in the mid-water community are the following: Family Carcharhinidae (gray sharks)—*C. melanopterus*, *C. menisorrhah*; Family Triakidae (smooth dogfishes)—*T. obesus*; Family Holocentridae (squirrel fishes)—*M. berndti*, *M. microphthalmus*; Family Aulostomidae (trumpet fish)—*A. chinensis*; Family Fistulariidae—*F. petimba*; Family Atherinidae (silversides)—*S. temmincki*; Family Scombridae (tunas)—*G. nuda*, *K. pelamis*, *E. a. yaito*; Family Sphyraenidae (barracuda)—*S. genie*; Family Carangidae (jacks)—*T. bailloni*, *C. f. jordani*, *C. melampygus*, *S. sanctipetri*, *E. bipinnulatus*; Family Serranidae (groupers)—*V. louti*, *P. leopardus*, *P. truncatus*; Family Lutjanidae (snappers)—*L. monostigmus*, *L. bohar*, *L. vitta*, *A. virescens*, *L. miniatus*.

FISH FAUNA ASSOCIATED WITH GLOMERATE CORAL HEADS

Because glomerate coral heads are generally devoid of interstices in which small organisms can hide, such heads are visited only by fish species intent upon browsing or grazing coral polyps. Most glomerate heads (*Porites*, *Astreopora*, *Coscinaraea*, *Cyphastrea*, *Goniastrea*, *Leptastrea*, *Pavona*) on luxuriant coral reefs are marred by paired tooth scrapings as a result of grazing on them by parrot fishes, trigger fishes, and others. Frequently such tooth marks are exceedingly abundant, indicating that the turnover rate of corals and coral feeding fishes must be running rather close to maximum sustaining capacity.

Fishes which browse the polyps without cropping too closely and getting particles of the calcareous corallite and corallum belong mostly to the family Chaetodontidae (butterfly fish). The most important grazers are the parrot fishes (Scaridae), the trigger fishes (Balistidae), and the puffers (Tetraodontidae).

Fig. 7 depicts the fish activity around a glomerate coral head. The significant species associated with such coral heads, all grazers or browsers except the pipe fish which merely hunt for small crustaceans on the surface of the head, are listed below: Family Syngnathidae (pipe fishes)—*C. i. waiti*, *C. f. conspicillatus*; Family Chaetodontidae (butterfly fishes)—*C. vagabundus*, *C. ephippium*, *C. citrinellus*, *C. auriga*, *C. lunula*, *M. strigangulus*; Family Scaridae—*C. spinidens*, *S. sordidus*, *S. bicolor*, *Scarus* sp. (7 unid. species); Family Balistidae (trigger fish)—*B. undulatus*; Family Tetraodontidae (puffers)—*A. meleagris*.

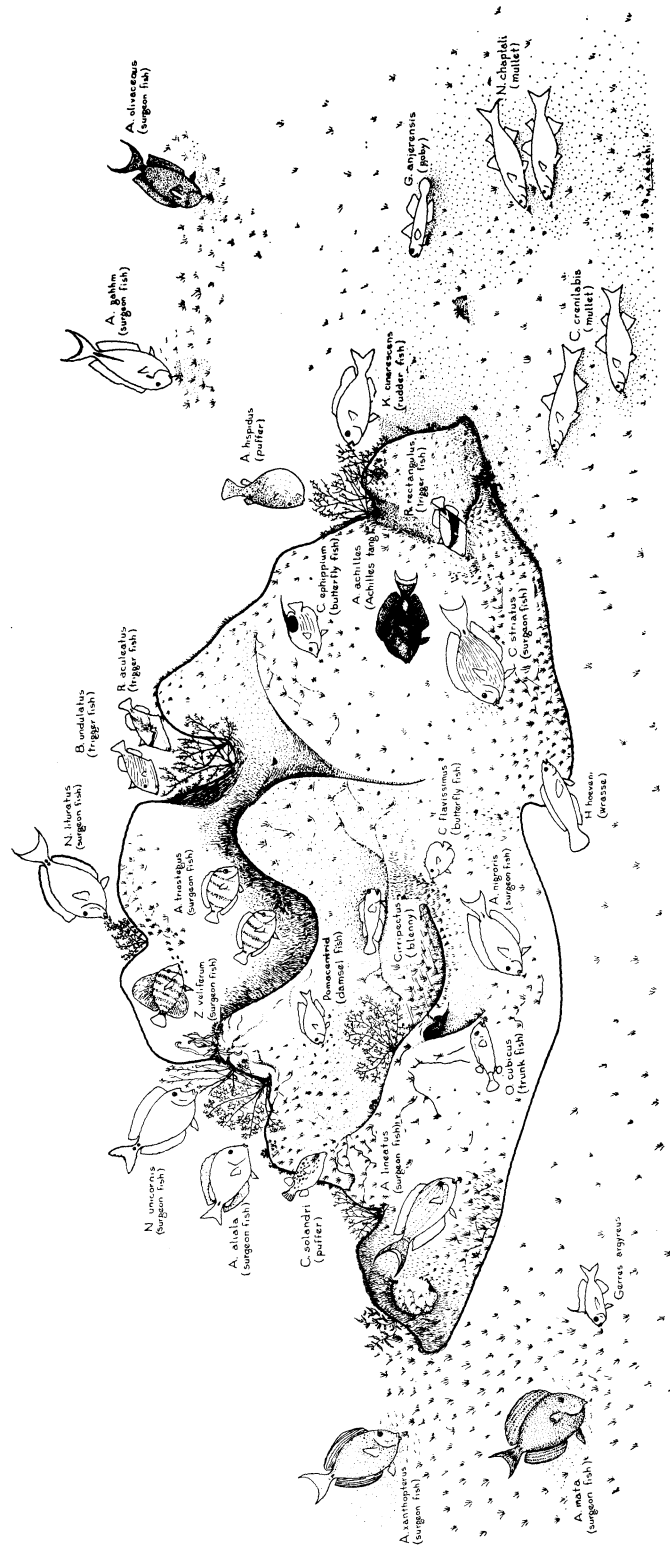


FIG. 5. Herbivorous fish in characteristic feeding attitudes.

FISH FAUNA ASSOCIATED WITH RAMOSE CORALS
AND THEIR DEAD BASES

An abundant fauna and flora are associated with branching or ramose types of coral heads. Not only is the coral head itself (polyps and contained zooxanthellae together with the filamentous algae living in the skeleton) almost a wholly contained ecological unit as stated by Odum & Odum (1955), but if we include the animal populations intimately associated with a branching head, it is even more complete as a contained ecological unit, and would justify community status by itself. Aside from the coral tissues themselves, there are among the fish associated with a single ramose head herbivores, carnivores, and omnivores. When we include the plethora of invertebrate types the community becomes more complex and complete. No doubt, a careful study of the microflora would reveal that it contains an adequate population of reducers too!

We have depicted the more important life about two types of ramose corals in Fig. 8. Comparatively few organisms are found in the interstices of the pedestal colonies of ramose corals because of their more exposed aspect. However, a number of species take refuge beneath the explanate head, and a large number of coral polyp feeders find such heads attractive because the branchlets are easily broken off, and, for some species, the terminal polyps are especially vulnerable for cropping.

In the ramose and cespitose heads with long branches, the interstices are attractive places of refuge for small crabs, shrimps, polychaetes, clams, and fishes. A number of highly carnivorous fish live within the interstices (*Gobiodon* spp., *Paragobiodon* spp., *Caracanthus* spp.) and do not venture outside the head. Other fishes such as the damsel fishes, *Dascyllus aruanus*, *Chromis caeruleus*, and *C. atripectoralis*, use the interstices only for protection, and swarm about just outside the head feeding on the abundant plankters. A number of carnivores such as the wrasses, *Gomphosus varius*, and *Epibulus insidiator*, and the butterfly fish, *Forcipiger longirostris*, have snouts either highly protractile or very elongate for probing deeply into the interstices in search of prey. Other wrasses constantly poke about amongst the branches searching for small crustaceans within reach.

On the bases of most of these heads algal filaments grow as a thin veneer. A number of herbivorous and omnivorous species graze and browse this material.

The following species are important members of the community of organisms associated with ramose coral heads:

Herbivores

Family Chaetodontidae (butterfly fishes)—*C. reticulatus*, *C. flavissimus*; Family Pomacentridae (damsel fishes)—*A. dicki*.

Carnivores

Family Muraenidae (moray eels)—*U. xanthopterus*, *R. marshallensis*, *G. buroensis*, *G. margaritophorus*, *G. fimbriatus*; Family Holocentridae (squirrel fishes)—*H. sammara*, *H. microstomus*, *H. laevis*, *H. diadema*, *H. spinifer*; Family Syngnathidae (pipefishes)—*C. i. waitei*, *C. f. conspicillatus*; Family Apogonidae (cardinal fishes)—*A. novemfasciatus*, *A. snyderi*, *A. exostigma*, *A. nigrofasciatus*, *A. novaeguineae*, *A. erythrinus*, *G. philippinus*, *P. quinquelineata*; Family Serranidae (groupers)—*C. urodelus*; Family Pseudochromidae—*P.*

melas, *P. polyacantha*, *P. tapeinosoma*; Family Pemphe-
ridae (sweepers)—*P. oualensis*; Family Lutjanidae
(snappers)—*S. cancellatus*; Family Cirrhitidae (hawk-
fish)—*A. arcatus*, *P. forsteri*, *C. aprinus*, *C. pinnulatus*;
Family Scorpaenidae (scorpion fishes)—*S. parvipinnis*;
Family Caracanthidae—*C. unipinnus*; Family Pomacen-
tridae (damsel fishes)—*C. caeruleus*, *C. atripectoralis*;
Family Labridae (wrasses)—*G. varius*, *C. oxycephalus*,
T. hardwickei, *T. quinquevittata*, *E. insidiator*, *H. mar-
garitaceus*, *N. taeniourus*; Family Gobiidae (gobies)—
G. rivulatus, *G. erythropsilus*, *P. echinocephalus*; Family
Balistidae (trigger fish)—*B. viridescens*; Family
Monacanthidae (file fishes)—*O. longirostris*; Family
Tetraodontidae (puffers)—*A. nigropunctatus*, *A. mele-
agris*.

Omnivores

Family Chaetodontidae (butterfly fishes)—*C. citrinel-
lus*, *C. auriga*; Family Pomacentridae (damsel fish)—
D. aruanus; Family Labridae (wrasses)—*T. lutescens*,
S. axillaris; Family Balistidae (trigger fish)—*R. aculea-
tus*, *B. undulatus*; Family Monacanthidae (file fish)—
A. carolae; Family Tetraodontidae (puffers)—*A. his-
pidus*; Family Canthigasteridae (sharp-backed puffers)
—*C. solandri*.

TROPHIC LEVELS

One of the prime objectives of this study was to determine to which trophic levels the more important fish species belonged. Moreover, among reef ecologists there has always been some question as to reasons why such an apparently large fish population could exist when the primary producers in evidence seemed to be far less abundant than they should be on theoretical grounds, as interpreted from a pyramid of biomass based on the standing crop. This latter question has been solved to a great extent at least by the brilliant research of Odum & Odum (1955) on Eniwetok reefs. There they found that in the living coral heads themselves the zooxanthellae contained in the tissues of polyps and, even more important, the filamentous algae growing in the pores of the inert skeleton in bands below the outer living animal tissue, actually made the coral head more plant than animal, i.e., more producer than consumer, by a ratio of about 3 to 1. In addition to the algae contained in coral heads, there is considerable filamentous algae in the sand, shingle or rubble, dead coral heads, and the porous reef floor, as well, of course, as in the algal mats and seaweed visible to the naked eye. As Odum & Odum (1955) point out, "From the standpoint of the entire reef ecosystem it does not matter how much food made by algae within the live coral head [or within porous rock, rubble, and sand] is used by coral animals [or other animals] directly. Only by considering the large amount of producer tissue in [these subsurface locations] it is possible to explain the great preponderance of organisms classed as animals."

The second important consideration in the balance sheet of the coral reef ecosystem is the fact that most of the fish protoplasm visible to a swimmer represents herbivorous types belonging to the second trophic level. Moreover, on a more quantitative basis, although admittedly rough, Odum & Odum (1955) found that among the fishes there was a striking predominance on a weight

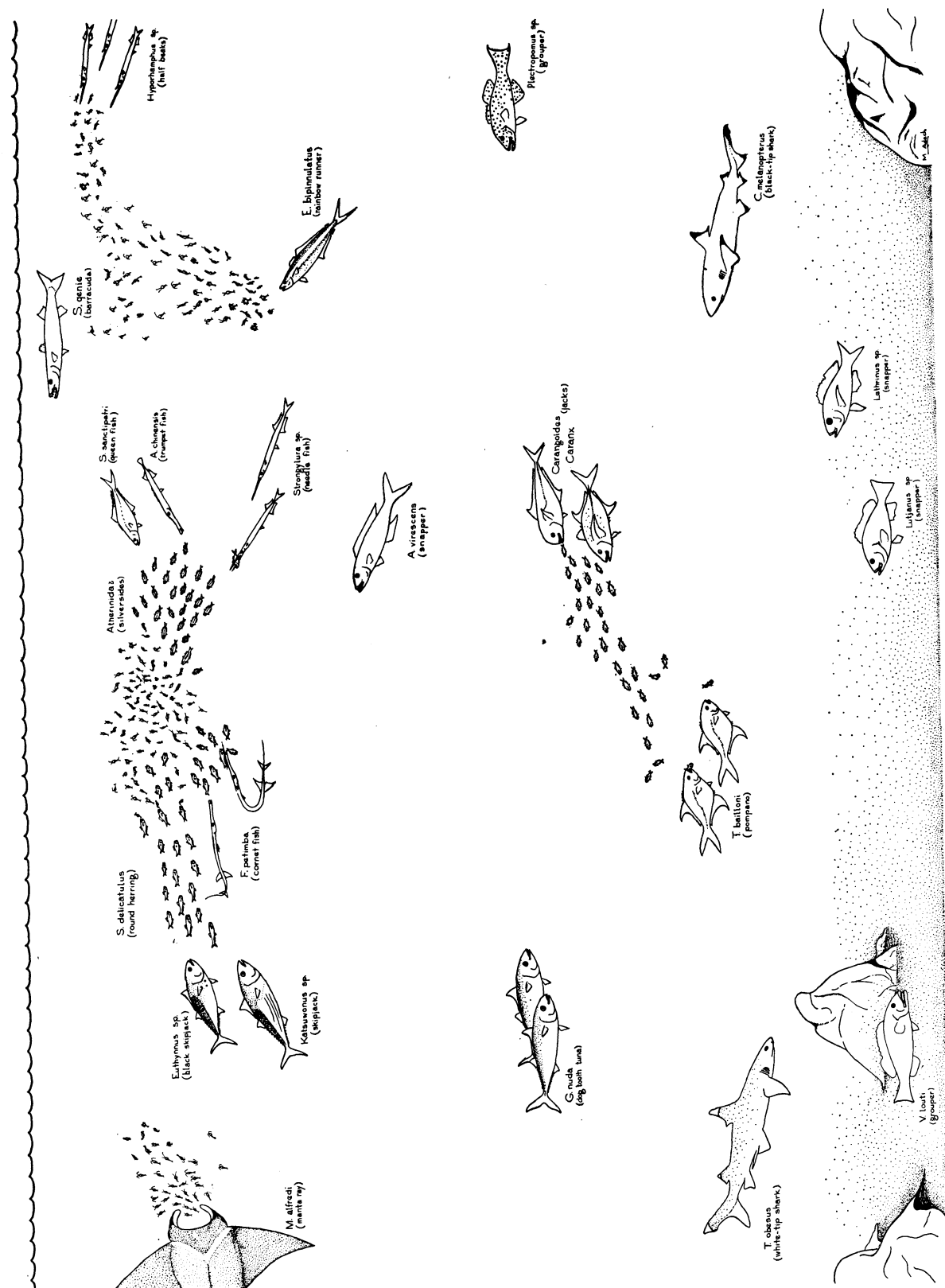


FIG. 6. The mid-water and surface community.

basis of herbivorous parrot fishes, surgeon fishes, damselfishes, and butterfly fishes in comparison to the wrasses, groupers, and other carnivores. The energetics of the system at this level are the most favorable in the entire food chain, regardless of the actual quantitative efficiency, since the herbivores are dependent upon the primary producers which, as in other ecosystems, have a much greater biomass than the carnivorous levels toward the apex of the pyramid.

Phylogenetically, certain interesting situations appear which are noteworthy. Our studies indicate that the more advanced and specialized fishes appear to be heading morphologically and physiologically toward the lower trophic levels where the stored energy in terms of food supply is in greater quantity. Note, for example, the foraging habits of the trigger fish (Balistidae), puffers (Tetraodontidae), etc., which have become omnivorous and frequently make entire meals on algae as well as on many little used invertebrates such as the sponges, coelenterates, echinoderms, and tunicates. Conversely, the most primitive fishes in the phylogenetic scale are exclusively carnivores, and usually so at the fourth or fifth trophic levels where comparatively little food is available. The more generalized species appear to fall mostly in the third and fourth trophic levels where a considerable amount of comparatively easy to get food items is available to them in the form of invertebrates or small fishes of the second and third trophic levels. The invertebrates comprise the greatest biomass of the second trophic level (Odum & Odum, 1955), and, although their detailed food habits are not accurately known, we are able to assign them arbitrarily to the second trophic level for the most part, although some comprise a portion of the third trophic level.

The fish families which comprise the bulk of the biomass at the second trophic level, surgeon fishes (Acanthuridae), damselfishes (Pomacentridae), and rabbit fishes (Siganidae) are rather highly evolved, specialized fishes also. The dental and other morphological modifications and physiological changes from the more primitive type fish are considerable, and these did not evolve in spite of the great mass of plant food available until comparatively lately as regards the evolutionary time scale of the group. It is still an enigma why the biomass of herbivorous fishes is so proportionately great on tropical reefs where larger seaweeds are not abundantly available, and so proportionately small along coastal shores in the temperate and arctic seas.

At the present time research on the primary producers of coral reef ecosystems in the Marshall Islands has reached a comparatively high level of understanding. The present studies should provide the framework for far greater knowledge at the higher trophic levels for the higher organisms, but there still remains to be known the role of the myriads of invertebrates which inhabit the reefs.

Below are listed the species comprising the several trophic levels on Marshallese reefs. It should be borne in mind that the trophic level into which a particular carnivore is placed frequently depends upon its growth stage. Many juvenile carnivores occupy a trophic level one or two levels below that eventually occupied as an adult. These changes have been taken into consideration when borne out by our analysis of their food and feeding habits.

First Trophic Level (Primary Producers)

Algae

Second Trophic Level (Primary Consumers; Herbivores)

Family Mugilidae (mullets)—*Crenimugil crenilabis*, *Neomyxus chaptali*; Family Leiognathidae (silver perch)—*Gerres argyreus*; Family Siganidae (rabbit fishes)—*Siganus rostratus*; Family Kyphosidae (pilot fish)—*Kyphosus cinerascens*; Family Chaetodontidae (butterfly fishes)—*Chaetodon auriga*, *C. ephippium*, *C. reticulatus*, *Centropyge flavissimus*; Family Acanthuridae (surgeon fishes)—*Acanthurus achilles*, *A. aliala*, *A. nigroris*, *A. xanthopterus*, *A. guttatus*, *A. lineatus*, *A. mata*, *A. gahm*, *A. olivaceus*, *A. t. triostegus*, *Ctenochaetus striatus*, *Naso lituratus*, *N. unicornis*, *Zebbrasoma veliferum*; Family Pomacentridae (damselfishes)—*Abudefduf amabilis*, *A. biocellatus*, *A. dicki*, *A. glaucus*, *A. lacrymatus*, *A. leucopomus*, *A. saxatilis*, *A. septemfasciatus*, *A. sordidus*, *Dascyllus aruanus*, *Pomacentrus albofasciatus*, *P. jenkinsi*, *P. nigricans*, *P. vaiuli*; Family Labridae (wrasses)—*Halichoeres hoeveni*; Family Blenniidae (blennies)—*Cirripectus sebae*, *C. variolosus*, *Exallias brevis*, *Istiblennius coronatus*, *I. paulus*; Family Balistidae (trigger fishes)—*Balistapus undulatus*, *Melichthys vidua*, *Rhinecanthus aculeatus*, *R. rectangulus*; Family Monacanthidae (file fishes)—*Amanes carolae*; Family Ostracionidae (trunk fishes)—*Ostracion cubicus*; Family Tetraodontidae (puffers)—*Arothron hispidus*; Family Canthigasteridae (sharp-backed puffers)—*Canthigaster solandri*.

Third Trophic Level (Secondary Consumers; Carnivores)

Family Mobulidae (manta rays)—*Manta alfredi*; Family Dussumieridae (round herrings)—*Spratelloides delicatulus*; Family Clupeidae (sardines)—*Harengula kunzei*; Family Ophichthidae (snake eels)—*Brachysomophis sauropsis*; Family Muraenidae (moray eels)—*Echidna leucotaenia*, *E. polyzona*, *E. zebra*, *Gymnothorax buroensis*, *G. flavimarginatus*, *G. javanicus*, *G. margaritophorus*, *G. pectli*, *Rabula marshallensis*, *Uropterygius xanthopterus*; Family Congridae (conger eels)—*Conger noordzieki*; Family Moringuidae (whip eels)—*Moringua macrochir*; Family Synodontidae (lizard fish)—*Synodus variegatus*; Family Hemiramphidae (half-beaks)—*Hyporhamphus affinis*, *H. laticeps*; Family Bothidae (flounders)—*Bothus mancus*; Family Holocentridae (squirrel fishes)—*Holocentrus diadema*, *H. lacteoguttatus*, *Holocentrus laevis*, *H. microstomus*, *H. spinifer*, *Myripristis berndti*, *M. micropthalmus*; Family Syngnathidae (pipefishes)—*Corythoichthys flavofasciatus*, *conspicillatus*, *C. intestinalis waitei*; Family Atherinidae (silversides)—*Pranncus pinguis*, *Allanetta ovalana*, *Stenatherina tcmmincki*; Family Polynemidae (threadfins)—*Polydactylus sexfilis*; Family Carangidae (jacks)—*Elaagatis bipinnulatus*, *Trachurops crumenophthalmus*; Family Apogonidae (cardinal fishes)—*Apogon erythrinus*, *A. exostigma*, *A. nigrofasciatus*, *A. novaequinae*, *A. snyderi*, *Cheilodipterus macrodon*, *Gymnapogon philippinus*; Family Serranidae (groupers)—*Cephalopholis argus*, *C. urodelus*, *Epinephelus hexagonatus*, *E. macrospilos*, *E. merra*, *E. spilatus*, *Variola louti*; Family Pseudochromidae—*Plesiops melas*, *P. nigricans*, *Pseudochromis tapeinosoma*, *Pseudogramma polyacanthus*; Family Pempheridae (sweepers)—*Pempheris ovalensis*; Family Lutjanidae (snappers)—*Gnathodentex aureolineatus*, *Gymnocranius griseus*, *Lutjanus gibbus*, *L. vaigiensis*, *L. vitta*, *Scolopsis caenellatus*; Family Leiognathidae (silver perch)—*Gerres argyreus*; Family

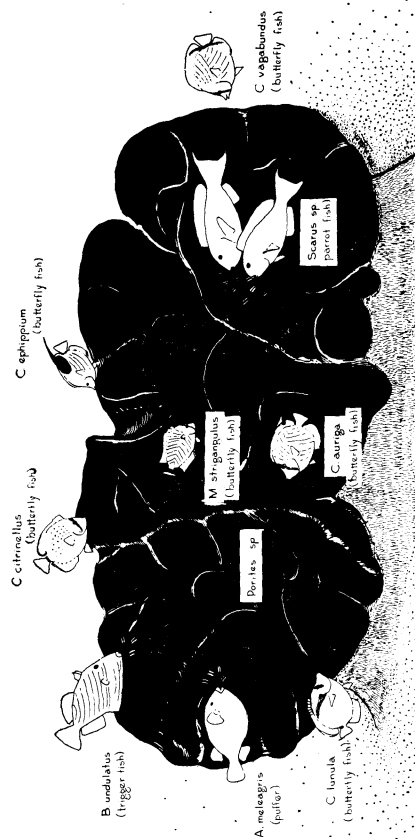


Fig. 7. Feeders upon glomerate corals.

Sparidae (snappers)—*Monotaxis grandoculis*; Family Mullidae (goat fishes)—*Mulloidichthys samoensis*, *Parupeneus barberinus*, *P. trifasciatus*, *Upeneus arge*; Family Cirrhitidae (hawkfish)—*Amblycirrhitus arcatus*, *Cirrhitichthys aprinus*, *Cirrhitus pinnulatus*; Family Chaetodontidae (butterfly fishes)—*Chaetodon auriga*; Family Scorpaenidae (scorpion fish)—*Pterois radiata*, *P. volitans*, *Scorpaenodes parvipinnis*; Family Caracanthidae—*Caracanthus unipinnus*; Family Platycephalidae (flatheads)—*Thysanophrys* sp.; Family Pomacentridae (damsel fish)—*Abudefduf glaucus*, *A. lacrymatus*, *A. leucopomus*, *A. saratilis*, *A. septemfasciatus*, *A. sordidus*, *Dascyllus aruanus*, *Chromis atripectoralis*, *C. caeruleus*, *Pomocentrus pavo*; Family Labridae (wrasses)—*Cheilinus chlorourus*, *C. oxycephalus*, *C. trilobatus*, *Coris angulata*, *C. gaimardi*, *Epibulus insidiator*, *Gomphosus varius*, *Halichoeres hoeveni*, *H. hortulanus*, *H. margaritaceus*, *H. marginatus*, *H. trimaculatus*, *Hemigymnus melapterus*, *Labroides dimidiatus*, *Macropharyngodon meleagris*, *M. pardalis*, *Novaculichthys taeniourus*, *Pseudocheilinus hexataenia*, *Stethojulis axillaris*, *Stethojulis* sp., *Thalassoma hardwicki*, *T. lucasanum marnae*, *T. lutescens*, *T. quinquevittata*, *T. umbrostigma*; Family Gobiidae (gobies)—*Bathygobius f. fuscus*, *Gnatholepis anjerensis*, *Gobiodon rivulatus*, *G. erythropsilus*, *Gobius ornatus*, *Paragobiodon echinocephalus*; Family Eleotridae (sleepers)—*Valenciennae strigata*, *V. violifera*; Family Microdesmidae—*Paragobioides grandoculis*; Family Parapercidae (sand perch)—*Parapercis cephalopunctatus*, *P. clathrata*; Family Blenniidae (blennies)—*Cirripectus sebae*, *Istiblennius paulus*; Family Brotulidae—*Dinematichthys ilucoeteoides*; Family Balistidae (trigger fish)—*Balistapus undulatus*, *Pseudobalistes flavimarginatus*, *P. fuscus*, *Rhinecanthus aculeatus*, *R. rec-*

tangulus; Family Ostracionidae (trunk fishes)—*Ostracion cubicus*; Family Tetraodontidae (puffers)—*Arothron hispidus*, *A. mappa*; Family Diodontidae (spiny puffers)—*Diodon hystrix*.

Fourth Trophic Level (Tertiary Consumers; Carnivores)

Family Carcharhinidae (gray sharks)—*Carcharhinus melanopterus*, *C. menisorrhah*; Family Triakidae (smooth dogfishes)—*Triaenodon obesus*; Family Muraenidae (moray eels)—*Gymnothorax javanicus*, *G. flavimarginatus*, *G. undulatus*; Family Synodontidae (lizard fishes)—*Synodus variegatus*, *Saurida gracilis*; Family Belontiidae (needle fishes)—*Strongylura incisa*, *S. gigantea*; Family Hemiramphidae (half-beaks)—*Hyporhamphus laticeps*; Family Bothidae (flounders)—*Bothus mancus*; Family Holocentridae (squirrel fishes)—*Holocentrus microstomus*; Family Aulostomidae (trumpet fishes)—*Aulostomus chinensis*; Family Fistulariidae (cornet fishes)—*Fistularia petimba*; Family Carangidae (jacks)—*Trachinotus bailloni*, *Carangoides ferdau jordanii*, *Caranx melampygus*; Family Apogonidae (cardinal fishes)—*Apogon novemfasciatus*, *Paramia quinque-lineata*; Family Priacanthidae (big eyes)—*Priacanthus cruentatus*; Family Serranidae (groupers)—*Epinephelus merra*, *E. fuscoguttatus*, *E. kohleri*, *E. hexagonatus*, *E. macrospilos*, *E. spilotos*, *Variola louti*, *Cephalopholis argus*, *Anypserodon leucogrammicus*, *Plectropomus truncatus*; Family Pseudochromidae—*Plesiops melas*; Family Pempheridae (sweepers)—*Pempheris ovalensis*; Family Lutjanidae (snappers)—*Lutjanus monostigmus*, *L. bohar*, *L. vitta*, *L. gibbus*, *Lethrinus microdon*; Family Mullidae (goat fishes)—*Parupeneus cyclostomus*; Family Cirrhitidae (hawkfishes)—*Paracirrhites forsteri*; Family Chaetodontidae (butterfly fishes)—*Chaetodon vaga-*

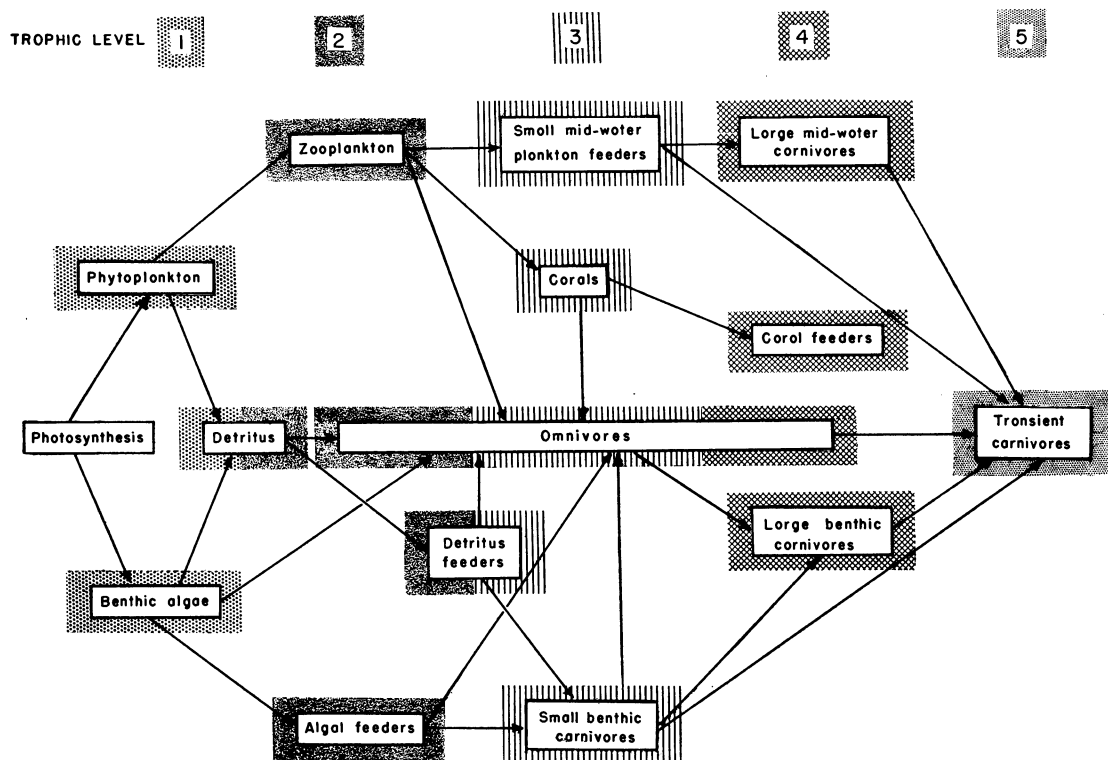


FIG. 9. The food web of Marshallese reefs.

bundus, *C. ephippium*, *C. citrinellus*, *C. auriga*, *C. lunula*, *Megaprotodon strigangulus*; Family Scorpaenidae (scorpion fishes)—*Scorpaenopsis gibbosa*, *Synanceja verrucosa*; Family Scaevidae (parrot fishes)—*Cryptotomus spinidens*, *Scarus sordidus*, *S. bicolor*; Family Paraperidae (sand perches)—*Paraperca cephalopunctatus*, *P. clathrata*; Family Blenniidae (blennies)—*Aspidontus taeniatus*; Family Balistidae (trigger fishes)—*Balistoides viridescens*, *Balistapus undulatus*; Family Monacanthidae (file fishes)—*Amanes carolae*, *Oxymonacanthus longirostris*; Family Tetraodontidae (puffers)—*Arothron nigropunctatus*, *A. meleagris*, *A. hispidus*, *Arothron* sp.

Fifth Trophic Level

(Quaternary Consumers; Roving Carnivores)

Family Carcharhinidae (gray sharks)—*Carcharhinus melanopterus*, *C. menisorrhynch*; Family Triakidae (smooth dogfishes)—*Triaenodon obesus*; Family Sphyracidae (barracudas)—*Sphyracna genie*; Family Scombridae (tunas)—*Gymnosarda nuda*, *Katsuwonus pelamis*, *Euthynnus affinis yaito*.

THE FOOD WEB

Figure 9 depicts in summarized form an overall picture of Marshallese food chains. For the sake of brevity various foraging activities have been combined under inclusive categories such as "algal feeders," etc. The reader is referred to earlier portions of the text for the specific constituents of these generalized categories. It is to be noted that only the major food pathways are shown in this food web, this being done for simplicity's sake because of the large number of species studied.

SUMMARY

1. Major gaps in our knowledge of coral reef ecology lie in our understanding of the taxonomic composition of the reef biota, the nature of biotic interaction between various trophic levels, and the specific community relationships obtaining in the several physiographic areas of a coral reef.

2. The present study attempts to fill these gaps by reporting upon the food, feeding habits, and ecological relationships of Marshallese fishes. The study was conducted at Bikini, Arno, and Eniwetok Atolls during the period 1947-1955. The geographical and physical aspects of these three atolls are described in detail along with descriptions of the various types of reefs encountered at each.

3. Fish examined for this study were obtained primarily by rotenone poisoning, with supplementary techniques (spears, hook and line, explosives) being used when warranted. Data recorded for each specimen were: standard length, sex, gonadal development, nature of alimentary tract, dentition, and type of food ingested. Over 2,000 individual stomachs were examined for the food study, and supplementing the laboratory work were hundreds of hours of underwater observation. We believe that combining the laboratory studies with the field observations enables us to present natural interpretations for the various ecological situations studied.

4. A discussion of food and feeding habits is presented for 56 families, 127 genera, and 233 species of Marshallese fishes, these figures representing more than half of the genera and somewhat less than half of the species known from the area. In addition to a discussion of each species, there are summaries by family and occasionally by genus.

5. The feeding habits of the species examined are categorized by foraging method as follows: algal feeders (consumers of unicellular algae, grazers, browsers, incidental algal feeders), detritus feeders, scavengers, zooplankton feeders, carnivores (feeders on fossorial, benthonic, and mid-water fauna, resident and transient roving carnivores), coral polyp feeders (browsers, grazers, and feeders on branching coral tips), and omnivores (facultative and incidental). Items frequently regarded as inedible (corals, echinoderms, sponges) were found to constitute significant portions of the diets of several fish groups.

6. The characteristic associations between fish and various coral reef habitats are illustrated and described for the following situations: supra- and intertidal pools, seaward reef flat, surf zone and surge channels, rocky and compacted sand substrates bearing algae, ledges and caverns, mid-water and surface communities, and glomerate and ramose coral heads and their bases.

7. The fishes considered are assigned to trophic levels as follows: primary consumers (herbivores), secondary and tertiary consumers (carnivores), and quaternary consumers (roving carnivores). Herbivorous species dominate Marshallese reefs because of favorable energetics between them and the great primary producer reef biomass. The more advanced fishes (trigger fish, puffers, surgeon fish, etc.) are typically members of the lower trophic levels, whereas the more primitive forms are carnivorous and frequently rank at the highest trophic levels.

8. A food web depicting energy flow in a coral reef ecosystem is presented.

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