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ECOLOGICAL RELATIONSHIPS IN HAWAIIAN AND  
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WITH EMPHASIS ON FOOD AND FEEDING HABITS.

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ECOLOGICAL RELATIONSHIPS IN HAWAIIAN AND  
JOHNSTON ISLAND ACANTHURIDAE (SURGEONFISHES) WITH  
EMPHASIS ON FOOD AND FEEDING HABITS

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By

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## ABSTRACT

Four genera and twenty species of the family Acanthuridae from Hawaii and Johnston Island are investigated for factors that might provide potential ecological separation of the species. The factors investigated are habitat "preference", foraging methods, food eaten, and possible morphological specialization for feeding.

On the basis of habitat "preference" the acanthurids may be divided into mid-water, sand patch, subsurge reef, and seaward reef or surge group forms. The habitats are defined in terms of acanthurid species composition and general physiography.

With regard to foraging methods, the Acanthuridae comprise zooplankton feeders, grazers, and browsers. The zooplankton feeders actively pursue and capture zooplankton components from the water column including copepods, decapod larvae, and the pelagic eggs of numerous animals. Grazers feed predominately on a calcareous substratum rich in diatoms and detritus. The browsers feed on multicellular benthic algae of two basic types based on size and morphology of the algae. One species complex feeds on leafy and fleshy algae such as Sargassum and Pocockiella

and the other feeds on filamentous algae such as Polysiphonia and Ectocarpus.

At the species level, several modifications in morphological characters related to feeding are found that suggest many of these fishes are able to handle their food in a different manner from other species. In several forms such characters as body shape, jaw position and structure, gill raker and pharyngeal tooth armament, gross structure and lining of the stomach, and length of the intestine showed possible correlation with foraging methods, food eaten, and in some cases habitat occupied.

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CHAPTER I  
INTRODUCTION

One of the largest groups of reef fishes in terms of species and biomass in the Hawaiian and Johnston Island marine environments is the family Acanthuridae. For the most part the species of this family are wide spread and frequently the most abundant of the diurnally active fishes in the littoral waters of these localities.

There are four genera and twenty species of these fishes many of which at first glance appear to be coexisting in identical habitats. This observation raises questions with regard to the well-known phenomenon of mutual exclusion attributed primarily to Gause (1934). Gause's Principle (Odum, 1953), as it is frequently referred to, notes that two or more closely related species cannot coexist in the same habitat or ecological niche.

The author has undertaken here an investigation of the species of the Acanthuridae to identify factors that might suggest ecological separation of these species.

Studies of this nature are virtually unknown in marine fishes. Some observations on the ecology of the Acanthuridae are found in the work of Randall (1955 a-d, 1956, 1961 a-c,

and 1965) and Hiatt and Strasburg (1960).

The primary emphasis of the investigation is on ecological separation by habitat, foraging methods, and food eaten. In addition, comparative studies of the gross mmorphology of the alimentary canals of the species have been undertaken as relevant parts of a study of feeding habits which might suggest possible "adaptations" in the feeding mechanisms of the species.

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## CHAPTER II

### HABITATS OCCUPIED BY ACANTHURIDS IN THE HAWAIIAN AND JOHNSTON ISLAND MARINE ENVIRONMENTS

#### GENERAL

If an observer swims from the shore out over the reef flat, marginal reef, and seaward slope areas it becomes apparent that species of the Acanthuridae are not distributed at random along such a transect. There are specific zones on the reef which are occupied by certain species of surgeonfishes. This observation is in agreement with those of Randall (1955a-d), Hiatt and Strasburg (1960), and Gosline (1965).

It should be pointed out here that the distribution of species in the various habitats is based on "centers of population." One should not be surprised to find a number of fishes that have been reported from the surge habitat, moving about in a reef-protected or subsurge area. There are then habitats in the Hawaiian and Johnston Island environments where one can predict the presence of particular acanthurid species. Randall (1961a) pointed out that these zones or habitats and the fishes that occupy them are more clearly defined around atolls than high island areas with less reef development. Hence the accuracy of these

predictions increases in the more precisely-zoned atoll environments. In Hawaii the differences between these habitats tend to be obscured as compared with the more atoll-like Johnston Island.

Before considering the individual habitats and fishes that occupy them it is useful to discuss Hawaii and Johnston Island geographically. Acanthurids within the scope of this study were observed and collected from stations on Oahu, Maui, Lanai, and Hawaii in the Hawaiian islands (Fig. 1) and from a series of stations around Johnston Island (Fig. 2).

The eastern Hawaiian islands (windward islands), including those mentioned above, are high volcanic islands. Coral reef platforms, barriers, and shallow water areas where coral dominates are not conspicuous (Gosline and Brock 1960). The three types of shoreline most frequently encountered are: steep, wave assaulted, lava cliffs and benches; beaches protected by fringing coral reef structures; and wave assaulted sand beaches often with submerged coral and basalt formations offshore.

Johnston Island is located about 450 miles southwest of the nearest of the Hawaiian Islands and is here considered

FIGURE 1. CHART OF HAWAIIAN ISLAND STATIONS

1-Kaena Pt.	11-Kaneohe Bay
2-Makaha	12-Kuloa Pt.
3-Waianae	13-Puuiki
Artificial Reef	14-Palaoa Pt.
4-Kewalo Basin	15-Puupehe Rock
5-Maunalua Bay	(Manele Bay)
6-Koko Head	16-Molokini
7-Hanauma Bay	17-La Perouse Bay
8-Makapuu Pt.	18-Honokaope Bay
9-Moku Manu	19-Kealakekua Bay
10-Kaneohe Outer Reef	



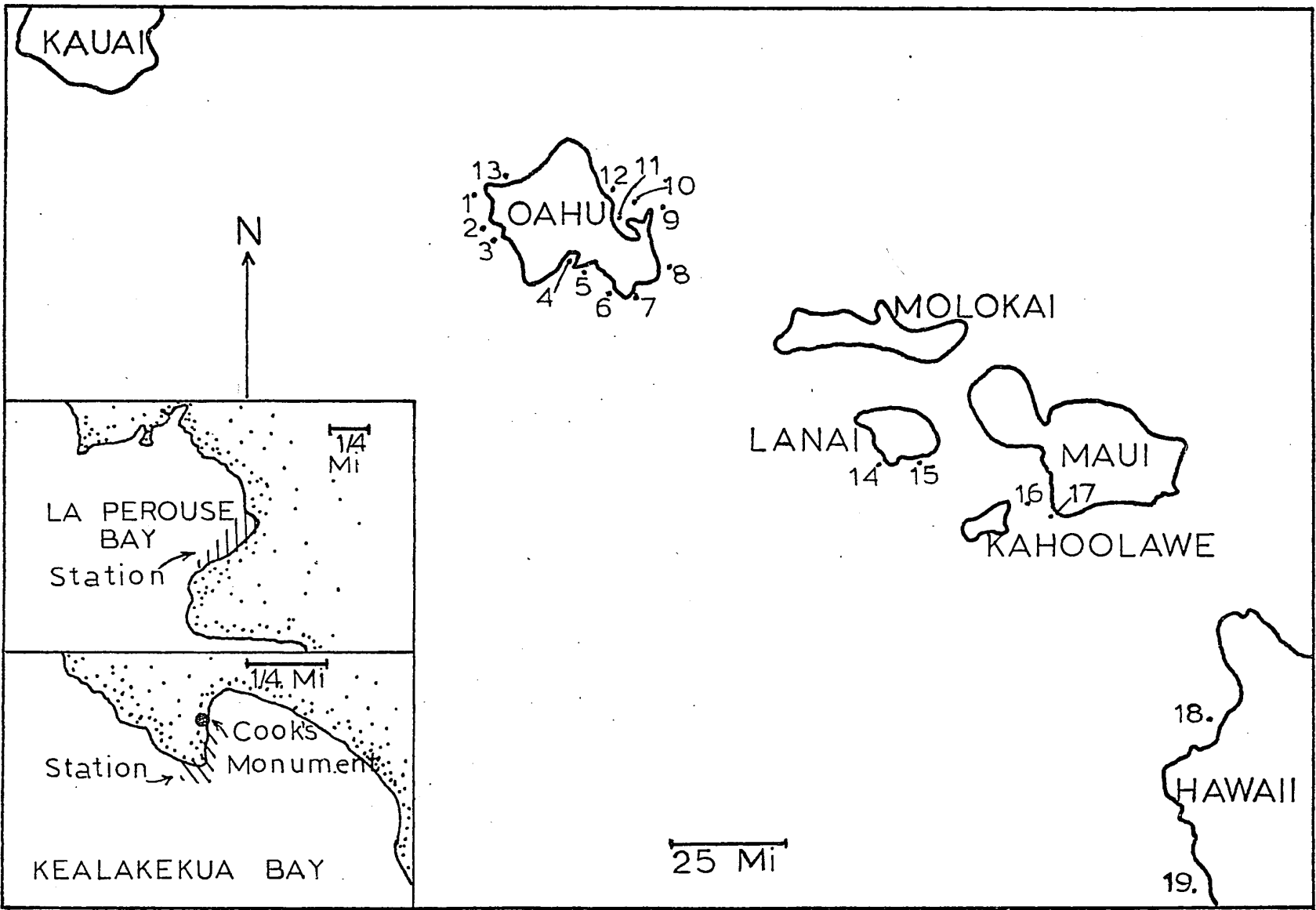
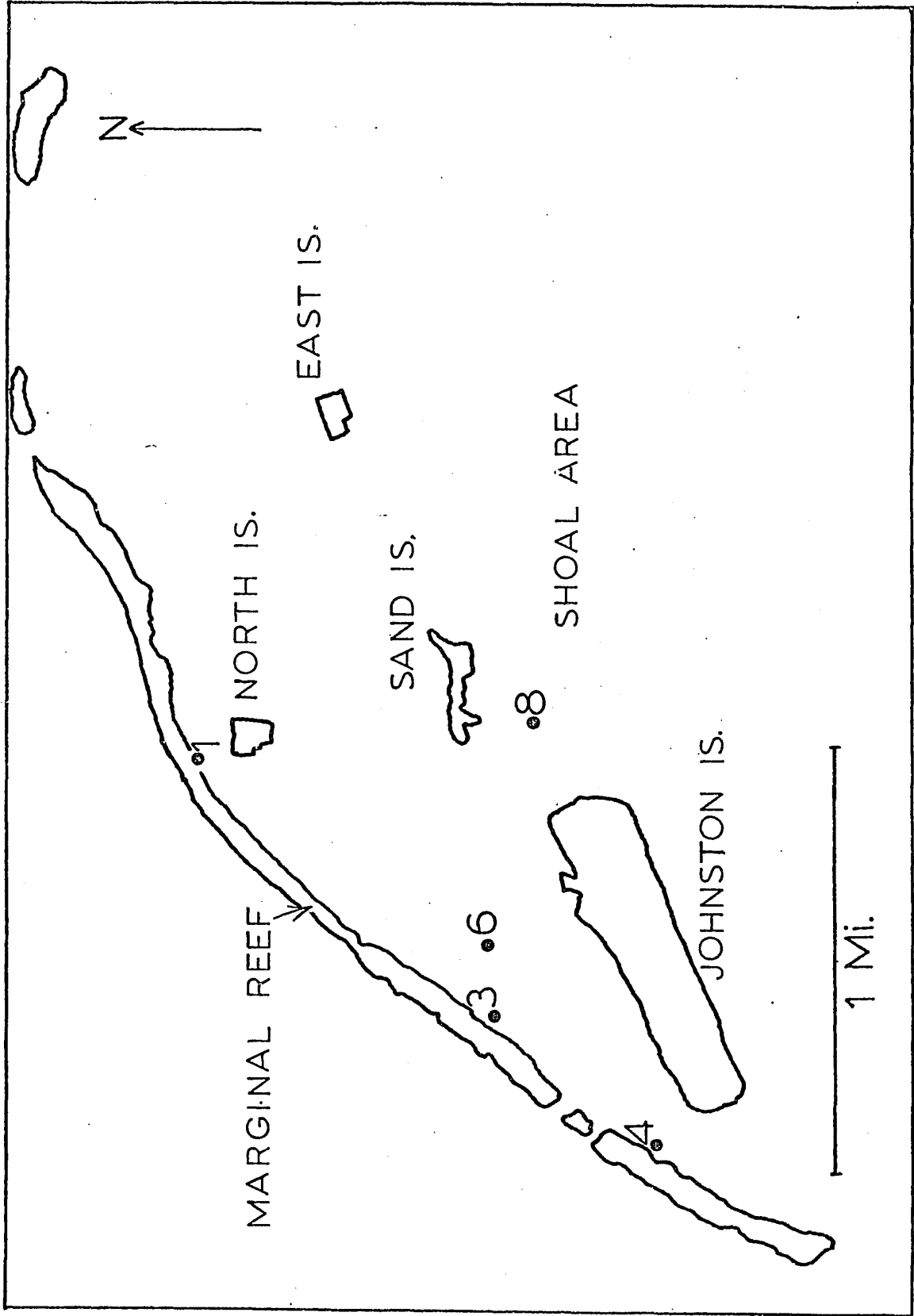


FIGURE 2. CHART OF JOHNSTON ISLAND STATIONS



part of the same faunal regime. It consists of an extensive coral reef area with its long axis oriented in a northeast-southwest direction (Fig. 2). The shoal is nine to ten miles long and seven to eight miles wide. The shoal area is divided into three major parts (Brock et al. 1965):

- 1) The marginal reef may be defined as a ridge of the coralline alga, Porolithon, that forms part of the northern and all of the northwestern boundary of the shoal.
- 2) The land masses are the natural islets of Johnston and Sand Island plus two recently man-made islets, North and East Islands.
- 3) The extensive submerged coral areas behind the marginal reef and surrounding the islets are generally quite shallow and the reef structure becomes less luxuriant as one proceeds downwind (in a southwesterly direction) from the marginal reef. The term "shoal" seems more applicable than "atoll" to Johnston Island. It differs from the "typical" atoll in lacking a deep central lagoon and a raised leeward reef. Wells (1954, in Brock et al. 1965) reported that Johnston Island like Yonge Reef (on the Great Barrier Reef) corresponds to a situation that would be produced if the Leeward half of an atoll was cut away. Though not exceedingly rich when compared with other central

Pacific faunal areas, Johnston Island has a much better developed coral growth than Hawaii.

All of the Acanthuridae found at Johnston Island are also found in Hawaii, except Ctenochaetus cyanoquttatus. The Hawaiian acanthurids that are as yet unknown from Johnston Island are Acanthurus dussumieri, A. leucopareius, A. nigrofuscus, A. thompsoni, A. xanthopterus, Naso brevirostris, and N. hexacanthus. Ctenochaetus striatus has been reported from Johnston Island (Halstead and Bunker, 1954), but this is possibly an error in identification. Similarly, Naso annulatus has been reported from Hawaii, but this record may also be in error (Gosline and Brock, 1960).

## MID-WATER HABITAT

GENERAL DESCRIPTION: The mid-water habitat is a sub-surge part of the Hawaiian environment (Fig. 3A). This habitat may be found near shore but is usually seaward of the surge or breaker zones. It sometimes occurs at considerable depths along the submerged island slopes. The fishes found in this habitat are usually associated with the water column itself rather than to the bottom community as is the case in all other acanthurids studied.

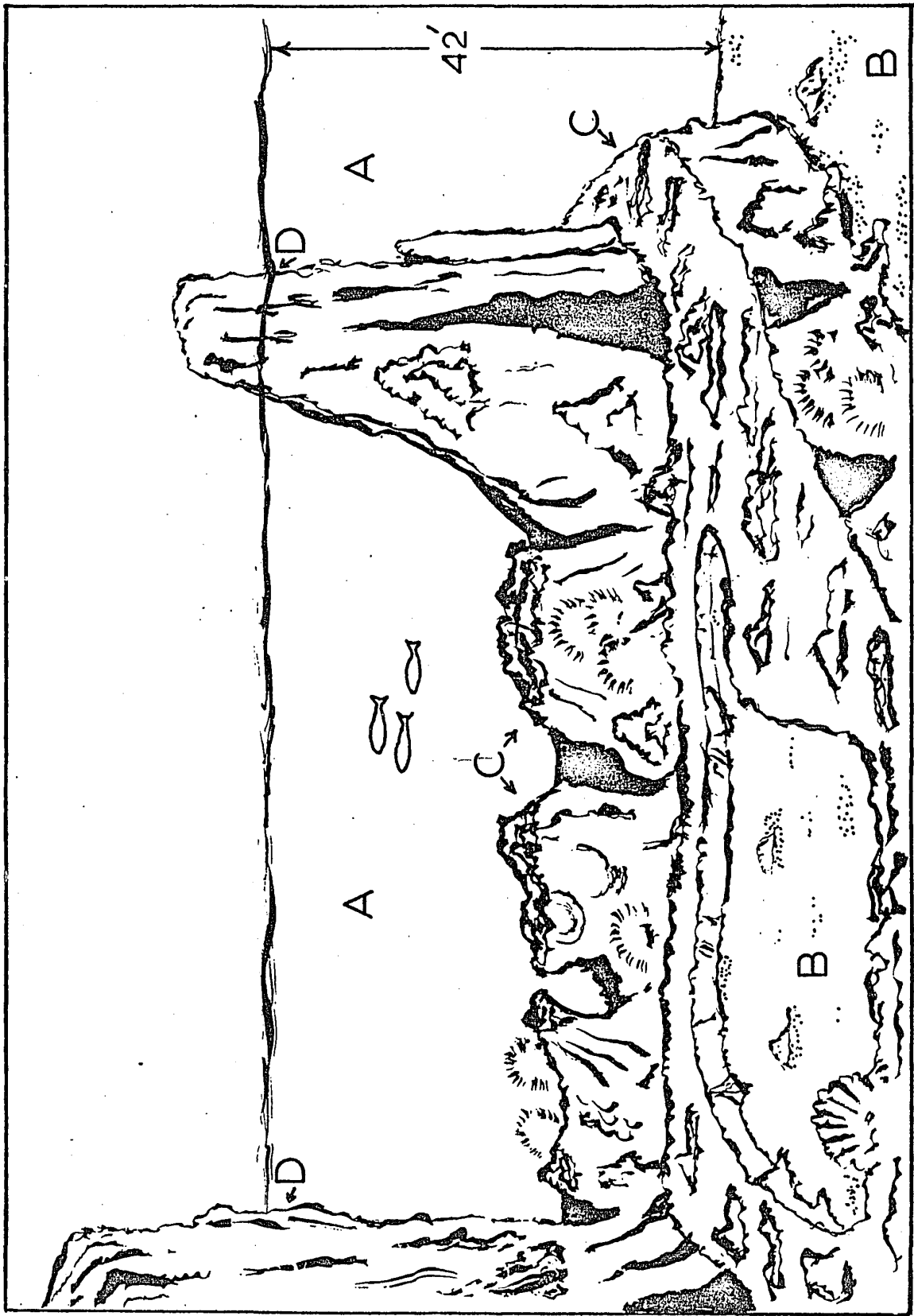
There is almost invariably nearby a steep slope of dark basalt and the substratum usually consists of broken basalt, often covered with patches of corals as Pocillopora damicornis and Porites compressa.

FISHES PRESENT: The acanthurid species most characteristic of this habitat are Acanthurus thompsoni and Naso hexacanthus. Also typical of the habitat are Hemitaurichthys zoster and Heniochus acuminatus of the Chaetodontidae, and Dascyllus albisella, Chromis ovalis, and C. verater of the Pomacentridae. These are the fish indicators, there are probably others.

The mid-water habitat with the associated species was encountered in the following areas (Fig. 1). On Oahu it

FIGURE 3. HABITATS ARE ILLUSTRATED IN THIS SKETCH.  
OPEN SEA IS TO THE RIGHT, THERE IS AN OFFSHORE  
ROCK AND SEA CLIFF AGAINST WHICH INCOMING WAVES  
BREAK.

A - Mid-Water Habitat  
B - Sand Patch "  
C - Subsurge Reef "  
D - Surge Zone "





was studied off Koko Head, in Hanauma Bay, off Moku Manu Island, and above the artificial reefs at Maunalua Bay and the Waianae Coast. On Lanai this habitat was observed off Palaoa Pt. and Puupehe Rock. On the Island of Hawaii one such habitat was investigated off the tip of the peninsula occupied by Cook's Monument in Kealahou Bay. The mid-water habitat with its particular association of fishes was not observed at Johnston Island.

AVAILABLE COVER: Cover is available in this habitat only in the coral and basalt formations at the base of the water column. Though this cover is occasionally used by Acanthurus thompsoni, more frequently the mid-water fishes appeared to make use of the open habitat for rapid maneuvering to avoid capture.

VERTICAL LIMITS: Data on the limits of the habitat are based on the limits observed for the above fishes. The habitat ranges from 20 to at least 450 feet. The maximum depth is based on research submarine dives made by D. S. Strasburg (MS). He observed Naso hexacanthus on all 14 dives off the Waianae Coast to a depth of 450 feet (Table I). It is reasonable from these observations to speculate that the lower limit of the mid-water habitat is even greater.

TABLE I. OBSERVATIONS ON FISHES MADE BY D. S.  
STRASBURG (MS) FROM THE RESEARCH SUBMARINE  
ASHERAH ON THE WAIANAE COAST OF OAHU

SPECIES OBSERVED	NUMBER OF DIVES ON WHICH OBSERVATIONS WERE MADE	DEPTH RANGE IN FEET
<u>Acanthurus</u> <u>glaucopareius</u>	2	160-220
<u>A. leucopareius</u>	1	280
<u>A. sandvicensis</u>	1	98-150
<u>A. dussumieri</u>	4	98-420
<u>A. olivaceus</u>	5	112-150
<u>A. xanthopterus</u>	7	150-298
<u>Ctenochaetus</u> <u>strigosus</u>	1	98-150
<u>Zebrasoma</u> <u>flavescens</u>	1	98-150
<u>Naso</u> <u>brevirostris</u>	1	98-150
<u>N. lituratus</u>	2	160-200
<u>N. hexacanthus</u>	14	50-450

## SAND PATCH HABITAT

GENERAL DESCRIPTION: In the Hawaiian Islands these areas are found inside fringing reefs, bays, or in the deeper waters of the suburge zone. They are found in the Johnston Island "shoal" environments. The habitat is made up of extensive sandy areas with interspersed coral or basalt structures (Fig. 3B).

FISHES PRESENT: The acanthurids that are characteristic of the sand patch habitat are Acanthurus dussumieri, A. mata, A. olivaceus, and A. xanthopterus (Randall, 1956 and Gosline, 1965).

AVAILABLE COVER: In the sand patch habitat per se there is essentially no cover. Fishes feeding in these areas stay near the reef and when disturbed leave the sand patch habitat and take refuge in coral or basalt holes in the reef.

VERTICAL LIMITS: The observed vertical limits of this habitat based on the fishes that characterize it were between 15 and 420 feet (Table I, for maximum depth).

## SUBSURGE REEF HABITAT

GENERAL DESCRIPTION: Basically this is the area one normally thinks of when discussing coral reef habitats. They are subsurge areas of moderate to dense coral growth (Fig. 3C). The areas correspond to the subsurge areas of fringing reefs, deep water reef patches, and reef filled bays (e.g., Kaneohe Bay) in the Hawaiian Islands, and to the coral rich parts of the "lagoon" areas of Johnston Island.

FISHES PRESENT: In this habitat are found a great number of fish species representing a large biomass of high density. The greatest number of acanthurid species are found here and include: Acanthurus nigrofuscus, A. nigroris, A. sandvicensis, Ctenochaetus hawaiiensis, C. strigosus, Naso brevirostris, N. lituratus (= Callicanthus, see Smith, 1966), N. unicornis, Zebrasoma flavescens, and Z. veliferum (sub-adults).

AVAILABLE COVER: The many holes and crevices in the basalt, coral, and coralline algae provide considerable cover for those species that require it.

VERTICAL LIMITS: The fishes defining the limits of this habitat are most commonly observed from depths of a few inches to about 100 feet. Although several of these species were reported at greater depths (Table I) these depths are considered to be below the limits of active coral growth and hence not within the normal habitat.

#### SURGE ZONE HABITAT

GENERAL DESCRIPTION: As the name implies this area is within the surge zone and is subjected to almost constant wave assault or other turbulence which frequently results in the presence of swarms of bubbles in the water. The surge habitat may be that part of a breaker-washed coral reef such as the outer part of fringing reefs, cliff areas, or large offshore rocks in Hawaii (Fig. 3D). At Johnston Island it corresponds to the marginal reef and to the tops of coral heads in the lagoon that may occasionally be awash.

FISHES PRESENT: The acanthurids most characteristic of this habitat are Acanthurus achilles, A. glaucopareius, A. guttatus, and A. leucopareius (Randall, 1956). I also

noticed on occasion the large adults of Zebrasoma veliferum in this habitat. Other acanthurids were seldom seen here except at times of flat calm seas or when passing over the reef from one side to the other. Several species approached quite near the backside of this habitat or near the steep face at the reef front to feed but rarely entered the turbulent parts when the above species were common.

AVAILABLE COVER: This habitat is usually honeycombed with numerous cracks and caves. At least one of the species, Acanthurus guttatus, seemed to use the most active part of the surge for cover.

VERTICAL LIMITS: This habitat is of course limited to the heavy surge areas of the reef and is by nature quite shallow. Most of the characteristic species are limited to about 20 feet. Some of Strasburg's (MS) observations (Table I) indicated that a few of these species were found occasionally at considerable depths.

CHAPTER III  
ANALYSIS OF FEEDING HABITS

GENERAL

It is the intent here to describe the acanthurid species complex of the various habitats based on foraging methods employed. The terminology of foraging methods is that used by Hiatt and Strasburg (1960).

FORAGING METHODS

ZOOPLANKTON FEEDERS: This category includes two fishes that actively pursue and capture individual zooplankters. The two fishes are of evolutionary interest because they represent convergence in this respect from two distinct genera. These species are the mid-water dwelling Acanthurus thompsoni and Naso hexacanthus. Brock (in Gosline and Brock 1960) offered the first clue to the existence of carnivorous acanthurids when he reported copepods and mollusc eggs in Acanthurus thompsoni. Recently Smith (1966) pointed out that certain species of the subfamily Nasinae had "predatory" food habits. I know of no other mention of carnivorous acanthurids in the literature.

The two Hawaiian zooplankton feeders are most frequently encountered off headlands, steep embankments,

and underwater ridges or reefs where current flow is intensified (Chapter II). It could be postulated that these are areas where large zooplankton concentrations would pass or occur.

Acanthurus thompsoni is the rarer of the two species and swims about the mid-water environment in loose aggregations, picking up suspended zooplankters. The fish dart about rapidly opening and closing the mouth as in the case of many holophagous fishes. The negative pressure produced by opening the mouth probably draws in these small food organisms. Naso hexacanthus differs from this only in that it travels in schools, breaking up occasionally to feed, then re-forming the school.

Both species contained crustacean remains for the most part. This material was basically derived from copepods, crab zoeae and megalops, and mysids. In addition, they contained a good many pelagic eggs and nematocysts. One small cephalopod was found in Acanthurus thompsoni. No attempt was made to identify or quantify this material.

The ability to feed on zooplankton probably allows these fishes to exist at depths that would exclude herbivorous acanthurids that feed on multicellular benthic algae.



This was evident in the "enormous numbers" of N. hexacanthus seen by Strasburg (MS) at considerable depths (Table I).

On one occasion I found two or three filaments of the red alga genus, Polysiphonia, and several sponge spicules in A. thompsoni. This suggests that the species may not be entirely dependent on zooplankton. (Fryer, 1959, a,b found this to be true in Lake Nyasa for zooplankton feeders that evolved from herbivorous fish stocks.)

GRAZERS: Fishes that pick up bits of the substratum while feeding are classified as grazers, irrespective of whether the material is rasped away from rock or picked up as loose sand.

Members of the group are the sand patch-feeding Acanthurus dussumieri, A. mata, A. olivaceus, and A. xanthopterus, and the reef-dwelling Ctenochaetus hawaiiensis and C. strigosus.

In all of the species of this feeding group there is a characteristic feeding behavior. The animals assume a near-vertical, head-down position applying the lips and teeth to the substratum. There follows an apparent coordinated sucking and rasping movement.

The Acanthurus are commonly seen moving over the bottom

in small to medium sized schools picking up mouthfuls of sand. On occasion they seem to stop and feed on and around rock and reef structures, but these structures on closer inspection are usually found to be covered with a layer of sand.

Ctenochaetus feeds over rocks and dead coral. It was never observed feeding in the sand patch area or on rocks with a sand covering. The feeding act in this genus looks remarkably as though the fish are "kissing" the substratum. Randall (1955d) conducted feeding experiments with C. strigosus in aquaria. He reported that the fine teeth of this species were ineffective in biting off filamentous algae and the teeth became entangled in the filaments. He further noted the possibility of a sucking mechanism being involved as well as a scraping one. Sand was avoided generally but if picked up was "forcefully ejected".

Randall (1956, p. 162) pointed out that the Acanthurus of the sand feeding group are found in bays and lagoons and the gut contents "generally contain a large percentage of hard, coarse, sedimentary material".

Hiatt and Strasburg (1960, p. 91) found A. mata to be a "strictly grazing herbivore on algal-covered, sandy

bottom". They noted the typical head-down feeding position and that great quantities of sand were ingested by the species.

Randall (in Gosline and Brock, 1960, p. 248) found "considerable inorganic sediment" in the diet of A. olivaceus. Hiatt and Strasburg (1960) found calcareous powder and algal scrapings in 100 percent of the A. olivaceus stomachs they examined at Eniwetok. Coralline algae, gastropods, and foraminifera were also found. They felt that the gastropods and foraminifera were inadvertently picked up. They reported (p. 91) that this fish, like A. mata, fed on "short algal cover on the compacted sandy bottoms, by swimming head-down, or it may scrape algae from coral rubble or the dead bases of coral heads".

Randall (1955b) found a yellowish particulate calcium carbonate material in the stomachs of A. xanthopterus from the Gilbert Islands. Dawson et al. (1955) noted a high percentage of the red alga, Jania, along with much calcareous debris in A. fuliginosus (= A. xanthopterus). They felt that the calcareous material might be Porolithon, the coralline alga. Hiatt and Strasburg (1960) found short algal filaments and much sand in A. xanthopterus

from Eniwetok. There were also some hydrozoan remains. They described the habits of this fish as similar to A. mata and stated that it frequently fed in the same area and in the same manner.

Similar results were obtained in this study. The members of the group almost invariably have the intestine packed with a large amount of calcareous debris and other matter discussed below.

The major difference most readily seen between Acanthurus and Ctenochaetus gut contents is the particle size of the sediment. It is coarse and grainy in Acanthurus and fine and powdery in Ctenochaetus.

Boaden (1962) reviewed grazing of animals in the "interstitial habitat". He described an invertebrate fauna that lives in marine sands and discussed the "epipsammon" or the upper layer of sand and the organisms associated with it.

These animals fed on detritus, fallen plankton, bacteria, and diatoms. "The film or organic matter around each grain consists of bacteria and detritus often with adhering autotrophs, especially diatoms" (p. 300). Blue green and green algae are also found in the upper layer.

One worker estimated 50,000 to 500,000 bacteria per cc of beach sand and another reported 20,000 diatoms per cc.

It is the opinion of this author that of the above components of the interstitial habitat, diatoms and detritus form the major part of the diet in the grazing Acanthurus and Ctenochaetus. Acanthurus get their food from among the sand grains, Ctenochaetus get theirs from a much finer calcareous matrix on the rock and dead corals of reefs. Strasburg (1953) referred to the detrital material as leptopel.

The upper layer of sand or epipsammon of the local environment in suburge areas is often bound together by blue green algae including Microcoleus and others. This along with the interstitial organisms, forms a thin layer that may be somewhat gelatinous in texture. Detritus is added to this material to provide what might, upon proper analysis, prove to be one of the richest food sources in the marine environment for those animals adapted to eating it. Dr. J. B. Lackey (personal communication) worked on this part of the Hawaiian environment and also looked at the stomach contents of some of these fishes. He indicated that the interstitial complex could be an adequate source

of nutrition for fishes. (It would be similar to "aufwuchs" eaten by many fishes in Lake Nyasa, Fryer, 1959, a and b.) Marshall (1965, p. 343) noted at Eniwetok "that organic matter, including aggregates, transported in suspension from the reefs to mid-atoll areas may constitute a substantial contribution to the trophic systems within the lagoon." Aggregates of carbon rich particles like those described by Riley (1963) were found interspersed with detritus. Detritus itself has been utilized by some marine animals (Strasburg, 1953, for some salarine blennies; and Whipple, 1966, for littorine snails).

Algae occurred in the stomachs of grazers from time to time. This has frequently been described by past authors as loose filaments of algae mixed with sand or detritus. By and large, "loose filaments of algae" are rare. Filamentous algae are firmly attached and must be bitten or scraped off the substratum. In these fishes in which algae were found, they were probably either taken accidentally along with interstitial material or purposely to supplement it. On two occasions Acanthurus dussumieri from Diamond Head and Maunalua Bay, Oahu, were found to contain large quantities of algae. The Diamond Head group had no sand

at all in the gut, hence it was concluded they were not grazing. The Maunalua Bay group had only a small amount of sand in the gut. These fish obviously had been feeding on the algae. Algae found in Maunalua Bay fish were by percent volume: Ulva 50, Acanthophora 25, Laurencia 10, Hypnea 10, and Dictyota 5. Normally, however, the intestines of the grazing Acanthurus were packed with sand, diatoms, and detritus with very few filaments of algae. These few algal fragments were usually one or more of the following:

Ectocarpus, Dictyota, Pocockiella, Sphacelaria, Caulerpa, Cladophora, Centroceras, Ceramium, Laurencia, Polysphonia, Tolypiocladia, Gelidium, Hypnea, Jania, and Lynqbya.

The ability to feed in the interstitial habitat probably enables these Acanthurus species to survive at depths below the zone of efficient algal production. This is in agreement with observations of Strasburg (MS) (Table I), who found many of these species at considerable depths. Brooks (1950) found that the benthic algae in Lake Baikal dropped out at 5 M but that benthic diatoms were found at 200-300 M. Wood (1956) was able to show that some diatoms might assume a heterotrophic existence and survive at considerable depth. He reported diatoms at 10,000 M.

It is of interest to point out that the Acanthurus grazers tend to reach the largest size of any others of the genus. Both these Acanthurus and Ctenochaetus lay down decidedly more fat around the intestines than the other Acanthuridae. It would seem, in view of the above, that the material these fishes are grazing on provides a highly nutritional diet. It is not here suggested that the large size of the Acanthurus was due to nutrition alone. It was more likely due to genetic factors but it is not unreasonable to assume that such large animals require a fairly efficient source of convertible energy for maintenance.

**BROWSERS:** The browsers are strict herbivores that bite and tear off bits of multicellular benthic algae without (or at least rarely) ingesting any of the inorganic substratum. The kinds of algae these fishes eat were attached to hard rock or coral surfaces. Hence the fishes themselves were restricted to areas with substrata of this nature.

Browsing species are Acanthurus achilles, A. glaucopareius, A. guttatus, A. leucopareius, A. nigrofuscus, A. nigroris, A. sandvicensis, Zebrasoma flavescens,



Z. veliferum, Naso brevirostris, N. lituratus, and N. unicornis.

Table II gives a general summary of the algae eaten by the herbivorous genera.

The significant features from this table are the relationships to size of food ingested rather than specific items. Hence, Naso tends to feed on larger algae of a leafy or fleshy nature. These include such genera as Pocockiella, Dictyota, Padina, and Sargassum of the brown algae, Rhizoclonium, Dictyosphaeria, Microdictyon, and Ulva of the greens, and Acanthophora, Champia, Laurencia and Hypnea of the reds.

Acanthurus and Zebrasoma are very similar in that they rely on the very fine filamentous genera of the algal Divisions. In cases where there is overlap between the Acanthurus/Zebrasoma group and the Naso group, the former tends to eat much smaller or immature members of the fleshy algae.

It is of interest to note that of the 160 odd algal genera available to the browsing Acanthuridae in Hawaii, only 40 were found during this study. Omitting those algae which were so rare as to be most likely accidentals

TABIE II. SUMMARY OF ALGAE EATEN BY THE  
HERBIVOROUS GENERA OF ACANTHURIDS

<u>Symbol</u>	<u>Acanthurus</u>	<u>Zebrasoma</u>	<u>Naso</u>
D-Dominant	84-93% <sup>1</sup>	84-100% <sup>2</sup>	81%
A-Abundant	65-78%	73-76 %	37-39%
C-Common	45-52%	49 %	18-24%
P-Present	14-31%	14-30 %	10-14%
R-Rare	1-11%	3-11 %	2-6 %

ALGAL DIVISIONS	ALGAL ORDERS	ALGAL GENERA	FISH GENERA: <u>ACANTHURUS</u> <u>ZEBRASOMA</u> <u>NASO</u>		
			No. of SPECIMENS :	N=197	N=37
PHAEOPHYTA	DICTYOTALES	<u>Pocockiella</u>	P	-	D
"	"	<u>Dictyota</u>	R	R	A
"	"	<u>Padina</u>	R	-	P
"	"	<u>Dictyopteris</u>	-	R	R
"	ECTOCARPALES	<u>Ectocarpus</u>	D	D	R
"	SPHACELARIALES	<u>Sphacelaria</u>	D	D	R
"	FUCALES	<u>Sargassum</u>	-	-	A
"	"	<u>Turbinaria</u>	-	-	R

TABLE II. (Continued) SUMMARY OF ALGAE EATEN BY THE  
HERBIVOROUS GENERA OF ACANTHURIDS

DIVISIONS	ALGAL ORDERS	ALGAL GENERA	FISH GENERA:		
			ACANTHURUS No. of SPECIMENS :	ZEBRASOMA N=37	NASO N=62
PHAEOPHYTA	DICTYOSIPNONALES	<u>Chnoospora</u>	-	-	R
CHLOROPHYTA	CLADOPHORALES	<u>Cladophora</u>	A	A	-
"	"	<u>Rhizoclonium</u>	-	-	P
"	SIPHONOCLADALES	<u>Cladophoropsis</u>	-	-	R
"	"	<u>Dictyosphaeria</u>	R	R	C
"	"	<u>Microdictyon</u>	-	R	C
"	ULVALES	<u>Enteromorpha</u>	C	C	-
"	"	<u>Ulva</u>	-	-	P
"	SIPHONALES	<u>Caulerpa</u>	P	R	R
"	"	<u>Codium</u>	R	P	-
"	"	<u>Udotea</u>	R	-	R
"	DASYCLADALES	<u>Acetabularia</u>	R	-	R

TABLE II. (Continued) SUMMARY OF ALGAE EATEN BY THE  
HERBIVOROUS GENERA OF ACANTHURIDS

ALGAL DIVISIONS	ALGAL ORDERS	ALGAL GENERA	FISH GENERA: <u>ACANTHURUS</u> <u>ZEBRASOMA</u> <u>NASO</u>		
			No. of SPECIMENS :	N=197	N=37
RHODOPHYTA	CERAMIALES	<u>Acanthophora</u>	R	-	P
"	"	<u>Acrochaetium</u>	P	A	-
"	"	<u>Alsidium</u>	R	R	-
"	"	<u>Centroceras</u>	A	D	-
"	"	<u>Ceramium</u>	A	D	-
"	"	<u>Champia</u>	R	P	P
"	"	<u>Chondria</u>	R	P	-
"	"	<u>Griffthsia</u>	R	P	-
"	"	<u>Laurencia</u>	P	R	C
"	"	<u>Polysiphonia</u>	D	D	R
"	"	<u>Spyridia</u>	R	-	R
"	"	<u>Tolypiocladia</u>	R	-	-

TABLE II. (Continued) SUMMARY OF ALGAE EATEN BY THE  
HERBIVOROUS GENERA OF ACANTHURIDS

ALGAL DIVISIONS	ALGAL ORDERS	ALGAL GENERA	FISH GENERA: <u>ACANTHURUS</u> <u>ZEBRASOMA</u> <u>NASO</u>		
			No. of SPECIMENS :	N=197	N=37
RHODOPHYTA	CRYPTONEMIALES	<u>Jania</u>	C	P	-
"	GELIDIALES	<u>Gelidium</u>	D	D	-
"	GIGARTINALES	<u>Hypnea</u>	R	P	C
CYANOPHYTA	OSCILLATORIALES	<u>Anabaena</u>	R	-	-
"	"	<u>Calothrix</u>	P	R	-
"	"	<u>Hydrocoleum</u>	R	-	-
"	"	<u>Lynqbya</u>	D	D	-
"	"	<u>Microcoleus</u>	R	-	-

1

The percents are based on percent occurrence of each algal genus in each fish genus.

<sup>2</sup>Because there are differences in selectivity between fish genera, the ranges of percentages upon which each category of abundance is based are different in each fish genus.

(i.e., Dictyopteris, Turbinaria, Chnoospora, Udotea, Acetabularia, Anabaena, Hydrocoleum, and Microcoleus) the number becomes 32 which represents only 20 percent of the algae available. In the individual algal Divisions 38 percent (6 of 16) of the available browns, 33 percent (9 of 27) of the greens, only 15 percent (15 of 97) of the reds and 8 percent (2 of 24) of the blue greens were eaten.

This suggests that though the food habits are variable, they are variable within a fairly narrow range of algae. Randall (1961a, p. 224) noted in feeding experiments that Acanthurus sandvicensis ate a great many species of algae and that "at least a few filaments of virtually every filamentous alga in the Hawaiian area can ultimately be found in the gut of the manini if enough specimens are examined." There is no reason to disagree with this statement per se, but the fact remains that quantitative data (Chapter IV) show that by and large the browsing Acanthuridae are selective in that they have a rather small range of algae over which they feed consistently. However, as Randall's statement implies, there will be at least a few other genera of algae not listed here that could be found in significant quantities in acanthurid gastrointestinal tracts if enough

specimens, localities, and time periods are investigated.

Finally, the failure of these species to utilize more of the larger fleshy algae does not seem to be related to morphological weakness in the fishes. Randall (1965) has shown that Atlantic species of Acanthurus were capable of biting off tough sea grasses like Thalassia and Cymodoce. Similarly the finding of large fleshy algae in A. dussumieri would be additional proof since the small teeth of this species would seem less "adaptive" for biting the larger algae than the true browsers (Chapter V). Why then do these species concentrate on filamentous algae and not more on the fleshy ones? Randall's (1961a) feeding experiments showed that when they have no choice, A. sandvicensis would feed on some of the fleshy algae. Hence there may be an enormous food reserve available should the supply of filamentous algae become limited.

#### BROWSERS---FEEDING ON LEAFY AND FLESHY ALGAE:

Naso lituratus and N. unicornis show considerable similarity in their feeding. Both species tend to feed in small roving groups. These schools swim well above the substratum diving occasionally to the bottom to feed around coral heads and basalt rocks. The fishes can be observed

cropping off bits of algae from the substratum. Much less data is available for N. brevirostris both in terms of observations and food eaten. N. brevirostris was observed only a few times. Gosline and Brock (1960) reported it as a rare fish in Hawaiian waters. The only specimens of N. brevirostris I was able to obtain were subadults and juveniles. Hence the food habits of the adults are as yet unknown. Feeding behavior of the juveniles and subadults is not unlike that of N. lituratus and N. unicornis. N. brevirostris was observed to feed in the benthic environment in 20 to 50 feet of water. Strasburg (MS) reported them on one dive down to 150 feet (Table I). Both N. lituratus and N. unicornis were observed feeding in waters of three to 50 feet.

Though the data at hand for N. brevirostris was inadequate, those that I have examined show a similarity in foods eaten with N. unicornis. Three specimens of N. brevirostris from Kaneohe Bay all contained 100 percent Dictyosphaeria which occurs there in great abundance. In all other cases (except Johnston Island where N. brevirostris is unreported and N. unicornis is rare) both had larger



amounts of Sargassum in their stomachs than any other acanthurid species. A collection of N. brevirostris from La Perouse Bay, Maui, contained about 90 percent by volume of Sargassum and about 10 percent Tolypiocladia.

The gastrointestinal tract of a single N. unicornis collected at Johnston Island was found to contain 100 percent Pocockiella. Collections of N. unicornis from Puuiki and Kuloa Pt., both on the north shore of Oahu, differed considerably in the ranking and generic composition of food (Table III).

Though there is some variability depending on locality, Table III indicates that Sargassum and Dictyota are the most common genera eaten by the N. unicornis specimens sampled. At Johnston Island the rarity of N. unicornis may be due to the absence of Sargassum and Acanthophora and the relative rarity of Dictyota (Buggeln and Tsuda, 1966). N. unicornis was presumably forced to eat Pocockiella and would thus be in strong competition with N. lituratus (see below), a situation that does not exist in Hawaii.

The preferred food of N. lituratus was Pocockiella; it was found in all of the 37 fish examined and in 25 of

TABLE III. COMPOSITION AND PROPORTION OF  
ALGAL GENERA EATEN BY NASO UNICORNIS  
BASED ON PERCENT WET WEIGHT

ALGAL GENERA	LOCALITY:	HAWAII				JOHNSTON IS.
	STATIONS:	LA PEROUSE BAY	KEALAKEKUA BAY	KULOA PT.	PUUIKI	4
No. of SPECIMENS:		N=2	N=1	N=5	N=5	N=1
<u>Dictyota</u>		59%	30%	0	21%	0
<u>Sargassum</u>		32%	50%	20%	74%	0
<u>Pocockiella</u>		9%	0	0	0	100%
<u>Padina</u>		0	10%	4%	0	0
<u>Acanthophora</u>		0	0	28%	0	0
<u>Laurencia</u>		0	0	13%	2%	0
<u>Hypnea</u>		0	0	18%	0	0
<u>Champia</u>		0	10%	5%	0	0
<u>Microdictyon</u>		0	0	6%	0	0
<u>Miscellaneous</u>		0	0	6%	3%	0

the 37 made up 100 percent of the stomach contents (Table IV).

The nearly equal amounts of Pocockiella, Sargassum, and Dictyota in La Perouse Bay (Maui) specimens may have been due to the fact that corals are not common there. The best stands of Pocockiella encountered during this study were growing on dead corals or at the base of live corals.

At Kealakekua Bay, Hawaii there is a rich growth of coral and good growth of Pocockiella on the dead parts of the coral heads. N. lituratus is common here.

At Johnston Island all the N. lituratus had 100 percent Pocockiella in their stomachs except those from Station 8 (Table IV), a leeward lagoon area (Brock et al. 1965). The largest populations of N. lituratus occur on the windward reef and in the windward lagoon where Pocockiella is common (Buggeln and Tsuda, 1966). Coral growth is reduced at Station 8, and the benthic fauna and flora there are in poor condition due to heavy siltation from the nearby dredged channels (Brock et al., 1965). N. lituratus is rare in this locality. The four specimens examined from Station 8 all had a mixed diet (Table IV).

TABLE IV. COMPOSITION AND PROPORTION OF  
 ALGAL GENERA EATEN BY NASO LITURATUS  
 BASED ON PERCENT WET WEIGHT

LOCALITY :	HAWAII		JOHNSTON IS.		
	STATIONS :	LA PEROUSE BAY	KEALAKEKUA BAY	1,3,4,6	8
ALGAL GENERA	No. of SPECIMENS:	N=3	N=5	N=25	N=4
<u>Dictyota</u>		35%	20-30%	0	0
<u>Sargassum</u>		30%	5%	0	0
<u>Pocockiella</u>		35%	60%	100%	50-70%
<u>Dictyosphaeria</u>		0	0	0	10-20%
Miscellaneous		0	0	0	10-20%

Though Pocockiella is by far the preferred food, Station 8 serves to adequately demonstrate that when faced with a poorly developed Pocockiella population, the fish can and will vary the diet somewhat.

BROWSERS--FEEDING ON FILAMENTOUS AND SMALL FLESHY ALGAE:

Fishes of the group include Acanthurus achilles, A. glaucopareius, A. guttatus, A. leucopareius, A. nigroris, A. sandvicensis, Zebrasoma flavescens, and Z. veliferum.

Table II shows that the diets of Acanthurus and Zebrasoma are quite similar. Zebrasoma eats relatively more Acrochaetium, Centroceras, Ceramium, Champia, Chondria, and Griffithsia. These differences are minor and a larger sample size is required to elucidate a possible ecological separation. Food organisms comprising the diets of the two genera are here considered virtually identical.

These fishes all remain closely associated with coral and basalt substratum. They browse with a series of pecking motions at the rock.

It was pointed out in Chapter II that the fishes of the surge zone habitat are capable of feeding in a breaking sea. The adversity of these surge areas would seem to exclude most of the other browsers from the area

leaving Acanthurus achilles, A. glaucopareius, A. guttatus, A. leucopareius, and the adults of Zebrasoma veliferum.

Observations show that Acanthurus achilles, A. guttatus, and A. leucopareius are remarkably adept at feeding in these areas. Feeding activity is "intense" between periods of heavy surge and breaking waves. The fishes break off feeding when the surge current is strongest and resume during the few seconds of slack before the next surge.

On calmer days A. achilles were seen to break off feeding and display aggressive behavior toward other acanthurids that ventured into and around the surge habitat. They consistently drive away other browsing surgeonfishes, particularly A. sandvicensis, A. nigroris, and A. leucopareius.

In the surge areas where A. guttatus feeds, there is often a considerable amount of loose and fairly coarse calcareous material being moved by the surge. This material is frequently caught in the algal turf and is ingested by A. guttatus. The other species most likely to feed in this area, A. achilles and A. leucopareius, apparently are better able to avoid this material (although some was infrequently found in A. leucopareius). G. Bakus

(personal communication) reported that A. guttatus at Eniwetok is a grazer taking "appreciable quantities of coral fragments along with benthic algae". Not being familiar with the Eniwetok fauna I do not know whether this is indeed grazing or a phenomenon similar to the one reported above. Hiatt and Strasburg (1960) also found calcareous material in the stomachs of these fish at Eniwetok admixed with filamentous algae. Randall (1955a) found in A. guttatus from the Gilberts calcareous material and several types of fine algae with Jania and Calothrix predominating.

Both A. nigroris and A. sandvicensis sometimes feed in areas outside their normal reef habitats. A. nigroris is frequently seen feeding in areas and in a manner that is strikingly like that of the sand patch group. On several occasions the gut was found to be full of coarse calcareous sand mixed with diatoms and detritus. It seems apparent that this animal is to a degree capable of switching from benthic algae to feeding in the interstitial habitat. Unlike A. guttatus, there is no question but that these fish were at times actively ingesting great quantities of sand.

A. sandvicensis similarly is observed in sand patch areas but remains a browser, picking algae from rocks that protrude up through the sand. This species will also approach the edges of the surge zone habitat where it frequently encounters aggressive resistance from A. achilles if the latter species is present in the area. A phenomenon characteristic of A. sandvicensis is the enormous feeding schools that move over the reef. The schools move along close to the substratum stopping now and then to feed. If one can postulate a kind of species pecking order within a genus, A. sandvicensis would most likely fall at the bottom of the one for Acanthurus. This species has been observed under aggressive attack from nearly all the other reef dwelling Acanthurus. An individual moving about the reef feeding is frequently attacked by other members of the genus, in particular A. achilles and A. nigrofuscus. As one of the large schools of A. sandvicensis moves along there is constant harassment by individuals of other species. These animals dash through the A. sandvicensis school with much ferocity as if trying to break it up. Under such circumstances an aggressor species has so many animals to attack that the task of



dispersing them is quite hopeless. While following these schools for some distance the author has observed many such attacks. On the average an aggressor fish can successfully interrupt the feeding of five to fifteen individuals. In a school of 200 (a conservative estimate) this would still allow over 90 percent of the remaining individuals to feed unharassed. Hence the schooling behavior may provide a distinct advantage for the species when feeding.

The tendency of Zebrasoma flavescens to be found on the leeward sides of islands (Brock, 1954) and in particular in areas of fairly luxuriant coral growth (e.g., Pocillopora damicornis and Porites compressa) may be correlated with its foraging habits. This species can and frequently does feed on algae growing exposed on basalt and dead coral heads like the browsing Acanthurus. But they were also seen to thrust their greatly produced snouts (Chapter V) among the interstices and at the base of dead corals to feed on stands of algae that cannot be reached by Acanthurus. Zebrasoma veliferum is similarly constructed.

Several of the above browsing species will be examined in detail in Chapter IV for food habits.

## CHAPTER IV

### DETAILED ANALYSIS OF ITEMS INGESTED BY ACANTHURID SPECIES BROWSING ON MULTICELLULAR BENTHIC ALGAE

#### GENERAL

Special attention was paid to this group of fishes for two reasons. First, the group contains the greatest number of acanthurid species. Second, it has been shown by Randall (1961c) and Stephenson and Searles (1960) that food of browsing herbivores may be limited by overbrowsing. These authors used wire screens to exclude browsers and noted great increase in the standing crop of protected filamentous algae when compared with the adjacent unscreened areas. Upon removal of the screens, browsing herbivores in these areas quickly reduced the algae to a short turf.

If food is limited and the species are all eating the same thing then there may be severe competition that could limit the number of species. Chapter III suggested that two of the browsing genera do in fact eat similar foods (Acanthurus and Zebrasoma).

It was hoped that a detailed study of the food eaten by possible competitors would suggest subtle differences in food habits and hence provide ecological separation of the species.

The browsing species of Naso already seemed fairly well separated ecologically by their food habits, hence were omitted here. Otherwise the study includes as many species as could be obtained, in reasonable numbers, of the group of fishes that feed on filamentous and small fleshy algae.

#### SPECIES CONSIDERED

The species considered were Acanthurus achilles, A. glaucopareius, A. leucopareius, A. nigrofuscus, A. nigroris, A. sandvicensis, and Zebrasoma flavescens. Acanthurus guttatus and Zebrasoma veliferum were not obtained in significant numbers. Two Hawaiian stations on Maui and Hawaii were studied. These stations were chosen so as to be as diverse as possible. They were La Perouse Bay on Maui and Kealakekua Bay on Hawaii. Both areas are remote with access only by boat or Jeep trail. Stations 1, 3, 4, 6, and 8 were studied at Johnston Island (See Brock et al., 1965 for details on these stations). Not all species were collected at every station and Acanthurus leucopareius and A. nigrofuscus are as yet unreported from Johnston Island.

Five specimens of each species were studied where possible at each station. These specimens were subjected to a rigorous analysis (See below). A total of 150

specimens were used in the analysis.

#### STATIONS

LA PEROUSE BAY: This station is bordered by a recent lava flow from the flank of Mt. Haleakala. This flow occurred in about 1790,  $\pm$  four years (Oostdam, 1965). The area was shallow, six to fifteen feet. Figure 1 (inset) shows the area studied. There was only a light surge at this leeward station. The relatively recent basalt surface has very little coral growth. Common fishes were Acanthurus nigrofuscus, A. nigroris, and A. sandvicensis. A. achilles, A. leucopareius, and Zebrasoma flavescens were rare.

KEALAKEKUA BAY: The Kealakekua Bay Station is bordered by a lava flow that is considerably older than the La Perouse flow. The Kealakekua lava is considered prehistoric by Stearns (1946). MacDonald (personal communication) suggested that it was at least several thousand years older than the La Perouse lava. Coral growth is luxurious and the species complex is the most advanced in ecological succession in the Windward Hawaiian Islands. Porites compressa and Pocillopora linguata are the dominant corals. The depth drops rapidly to about 70-80 feet. Breaking seas and

a strong surge frequently occurs on the Point (Fig. 1, inset). Common fishes were Acanthurus achilles, A. nigrofuscus, A. sandvicensis, and Zebrasoma flavescens. Acanthurus leucopareius and A. nigroris were present but not common.

Detailed descriptions of the five Johnston Island stations may be found in Brock et al. (1965). General descriptions are as follows:

STATION 1 is located just inside the marginal reef (windward side) and due north of North Island (Fig. 2). The marginal reef is made up primarily of coralline algae. The area of the lagoon side of the marginal reef has a short talus slope followed by large mounds or coral knolls almost completely covered with very large table-shaped Acropora heads. Station 1 has luxuriant coral and fish fauna. Collections were made with spear and poison in an area that included part of the seaward reef, talus slope, and coral knolls. Acanthurus achilles is extremely abundant on the edge of the seaward reef and the population extended back somewhat into the lagoon areas.

A. sandvicensis and A. nigroris are common and A. glaucopareius is present in the immediate backslope areas. Zebrasoma flavescens is quite common in sheltered areas

behind coral knolls.

STATION 3 (Fig. 2) is located just inside the marginal reef and due north of Johnston Island. Coral knolls are common here as at Station 1 but tend to be connected to form winding ridges. The ridges are interspersed with narrow sand and coral talus channels. This area is about 30 meters leeward of the marginal reef. Fishes were collected with spears. Acanthurus sandvicensis is the most abundant fish. A. achilles is also quite abundant due to the proximity of the seaward reef. A. nigroris and Zebrosoma flavescens are common.

STATION 4 is located just southwest of the small boat channel (Fig. 2). During earlier work this was found to be an extremely rich area in terms of the coral and fish fauna. Later dredging operations in the Johnston Island ship anchorage resulted in considerable siltation. The once flourishing coral fauna has been considerably reduced. The area is characterized by rough massive coral formations covered by a thin layer of dredge spoil (Brock et al., 1965). Fish specimens were collected by spearing and poisoning. Acanthurus achilles, A. sandvicensis, and Zebrosoma flavescens are all abundant. Acanthurus nigroris

is fairly well represented.

STATION 6 is located on the edge of the ship anchorage and due north of Johnston Island (Fig. 2). Prevailing tidal currents in this area have kept it relatively free of siltation from nearby dredging. It is about 300 meters inside the marginal reef. This is considered a windward lagoon area. The station has winding flat topped coral ridges. These ridges are interspersed with patches of coral sand and low clumps of coral. All fishes collected were speared. Acanthurus sandvicensis is dominant. A. nigroris and Zebrasoma flavescens are common. Acanthurus achilles is not uncommon but considerably reduced in numbers when compared with the above three stations nearer the marginal reef.

STATION 8 (Fig. 2) is located just south of Sand Island and east of the ship channel. It is considered a leeward lagoon station. The area is characterized by shallow elongate coral ridges on a pavement-like calcareous bottom. The ridges are somewhat sinuous but basically run parallel to one another (east to west). Coral formations are small. The station has been under serious siltation from dredging. Many of the corals are dead and the invertebrate fauna

and algal turf reduced. Fishes were speared and poisoned. Acanthurus sandvicensis is the most abundant acanthurid. A. nigroris is fairly common and both A. achilles and Zebrasoma flavescens are rare and were not collected.

#### STOMACH ANALYSIS TECHNIQUE

Review of the literature (good reviews of methods of stomach analyses are found in Hynes, 1950 and Pillay, 1953) has revealed that quantitative analysis of gut contents of animals feeding on benthic algae is virtually unknown. Even if the algae are readily identified they are not easily separated for determination of the quantity of each kind. Some of the methods commonly found in other works have been as follows:

1. The percent by weight or volume of "filamentous algae" in a stomach sample may be visually approximated. This method is useful in so far as one can determine whether or not a fish is a herbivore or to what degree it is dependent upon plant material for food. This technique was used in Tables III and IV.

2. The frequency of occurrence of each algal genus or species in a series of fish stomachs may also be subjectively estimated. A certain amount of reliable infor-



mation may be gained from this (e.g., see Table II) but all too often a diminutive alga may appear in 100 percent of the fish and yet represent only a small biomass, perhaps having no nutritive significance at all.

3. A generic or specific list of the algal components found in a series of stomachs from a fish species may be given. This is probably the least useful, but most frequent method employed. A few filaments of one genus appearing in only one or two stomachs would be given equal weight with a genus found in great abundance in all stomachs.

Attempts to find a more sensitive method than those given above has proved to be extremely time consuming. Physical separation of the various algal genera is virtually impossible due to their frequent microscopic size.

An empirical approach or direct count was considered to be the most feasible. A fragment of a multicellular alga is not as clearly defined a unit as is a small animal swallowed intact by a carnivore. However it is a reasonable assumption that an entire thallus need not be ingested for it to be considered significant enough to be counted. Hence, each algal filament or fragment bitten

off by a fish may be viewed as a single countable unit for measuring abundance. An additional complication is encountered here because there is some pharyngeal mastication that further divides an algal filament into smaller pieces. In this respect, genera such as the "jointed" Jania and the easily fragmented Lynqbya would provide outrageously incorrect counts. Finally, the morphological difference in size of the various algae make a one to one count of a piece of Laurencia (large) to a piece of Lynqbya (small), somewhat ludicrous in terms of biomass. A direct count of algal filaments may therefore be virtually meaningless.

In consideration of the above, three approaches to quantification were attempted. These were all based on slides made from stomach contents.

1. Algal genera were ranked by order of decreasing dominance from a subjective estimate of the biomass of each algal genus in the sample. Spearman's rank correlation method (in Siegal, 1956) was used to provide a measure of similarity of food and feeding habits between each species of surgeonfishes. A matrix of the rank correlation coefficients between each species was then constructed. Fishes with the closest correlation coefficients

were clustered and presented in dendrograms according to methods reviewed by Sokal and Sneath (1963).

The procedure proved a simple operative technique, yet two major drawbacks were encountered. First, no two researchers would ever subjectively draw identical conclusions about the estimated algal biomass. Secondly, there was no way to place a numerical value on the distance between the ranked algal genera. For example, if Polysiphonia makes up 90 percent of the stomach contents of a fish and Ectocarpus makes up only 10 percent, then ranking them first and second would be a misrepresentation of the true value of each algal genus to the fish.

2. A consideration was also given to subjectively estimating percent biomass of each alga in the sample. Again the possibility of two independent researchers attaining comparable results was doubtful. The method proved incidentally, to give reproducible results, yet a more standardized technique was called for.

3. As a compromise the following procedure was employed: The esophagus and stomach from the anterior end of the esophagus to the region of the pyloric caeca were removed from each fish. The excised portion of the gut

was split open and the contents washed into a petri dish. This material was thoroughly mixed and all clumps broken up. Three drops of this slurry were taken from three different parts of the petri dish and placed on three glass slides. The material was spread in part by a dissecting needle and in part by placement of the coverglass. The homogeneity of the samples can be questioned, but the random manner of preparation is considered relatively free from bias. Therefore, the ratio of algal genera on the slides is believed to be representative of the ratio of algal genera in the stomachs. Results from preparations done in triplicate were found to be more accurate than using one. Estimated error was about  $\pm 5$  to 10 percent.

Each of the three slides was examined under a compound microscope equipped with a 1 mm ocular grid. The slides were manipulated with a stage micrometer. Nine areas on each slide were studied (Fig. 4a). The grid was positioned over each one of these points. The grid itself has nine vertical and nine horizontal lines each 0.1 mm apart. The central vertical and horizontal lines each make eight points of intersection with the lines in the opposite plane plus one intersection with each other

(Fig. 4b). This results in 17 points of intersection. If an algal genus fell on any one or more of these points the number of intersections was counted and recorded for that genus.

Thus there were 17 points of intersection per grid counted, there were nine grids per slide and 27 grids in three slides. The result was a total of 459 points of intersection examined per fish. The principal behind the technique was similar to determining area under a grid by square counting. This method considers the cross sectional area occupied by each algal genus. The more points that are considered, the more accurate would be the count. Figure 4b shows a hypothetical example of this technique.

The following relationships may be calculated from these counts.

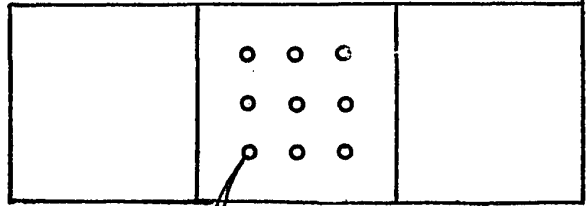
$$\frac{\# \text{ intersections with algae}}{459} = \text{relative algal density of the sample}$$

$$\frac{\# \text{ intersections with alga A}}{\# \text{ intersections with all algae}} = \text{Frequency of alga A in the fish stomach relative to the other algae. Frequency} \times 100 = \text{percent frequency of A in the stomach}$$

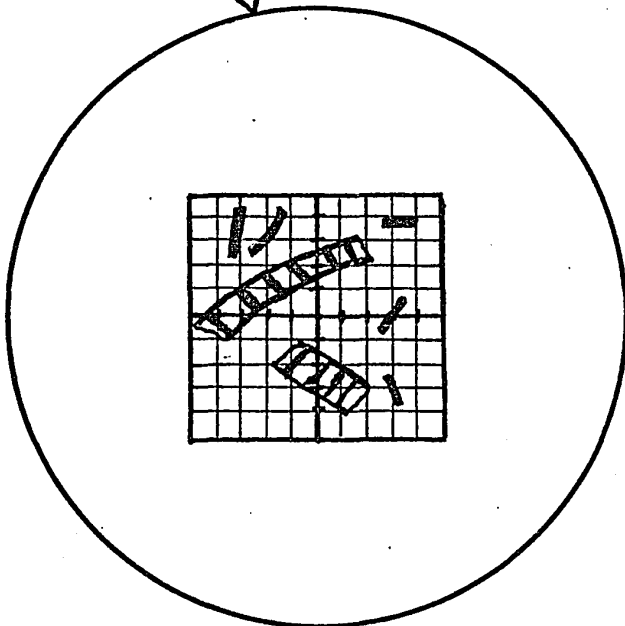
FIGURE 4. PART OF STOMACH ANALYSIS TECHNIQUE



a. Microscope slide and coverglass with sampling points shown as circles, b. One of the sampling points enlarged to show the ocular grid and method of counting.

a.



b.



 Alga A=5  
 Alga B=1

The advantage of the direct count method is that it allows for agreement between two researchers using the same material. It must be understood that some variability results from preparation of the slides. Using three slides increases the chance of having representative material. The data obtained were relative and not based directly on the total physical biomass of each alga in the stomach.

Employing this technique, three possible comparisons may be made:

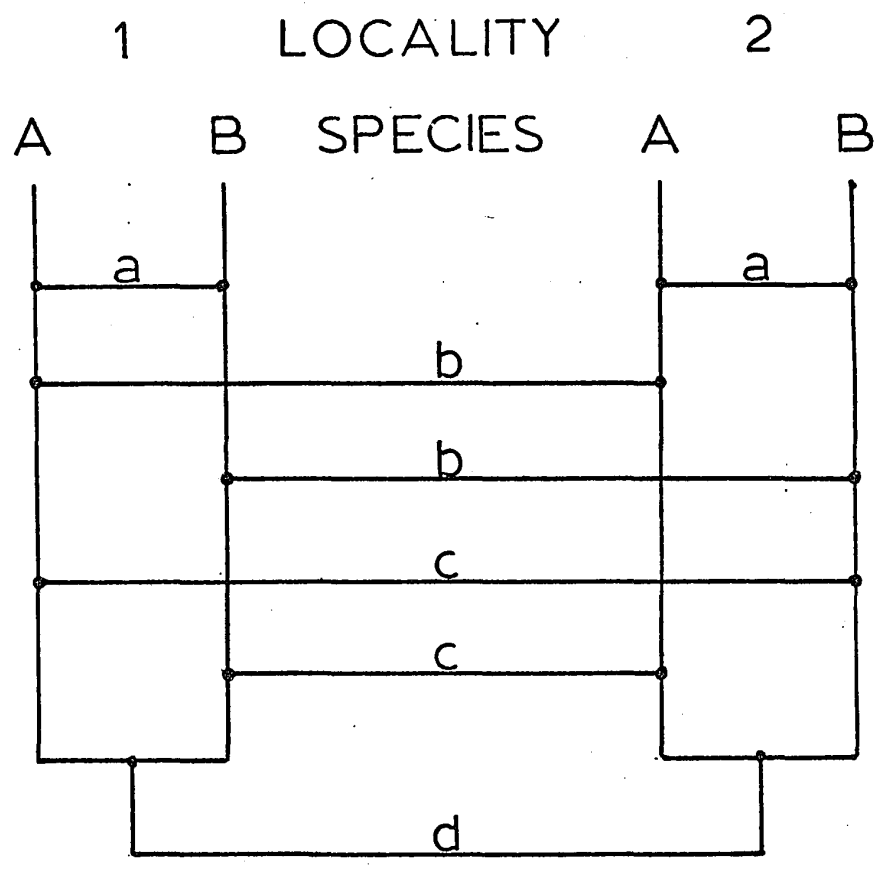
1. The food habits among fish species of the same station may be compared. This would be an interspecific/intrastation comparison (Fig. 5a). This is a logical comparison because each species is exposed to the same algal community and would theoretically have the same food gathering opportunities. Therefore, expected differences in food habits would then be a reflection of the different physiology and behavior of each species.

2. An intraspecific/interstation comparison may be employed where fish of the same species are compared between stations (Fig. 5b). If there is a tendency to select specific foods, there should be a high degree of overlap in one species over several stations. The primary variable



## FIGURE 5. POSSIBLE COMPARISONS FOR FOOD HABITS

a. Interspecific/intrastation, b.  
intraspecific/interstation, c. interspecific/  
interstation, d. interspecific pairs/  
interstation



is that populations of the same species are exposed to entirely different algal communities at different stations.

3. The interspecific/interstation comparison is the most illogical approach (Fig. 5c). Comparison of genetically different fishes from floristically different stations is made. This might be a valid comparison if a relationship could be determined between two species at one station and this relationship compared with that of the same species pair from a different station (Fig. 5d). This is undoubtedly a complex and difficult relationship to deal with and it will not be further considered.

The percent frequency data, gotten from the intersection counting method and averaged for five fish samples, were rounded off to the nearest five percent. Algae in each species were divided into primary and secondary foods (Dumas, 1956). These categories were arbitrarily based on the ten percent level of algal frequency in each species. If an algal (rounded to the nearest five percent) did not reach the ten percent level it was considered a secondary food of little importance to the animal's immediate basic nutrition. Food items reaching the ten percent level and

above were considered primary. This is based on the assumption that all the ingested algae have the same food value.

The average percent frequencies of primary foods for each species and each station are plotted in the pie diagrams (Fig. 6-12).

Total percent of primary food was calculated for each species at each station. The percent overlap of primary food was calculated between each species and the combined acanthurid community at each station. These figures were divided by the amount of primary food to remove the effect of secondary food and to standardize the values on primary foods. Table V is an example of this operation using data from the Kealakekua Bay Station. These data are normally recorded at the bottom of Tables VI-XI.

Matrices (Tables VI-XII) were constructed to compare each species from a Station with every other species from the same Station. Percent overlap of primary food was computed between each species and divided by the total percent of primary food in each subject species under study.

The intraspecific/interspecific comparisons were made in a similar manner for Acanthurus achilles, A. nigroris, and A. sandvicensis (Table XIV-XVI). The percent overlap

TABLE V. SAMPLE COMPUTATIONS OF OVERLAP  
 DATA MADE ON KEALAKEKUA BAY SPECIMENS  
 (FIVE SPECIMENS OF EACH SPECIES WERE USED)

SPECIES	TOTAL PERCENT OF PRIMARY FOOD	PERCENT OF PRIMARY FOOD OVERLAPPED BY THE COMBINED ACANTHURID COMMUNITY	TOTAL PERCENT OVERLAP CORRECTED
<u>Acanthurus</u> <u>achilles</u>	85	75	88 <sup>1</sup>
<u>A. leucopareius</u>	85	70	82
<u>A. nigrofuscus</u>	80	70	88
<u>A. nigroris</u>	85	50	59
<u>A. sandvicensis</u>	75	65	87
<u>Zebrasoma</u> <u>flavescens</u>	70	65	93

<sup>1</sup>  
 Computed as  $\frac{.75}{.85} \times 100 = 88$  percent

was computed for each species with the same species from different stations. Again this overlap was corrected to primary food by dividing by the total primary food in the species under consideration.

In Tables XIII and XVII the percent overlap data for interspecific/intrastation and intraspecific/interstation comparisons are averaged for each station and then the averages for all stations are computed.

#### INTERSPECIFIC/INTRASTATION COMPARISONS

The pie diagrams illustrated in Figures 6-12 demonstrate several general points. The number of algal genera eaten by the Hawaiian species (Figs. 6-7) usually outnumber those eaten by Johnston Island species (Figs. 8-12).

Polysiphonia was found in every fish species considered and in only one instance (Fig. 7, Acanthurus nigroris) was it below 15 percent occurrence.

In most of the Kealakekua Bay species Gelidium was important and in the La Perouse Bay species, Laurencia. Neither genus reached the primary food level in the Johnston Island species. Buggeln and Tsuda (1966) listed Laurencia sp. as dominant at Johnston Island Station 1. Yet Laurencia was not represented in any of the acanthurids

studied there. Whether this is an unpalatable species or the Johnston Island fishes are not conditioned to eat Laurencia is a debatable point. Gelidium has not been reported as dominant from any Johnston Island Station.

The question frequently arises as to whether or not herbivorous fishes eat the dominant algae in their environment. In Figures 8-12 an asterisk is used to designate those algae that were recorded as dominant for each Johnston Island Station by Buggeln and Tsuda (1966).

In several cases (Figs. 8, 9, 11, and 12) algae which were reported dominant at the stations were indeed found in the fishes. Only at Station 4 (Fig. 10) did a dominant alga fail to appear in at least one fish species. But it was equally clear that not all of the primary foods eaten by the fish were recorded as dominant in the environment. In fact Polysiphonia, the dominant alga in three of the four species at Station 4 (Fig. 10) was not even reported at this Station in the above floristic study.

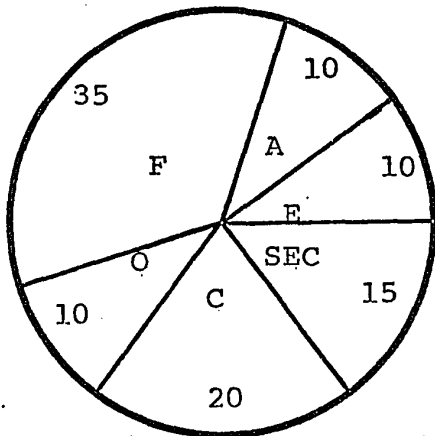
Acanthurus nigroris was the only species that seemed to be at all separated from the other species in terms of food habit. The dominant algae were highly variable in this species. In the Hawaiian localities it contained significant

FIGURE 6. PERCENT OF PRIMARY FOODS EATEN BY THE SPECIES AT KEALAKEKUA BAY, HAWAII

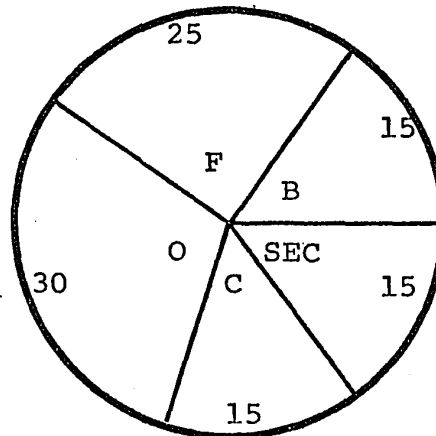
Key to Primary Algae

- A-Sphacelaria
- B-Centroceras
- C-Lyngbya
- D-Jania
- E-Ectocarpus
- F-Polysiphonia
- I-Acrochaetium
- J-Ceramium
- K-Hypnea
- O-Gelidium
- Q-Cladophora
- R-Enteromorpha
- T-Laurencia
- V-Dictyosphaeria
- Z-Dictyota
- LL-Tolypiocladia
- SEC-Secondary foods

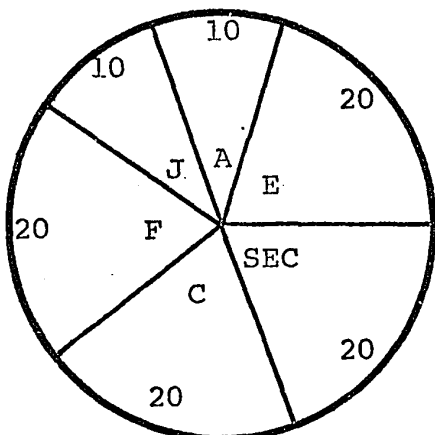




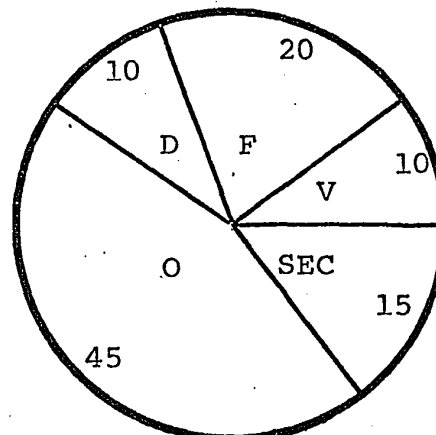
A. achilles



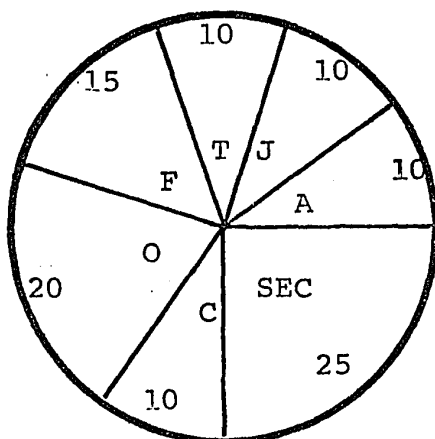
A. leucopareius



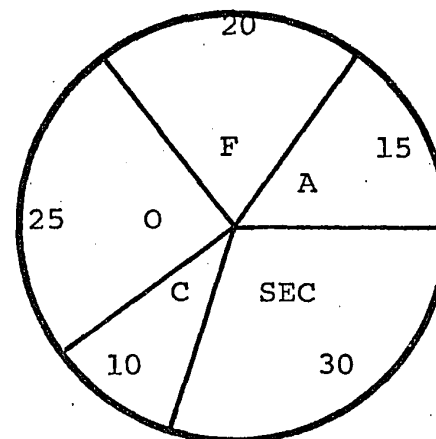
A. nigrofuscus



A. nigroris

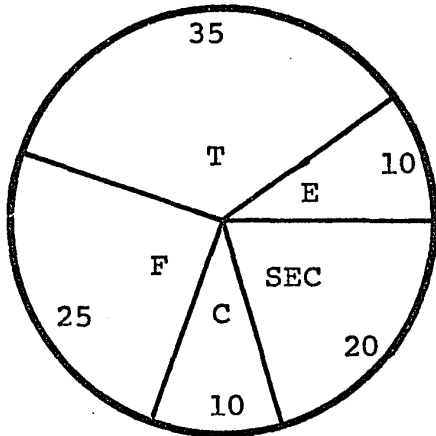


A. sandvicensis

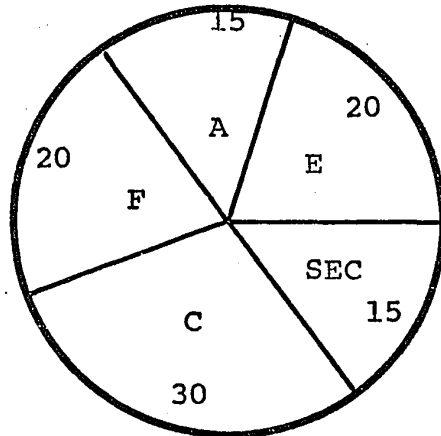


Z. flavescens

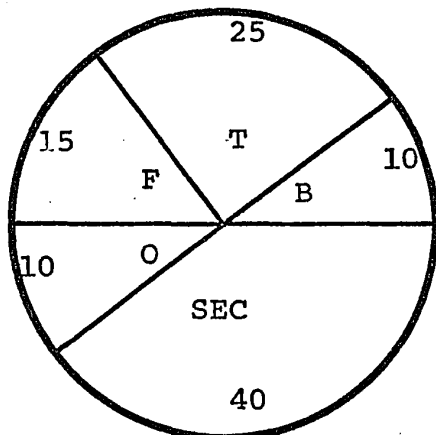
FIGURE 7. PERCENT OF PRIMARY FOODS EATEN BY THE  
SPECIES AT LA PEROUSE BAY, MAUI (SEE FIG. 6  
FOR KEY TO THE PRIMARY ALGAE)



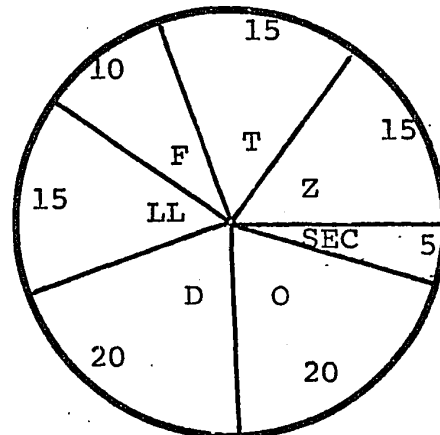
A. achilles



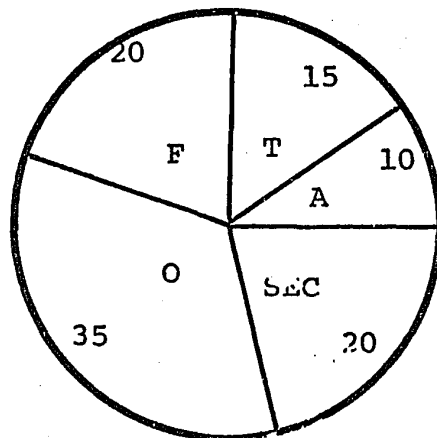
A. leucopareius



A. nigrofuscus



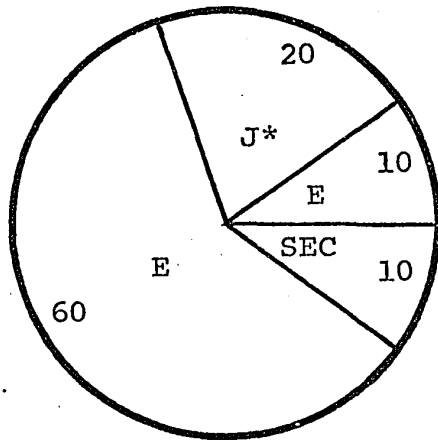
A. nigroris



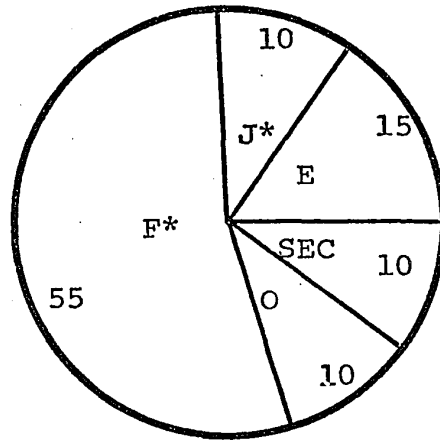
A. sandvicensis

FIGURE 8. PERCENT OF PRIMARY FOODS EATEN BY THE  
SPECIES AT JOHNSTON ISLAND STATION 1 (SEE FIG.  
6 FOR KEY TO THE PRIMARY ALGAE)

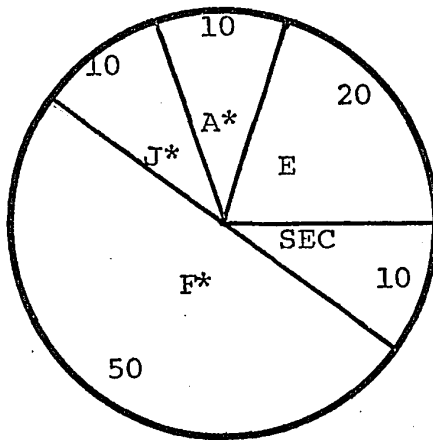
An asterisk (\*) denotes algae that were found to  
be dominant by Buggeln and Tsuda (1966) at the  
Johnston Island Stations studied.



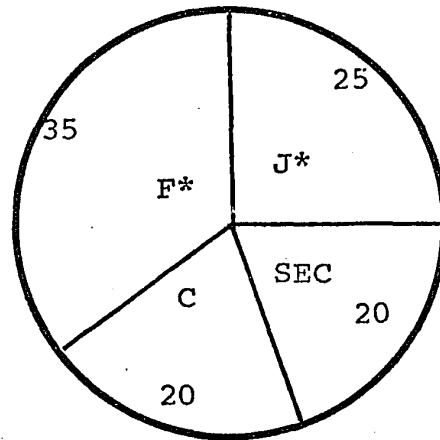
A. achilles



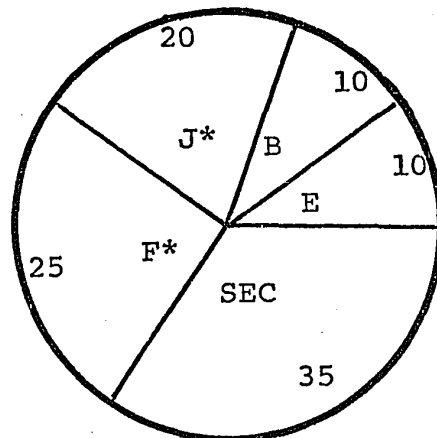
A. glaucopareius



A. nigroris

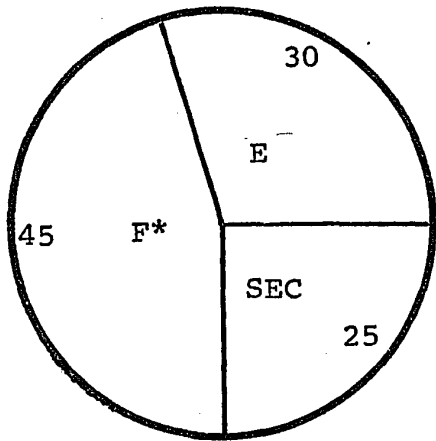


A. sandvicensis

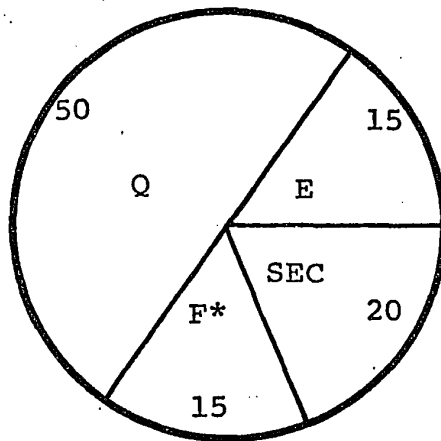


Z. flavescens

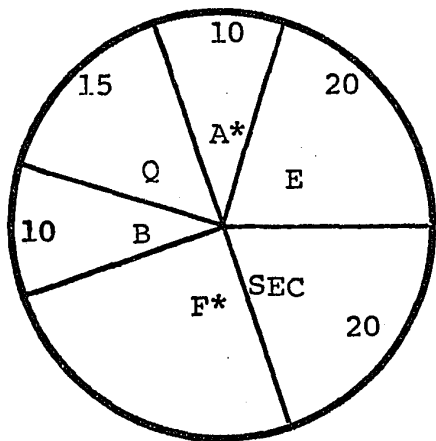
FIGURE 9. PERCENT OF PRIMARY FOODS EATEN BY THE  
SPECIES AT JOHNSTON ISLAND STATION 3 (SEE FIG.  
6 FOR KEY TO THE PRIMARY ALGAE)



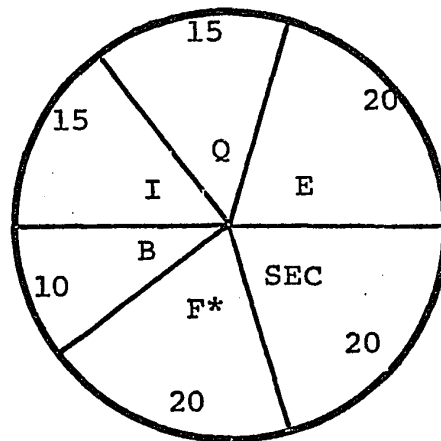
A. achilles



A. nigroris



A. sandvicensis



Z. flavescens

FIGURE 10. PERCENT OF PRIMARY FOODS EATEN BY THE  
SPECIES AT JOHNSTON ISLAND STATION 4 (SEE FIG.  
6 FOR KEY TO THE PRIMARY ALGAE)



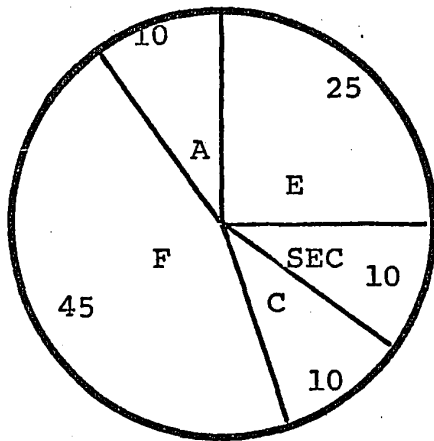
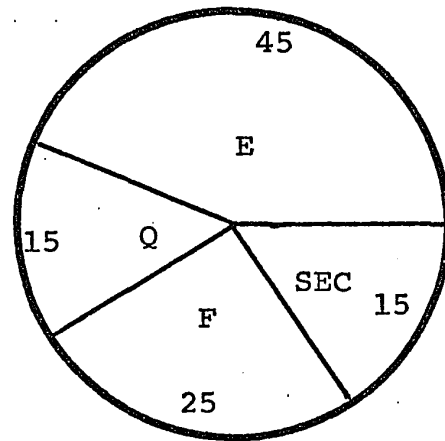
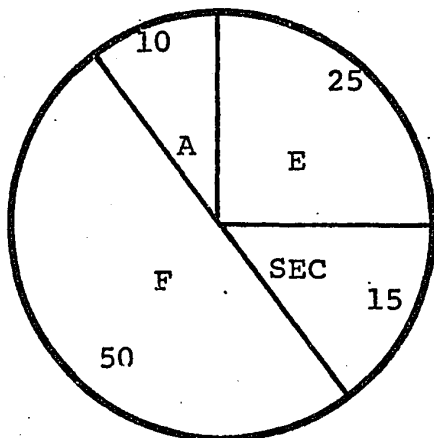
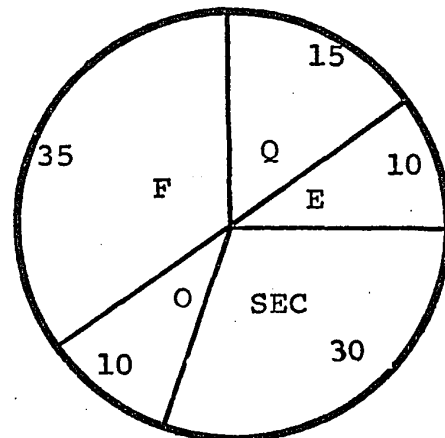
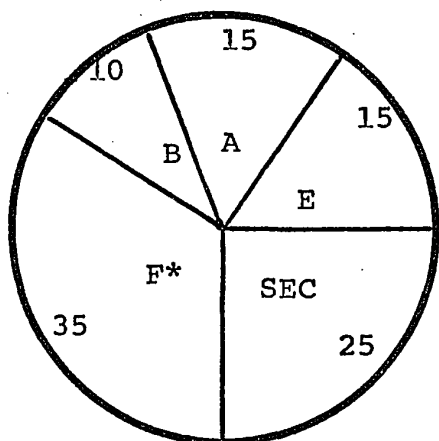
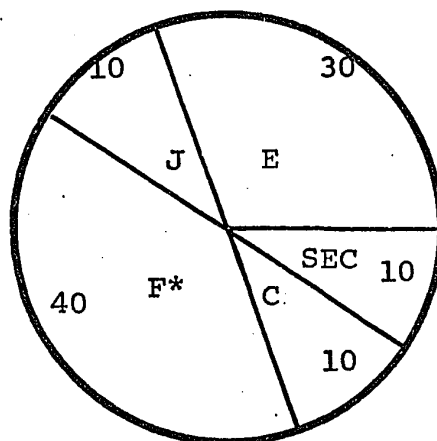
A. achillesA. nigrorisA. sandvicensisZ. flavescens

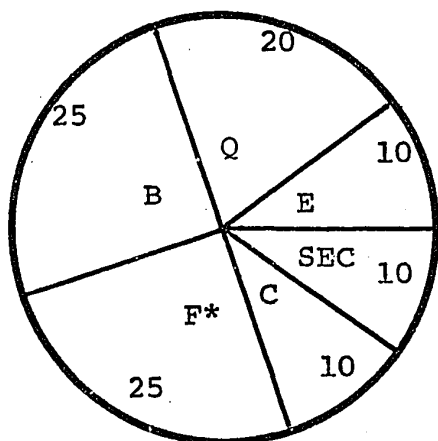
FIGURE 11. PERCENT OF PRIMARY FOODS EATEN BY THE  
SPECIES AT JOHNSTON ISLAND STATION 6 (SEE FIG.  
6 FOR KEY TO THE PRIMARY ALGAE)



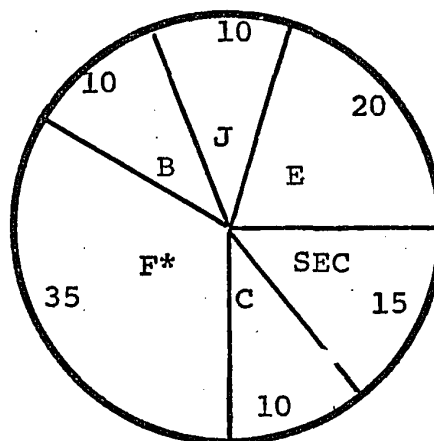
A. achilles



A. nigroris

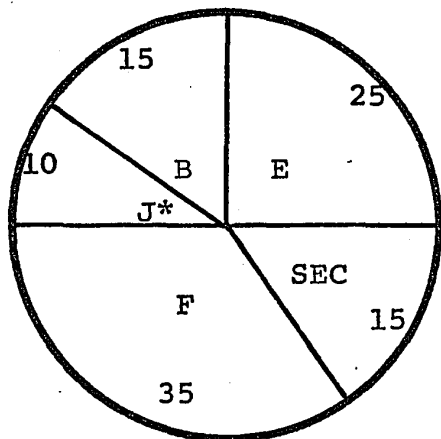


A. sandvicensis

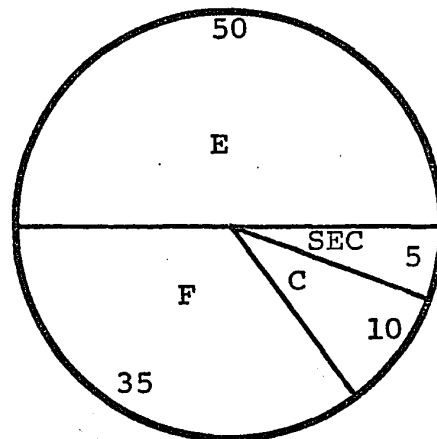


Z. flavescens

FIGURE 12. PERCENT OF PRIMARY FOODS EATEN BY THE  
SPECIES AT JOHNSTON ISLAND STATION 8 (SEE FIG.  
6 FOR KEY TO THE PRIMARY ALGAE)



A. nigroris



A. sandvicensis

quantities of Dictyota, Dictyosphaeria, Jania, and Tolypiocladia. These genera were not found in the other species. At Johnston Island though its food habits were not as divergent from the other species, it still tended to differ considerably. It was the least specialized of the species investigated, feeding on 14 different primary algae. A. achilles was the most highly specialized feeding only on seven algal genera. A. sandvicensis and Zebrasoma flavescens were also quite variable in their feeding habits.

Except for Acanthurus nigroris, these fishes all eat very nearly the same algae at one time or another. However, there was no consistency in terms of composition or proportion in any of the fishes.

Tables VI to XII give information on overlap of primary foods between each species, and between each species and the rest of the acanthurid community at a particular station. Except in Acanthurus nigroris which had low overlap values with most other species and at most other stations, no other species ranked consistently high or low in terms of overlap. The overlap values between species vary considerably from station to station.

The average overlap values in Table XIII are no more

TABLE VI. PERCENT OVERLAP OF PRIMARY FOODS BETWEEN SPECIES FROM KEALAKEKUA BAY, HAWAII

	<u>A. ach.</u>	<u>A. leu.</u>	<u>A. nigf.</u>	<u>A. nigr.</u>	<u>A. san.</u>	<u>Z. fla.</u>
<u>A. ach.</u> <sup>1</sup>	X	59	75	35	60	71
<u>A. leu.</u>	59 <sup>2</sup>	X	44	59	60	79
<u>A. nigf.</u>	71	41	X	25	60	57
<u>A. san.</u>	53	53	56	41	X	79
<u>Z. fla.</u>	59	65	50	53	73	X
VS. ENTIRE ACANTHURID COMMUNITY	88 <sup>3</sup>	82	88	59	87	93
TOTAL PERCENT OF PRIMARY FOOD	85 <sup>4</sup>	85	80	85	75	70

<sup>1</sup> Abbreviations for species are A. ach.-Acanthurus achilles, A. leu.-A. leucopareius, A. nigf.-A. nigrofuscus, A. nigr.-A. nigroris, A. san.-A. sandvicensis, Z. fla.-Zebrasoma flavescens.

<sup>2</sup> This number represents the percent overlap of primary food between the species listed on the side of the table and those listed at the top (e.g., A. leucopareius eats 59 percent of the primary food eaten by A. achilles).

<sup>3</sup> This number represents the percent of primary food eaten in common between the species listed at the top of the table and the combined acanthurid community at this Station.

<sup>4</sup> The total percent of primary food found in the species listed at the top of the table.

TABLE VII. PERCENT OVERLAP OF PRIMARY FOODS BETWEEN SPECIES FROM LA PEROUSE BAY, MAUI (SEE TABLE VI. FOR COMPLETE EXPLANATION OF ENTRIES AND SPECIES ABBREVIATIONS).

	<u>A. ach.</u>	<u>A. leu.</u>	<u>A. niqf.</u>	<u>A. nigr</u>	<u>A. san.</u>
<u>A. ach.</u>	X	47	67	26	44
<u>A. leu.</u>	50	X	25	10	38
<u>A. niqf.</u>	50	18	X	37	50
<u>A. nigr.</u>	31	12	58	X	56
<u>A. san.</u>	44	35	67	47	X
VS. ENTIRE ACANTHURID COMMUNITY	81	59	83	47	81
TOTAL PERCENT OF PRIMARY FOOD	80	85	60	95	80



TABLE VIII. PERCENT OVERLAP OF PRIMARY FOODS BETWEEN SPECIES FROM JOHNSTON ISLAND STATION 1 (SEE TABLE VI FOR COMPLETE EXPLANATION OF ENTRIES AND SPECIES ABBREVIATIONS).

	<u>A. ach.</u>	<u>A. gla.</u>	<u>A. nigr.</u>	<u>A. san.</u>	<u>Z. fla.</u>
<u>A. ach.</u>	X	83	78	69	65
<u>A. gla.</u> <sup>1</sup>	83	X	83	56	53
<u>A. nigr.</u>	78	83	X	56	53
<u>A. san.</u>	61	50	50	X	53
<u>Z. fla.</u>	61	50	50	56	X
VS. ENTIRE ACANTHURID COMMUNITY	94	89	83	69	85
TOTAL PERCENT OF PRIMARY FOOD	90	90	90	80	65

<sup>1</sup>A. gla-Acanthurus glaucopareius

TABLE IX. PERCENT OVERLAP OF PRIMARY FOODS BETWEEN SPECIES FROM JOHNSTON ISLAND STATION 3 (SEE TABLE VI FOR COMPLETE EXPLANATION OF ENTRIES AND SPECIES ABBREVIATIONS).

	<u>A. ach.</u>	<u>A. nigr.</u>	<u>A. san.</u>	<u>Z. fla.</u>
<u>A. ach.</u>	X	38	56	50
<u>A. nigr.</u>	40	X	56	56
<u>A. san.</u>	60	56	X	81
<u>Z. fla.</u>	53	56	81	X
VS. ENTIRE ACANTHURID COMMUNITY	60	56	88	81
TOTAL PERCENT OF PRIMARY FOOD	75	80	80	80

TABLE X. PERCENT OVERLAP OF PRIMARY FOODS BETWEEN SPECIES FROM JOHNSTON ISLAND STATION 4 (SEE TABLE VI FOR COMPLETE EXPLANATION OF ENTRIES AND SPECIES ABBREVIATIONS).

	<u>A. ach.</u>	<u>A. nigr.</u>	<u>A. san.</u>	<u>Z. fla.</u>
<u>A. ach.</u>	X	59	94	64
<u>A. nigr.</u>	56	X	59	71
<u>A. san.</u>	89	59	X	64
<u>Z. fla.</u>	50	59	52	X
<u>VS. ENTIRE</u>				
<u>ACANTHURID</u>	89	76	94	86
<u>COMMUNITY</u>				
<u>TOTAL</u>				
<u>PERCENT OF</u>	90	85	85	70
<u>PRIMARY</u>				
<u>FOOD</u>				

TABLE XI. PERCENT OVERLAP OF PRIMARY FOODS BETWEEN SPECIES FROM JOHNSTON ISLAND STATION 6 (SEE TABLE VI FOR COMPLETE EXPLANATION OF ENTRIES AND SPECIES ABBREVIATIONS).

	<u>A. ach.</u>	<u>A. nigr.</u>	<u>A. san.</u>	<u>Z. fla.</u>
<u>A. ach.</u>	X	56	50	71
<u>A. nigr.</u>	67	X	50	76
<u>A. san.</u>	60	50	X	65
<u>Z. fla.</u>	80	72	61	X
VS. ENTIRE ACANTHURID COMMUNITY	80	72	61	88
TOTAL PERCENT OF PRIMARY FOOD	75	90	90	85

TABLE XII. PERCENT OVERLAP OF PRIMARY FOODS BETWEEN SPECIES FROM JOHNSTON ISLAND STATION 8 (SEE TABLE VI FOR COMPLETE EXPLANATION OF ENTRIES AND SPECIES ABBREVIATIONS).

	<u>A. nigr.</u>	<u>A. san.</u>
<u>A. nigr.</u>	X	63
<u>A. san.</u>	71	X
TOTAL PERCENT OF PRIMARY FOOD	85	95

TABLE XIII. AVERAGE OVERLAP DATA FOR  
 INTERSPECIFIC/INTRASTATION COMPARISONS  
 (SEE TABLES VI AND XIV FOR ABBREVIATIONS).

	<u>A. ach.</u>	<u>A. gla.</u>	<u>A. leu.</u>	<u>A. nigf.</u>	<u>A. nigr.</u>	<u>A. san.</u>	<u>Z. fla.</u>	STATION OVERLAP	LOCALITY OVERLAP
KB	55 <sup>1</sup>	X	55	50	43	60	70	55 <sup>2</sup>	48 <sup>3</sup>
LPB	44	X	28	54	33	47	X	41	
JI 1	71	66	X	X	65	59	56	63	
JI 3	51	X	X	X	50	64	62	57	
JI 4	65	X	X	X	59	68	66	64	62
JI 6	69	X	X	X	59	54	71	63	

<sup>1</sup>Average percent overlap between each species and the rest of the acanthurid community at each station (e.g., A. achilles food was overlapped by other fish by 55 percent).

<sup>2</sup>Average percent overlap for all species at each station.

<sup>3</sup>Average percent overlap for all species at each locality (Hawaii and Johnston Island).

rewarding than the above. In general the Hawaiian populations showed less overlap (48 percent) than the Johnston Island populations (62 percent). Finally the data would seem to indicate that though there was considerable overlap and similarity in diet for these fishes no two species were completely identical at any station for composition or amount of food.

#### INTRASPECIFIC/INTERSTATION COMPARISONS

Only three species were collected consistently from all stations, these were Acanthurus achilles, A. nigroris, and A. sandvicensis.

A. achilles had an average overlap of 60 percent (Table XVII). Greatest overlap would occur between Johnston Stations 3 (93 percent) and 4 (78 percent) if the populations were brought together (Table XIV). The least amount of overlap occurred between Johnston Island Station 1 (40 percent) and La Perouse Bay (45 percent).

A. nigroris had an average overlap of only 33 percent (Table XVII). Greatest overlap (78 percent) was between Johnston Island Stations 1 and 6 (Table XV). Johnston Island and La Perouse Bay specimens generally overlapped

TABLE XIV. PERCENT OVERLAP OF PRIMARY FOODS  
 BETWEEN POPULATIONS OF ACANTHURUS ACHILLES  
 FROM DIFFERENT STATIONS.

	KB	LPB	JI 1	JI 3	JI 4	JI 6
KB <sup>1</sup>	X	56	50	60	72	73
LPB	53	X	39	47	50	47
JI 1	53	44	X	73	61	60
JI 3	53	44	61	X	78	73
JI 4	76	56	61	93	X	80
JI 6	65	44	50	73	67	X

<sup>1</sup>Abbreviations for Stations are: KB-Kealakekua Bay, Hawaii; LPB-La Perouse Bay, Maui; JI 1-Johnston Island Station 1 (etc.).



TABLE XV. PERCENT OVERLAP OF PRIMARY FOODS  
 BETWEEN POPULATIONS OF ACANTHURUS NIGRORIS  
 FROM DIFFERENT STATIONS (SEE TABLE XIV  
 FOR STATION ABBREVIATIONS).

	KB	LPB	JI 1	JI 3	JI 4	JI 6
KB	X	42	22	19	24	22
LPB	47	X	11	12	12	11
JI 1	24	10	X	38	53	78
JI 3	18	10	33	X	53	33
JI 4	24	10	50	56	X	61
JI 6	24	10	78	38	65	X

TABLE XVI. PERCENT OVERLAP OF PRIMARY FOODS  
 BETWEEN POPULATIONS OF ACANTHURUS SANDVICENSIS  
 FROM DIFFERENT STATIONS (SEE TABLE XIV  
 FOR STATION ABBREVIATIONS).

---

	KB	LPB	JI 1	JI 3	JI 4	JI 6
KB	X	69	44	31	29	28
LPB	73	X	25	25	35	22
JI 1	47	25	X	31	41	39
JI 3	33	25	31	X	65	67
JI 4	33	38	44	69	X	39
JI 6	33	25	44	75	41	X

---

only 19 percent.

A. sandvicensis had an average interstation overlap value of 41 percent (Table XVII). The greatest overlap (Table XVI) was only 73 percent between Kealakekua Bay and La Perouse Bay specimens (not reciprocal) and between Johnston Island Station 3 (75 percent) and 6 (not reciprocal).

Only A. achilles showed any degree of stability between stations. Figures 6-11 show that they are fairly consistent over the algae they eat. This evidence plus the complete disparity of data for A. nigroris (33 percent) and A. sandvicensis (41 percent) would indicate that the diet of these fishes, within limits, depends largely on the environment (Table XVII).

TABLE XVII. AVERAGE OVERLAP DATA FOR  
INTRASPECIFIC/INTERSTATION COMPARISONS.

	<u>Acanthurus</u> <u>achilles</u>	<u>A.</u> <u>nigroris</u>	<u>A.</u> <u>sandvicensis</u>
KEALAKEKUA BAY	60 <sup>1</sup>	27	44
	54 <sup>2</sup>	22	40
LA PEROUSE BAY	49	16	36
	60 <sup>3</sup>	33	41
JOHNSTON IS. 1	52	39	37
JOHNSTON IS. 3	69	33	46
	64	38	41
JOHNSTON IS. 4	66	41	42
JOHNSTON IS. 6	67	41	39

<sup>1</sup>Average percent overlap for each species population and each station.

<sup>2</sup>Average percent overlap for each species and all stations in one locality (e.g., Hawaii and Johnston Island).

<sup>3</sup>Average percent overlap for each species and all stations in both localities.

## CHAPTER V

### COMPARATIVE GROSS MORPHOLOGY

#### GENERAL

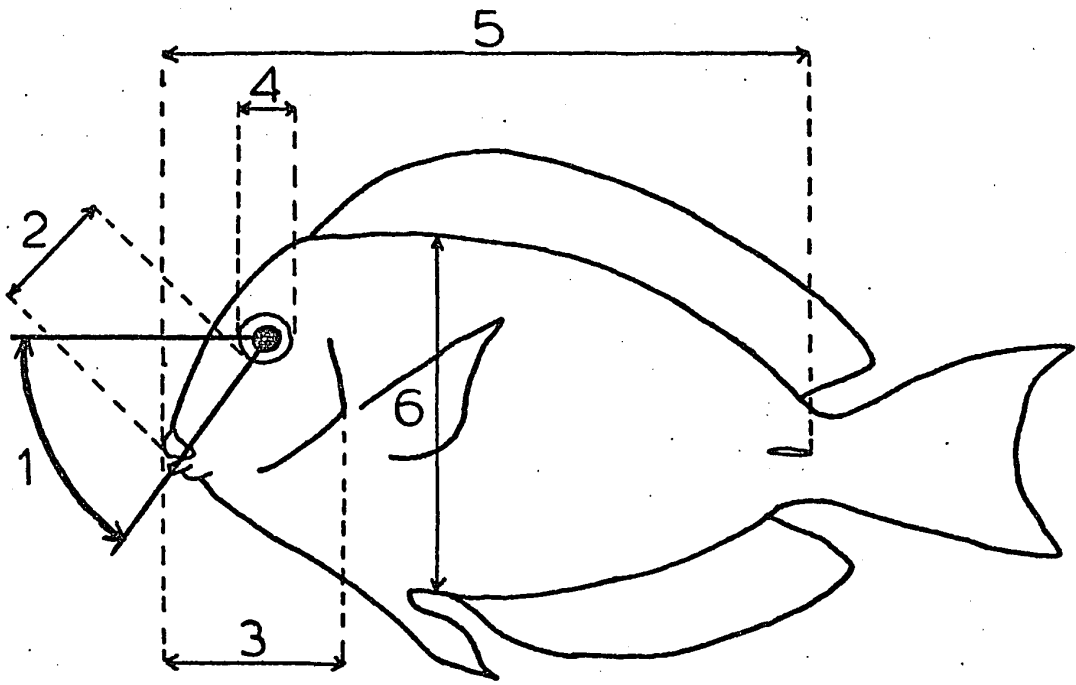
Field observations and stomach analyses made during this study have shown that many of the Acanthuridae have different foraging methods and that they frequently feed on different foods (Chapters III and IV). As an integral part of this study an investigation of the comparative morphology, primarily of the alimentary canal system, was carried out and is reported here. It would seem highly unlikely that variations in the alimentary canal systems of the species would have no adaptive significance. It is here postulated that when these variations occur between acanthurid species, they suggest species specific differences in handling food material. Thus even though two species might be eating essentially the same food, there are modifications in the food handling apparatus that result in each species being more adept in certain aspects of feeding than the others.

#### EXTERNAL MORPHOLOGY

**BODY SHAPE:** The shape or general body form is often correlated with the habitat occupied by a fish (Fryer,

FIGURE 13. A GENERALIZED ACANTHURID SHOWING SOME  
OF THE MEASUREMENTS USED IN DISCUSSION OF  
MORPHOLOGICAL ADAPTATIONS FOR FEEDING

- 1-Eye/mouth angle
- 2-Snout length
- 3-Head length
- 4-Diameter of the eye
- 5-Standard length
- 6-Body depth



1959b and Keast, 1966). Body depth into standard length was used as an indication of body shape (Fig. 13 and Table XVIII).

The mid-water dwellers, Acanthurus thompsoni (Fig. 14f) and Naso hexacanthus (Fig. 16c) are among the most elongate species of their respective genera (Table XVIII). The mid-water existence and active zooplankton feeding habits of these animals may be correlated with the body shape.

The species of Acanthurus found over or around sandy areas (A. dussumieri, Fig. 14e; A. mata; A. olivaceus; and A. xanthopterus) are slightly more elongate than most of the remaining members of this genus (Table XVIII).

Fishes most closely associated with reef and rocky substrata tend to be deeper bodied. These animals rarely swim in open water or over open bottom; hence they are never far from cover. This group includes A. achilles (Fig. 14a) A. glaucopareius, A. guttatus (Fig. 14b), A. leucopareius, A. nigroris, A. sandvicensis (Fig. 14c), Ctenochaetus hawaiiensis (Fig. 15a), C. strigosus (Fig. 15b), Zebrasoma flavescens (Fig. 17a), and Z. veliferum. However, the reef-dwelling Acanthurus nigrofuscus (Fig. 14d) is very nearly as elongate as the mid-water form, A. thompsoni (Fig. 14f).



TABLE XVIII. PROPORTIONAL MEASUREMENTS AND ANGLES OF POSSIBLE SIGNIFICANCE IN FEEDING (SEE FIGURE 13): BD-MAXIMUM BODY DEPTH INTO STANDARD LENGTH, SNT-SNOUT INTO HEAD, EYE-EYE DIAMETER INTO SNOUT, EYE/MOUTH-ANGLE BETWEEN THE EYE AND THE MOUTH (TWO TO FIVE SPECIMENS OF EACH SPECIES WERE USED AND THE MEASUREMENTS AVERAGED).

<u>SPECIES</u>	<u>BD</u>	<u>SNT</u>	<u>EYE</u>	<u>EYE/MOUTH</u>
<u>Acanthurus thompsoni</u>	2.3	8.0	1.7	48°
<u>A. achilles</u>	1.8	4.0	3.2	62°
<u>A. glaucopareius</u>	1.8	4.1	2.8	62°
<u>A. guttatus</u>	1.6	3.9	3.8	62°
<u>A. leucopareius</u>	1.8	4.2	3.0	62°
<u>A. nigrofuscus</u>	2.2	4.6	2.6	56°
<u>A. nigroris</u>	1.9	4.2	3.2	58°
<u>A. sandvicensis</u>	1.9	4.8	2.7	55°
<u>A. dussumieri</u>	2.0	4.4	3.4	50°
<u>A. mata</u>	2.0	4.4	3.2	50°
<u>A. olivaceus</u>	2.4	4.7	3.2	50°
<u>A. xanthopterus</u>	2.1	4.9	3.2	52°
<u>Ctenochaetus hawaiiensis</u>	1.8	3.7	3.8	50°
<u>C. strigosus</u>	1.9	4.6	3.2	55°
<u>Naso brevirostris</u>	2.8	6.0	2.0	33°

TABLE XVIII. (Continued) PROPORTIONAL MEASUREMENTS AND ANGLES OF POSSIBLE SIGNIFICANCE IN FEEDING (SEE FIGURE 13): BD-MAXIMUM BODY DEPTH INTO STANDARD LENGTH, SNT-SNOUT INTO HEAD, EYE-EYE DIAMETER INTO SNOUT, EYE/MOUTH-ANGLE BETWEEN THE EYE AND THE MOUTH (TWO TO FIVE SPECIMENS OF EACH SPECIES WERE USED AND THE MEASUREMENTS AVERAGED).

<u>SPECIES</u>	<u>BD</u>	<u>SNT</u>	<u>EYE</u>	<u>EYE/MOUTH</u>
<u>N. hexacanthus</u>	3.0	6.6	2.0	27°
<u>N. lituratus</u>	2.7	4.3	3.1	33°
<u>N. unicornis</u>	2.8	4.4	3.3	38°
<u>Zebrasoma flavescens</u>	1.7	4.3	3.1	47°
<u>Z. veliferum</u>	1.8	4.6	3.3	45°

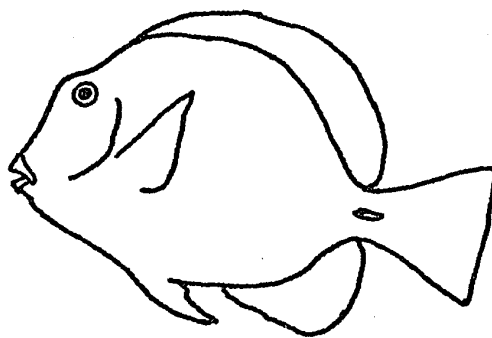
FIGURE 14. REPRESENTATIVE SPECIES OF ACANTHURUS

a. A. achilles, b. A. guttatus, c. A. sandvi-  
censis (After Randall, 1956)

a.



b.



c.

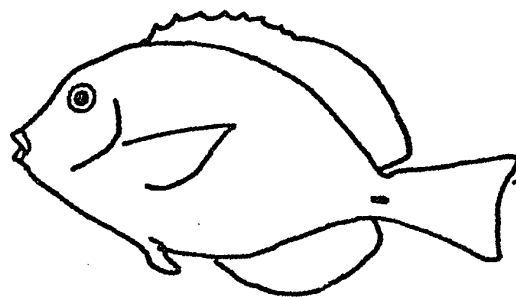


FIGURE 14 (Continued) d. A. nigrofuscus (profile retouched), e. A. dussumieri, f. A. thompsoni (d and f after Randall, 1956).

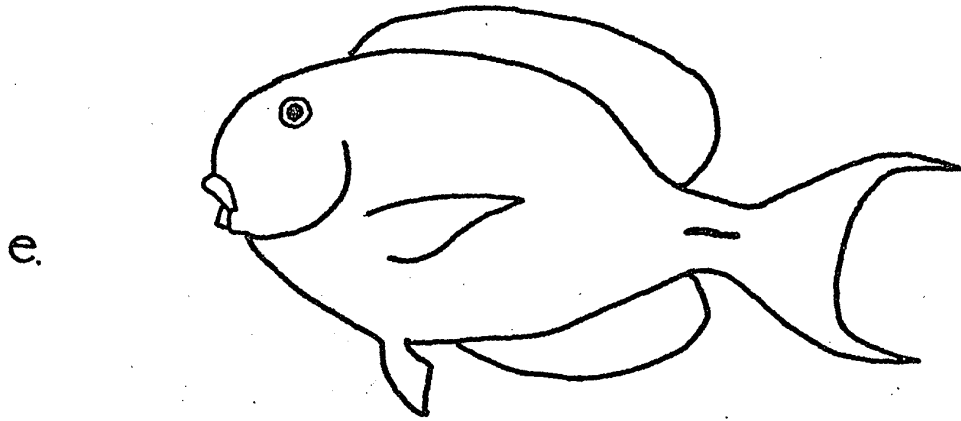
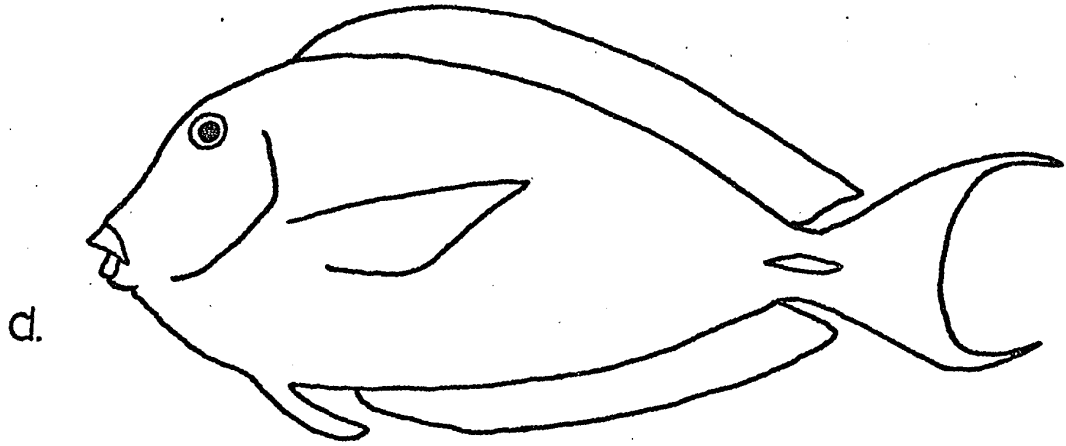
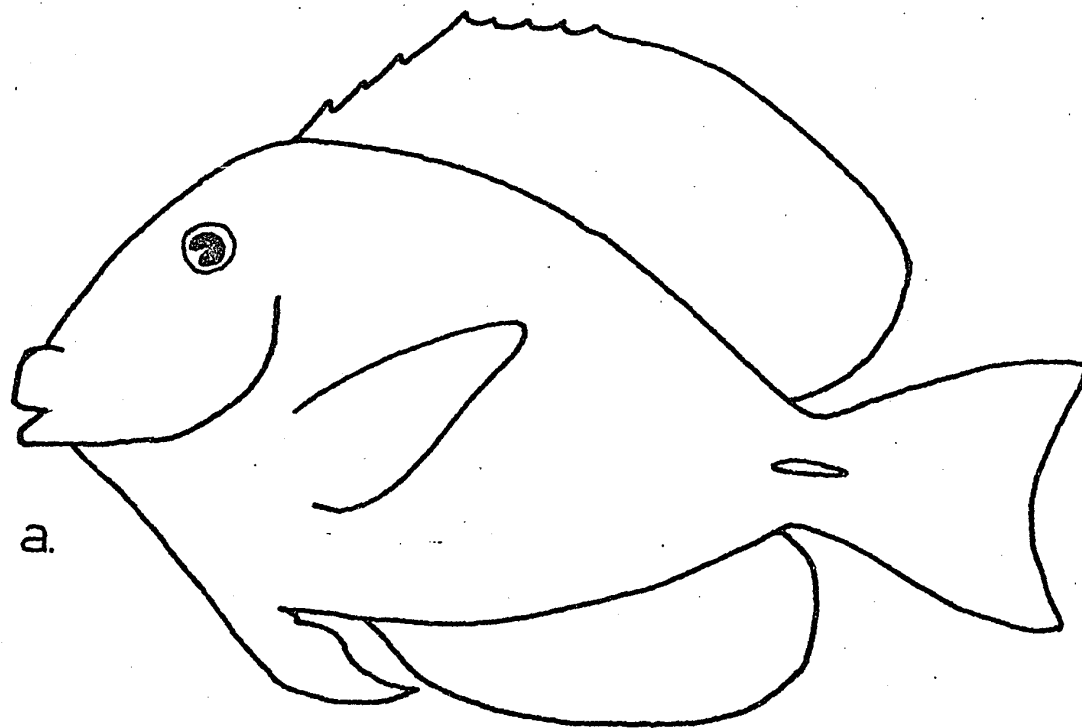
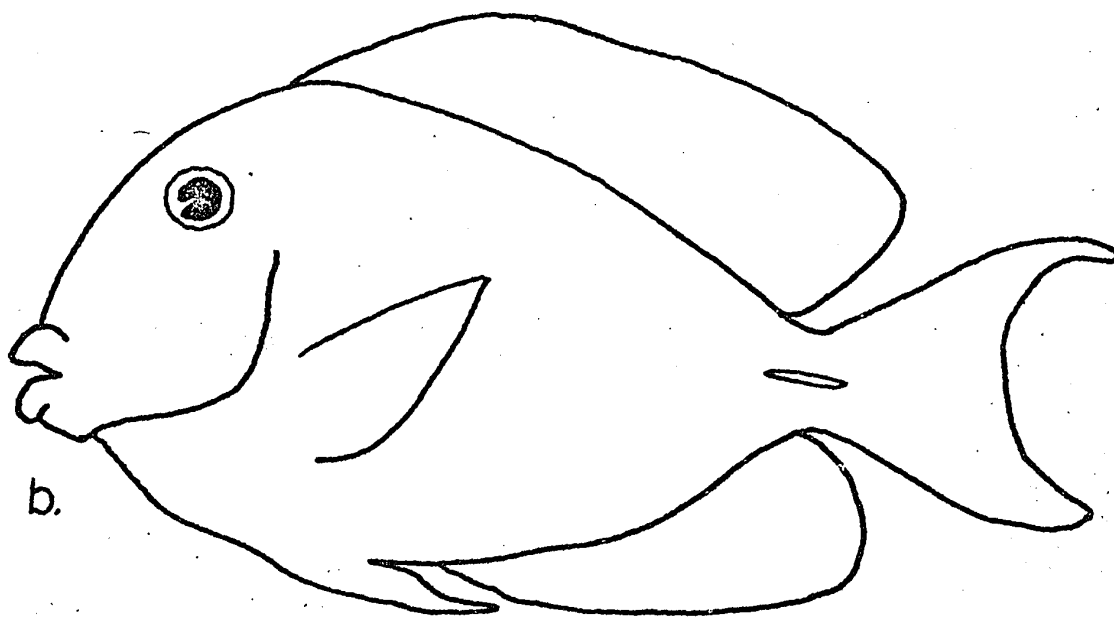


FIGURE 15. REPRESENTATIVE SPECIES OF CTENOCHAETUS

a. C. hawaiiensis, b. C. strigosus  
(After Randall, 1955d).



a.

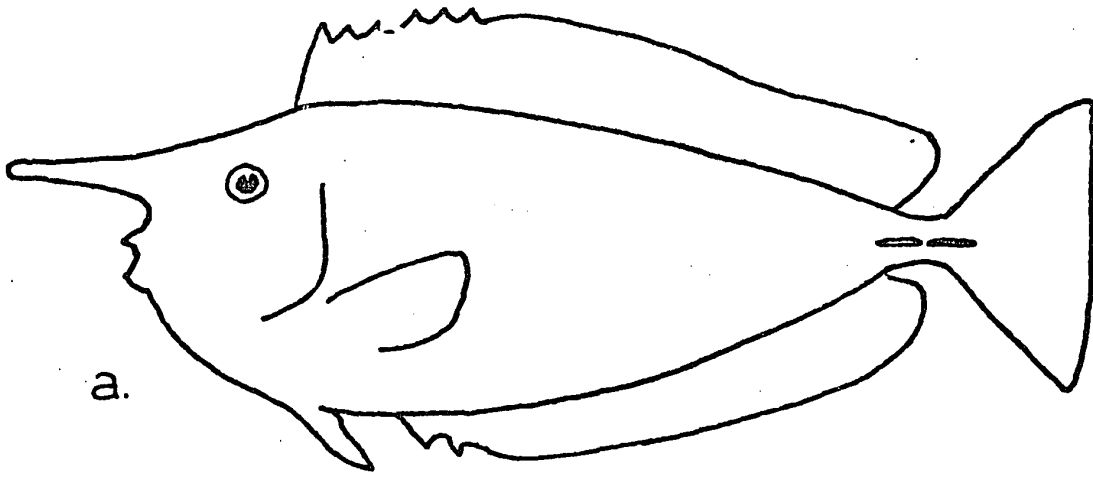


b.

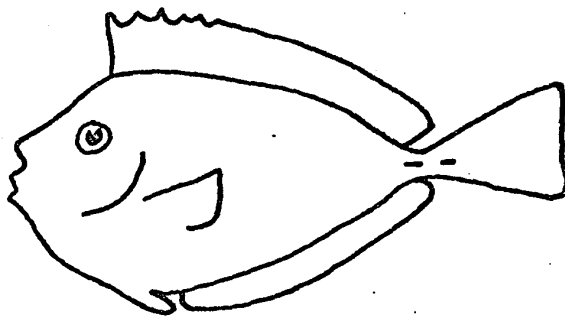


FIGURE 16. REPRESENTATIVE SPECIES OF NASO

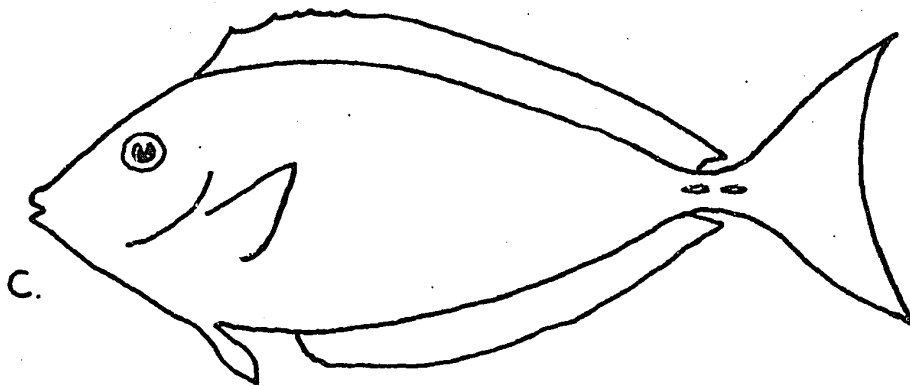
- a. N. brevirostris adult (556mm),
- b. subadult (140mm), c. N. hexa-  
canthus (400mm) (After Smith, 1966).



a.



b.



c.

FIGURE 16. (Continued) d. N. lituratus  
(604mm), e. N. unicornis (604mm)  
(After Smith, 1966, Caudal fila-  
ments eliminated in d.).

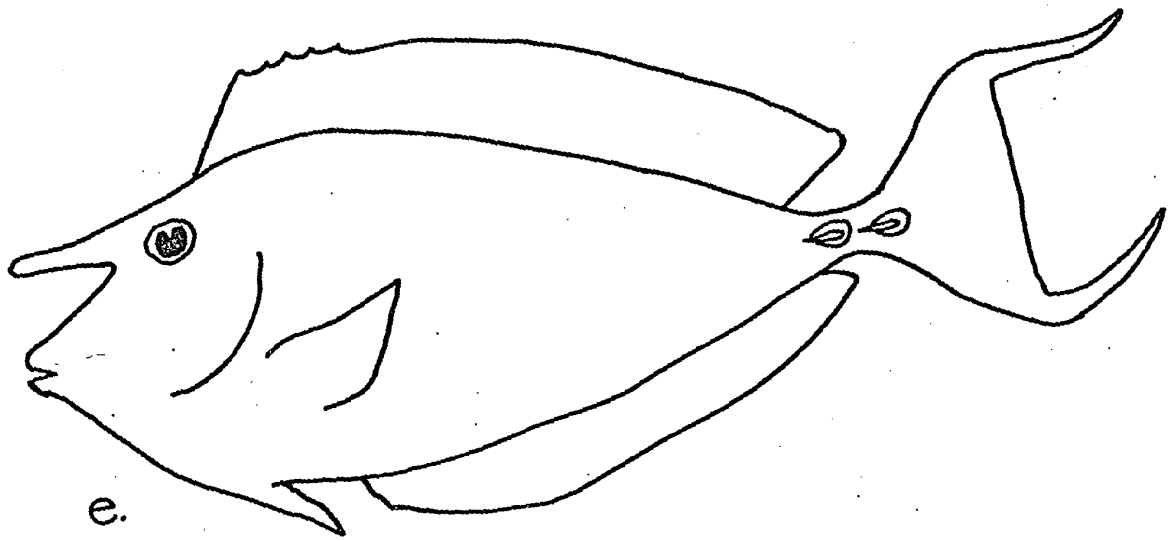
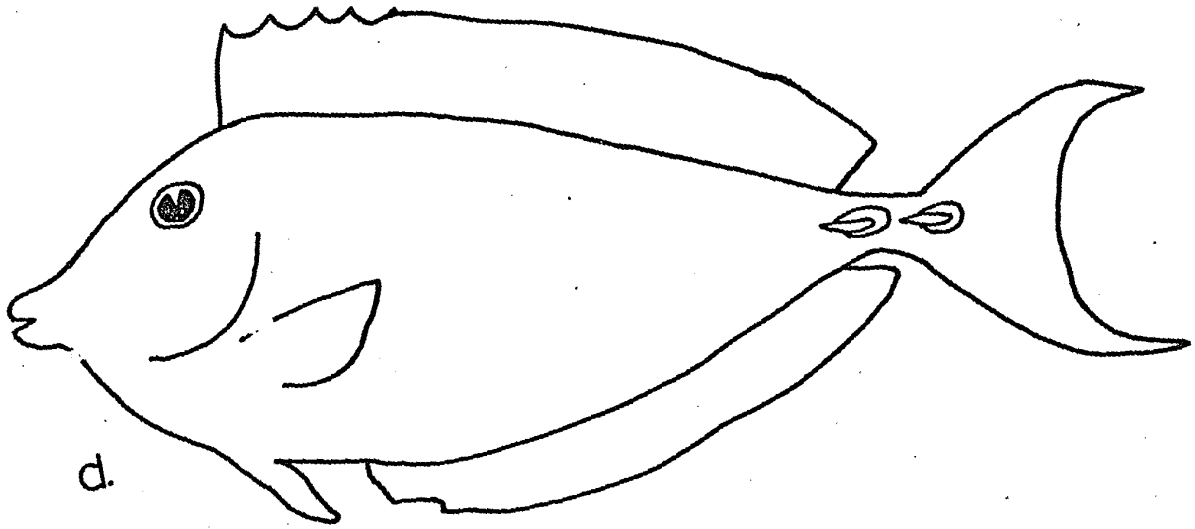
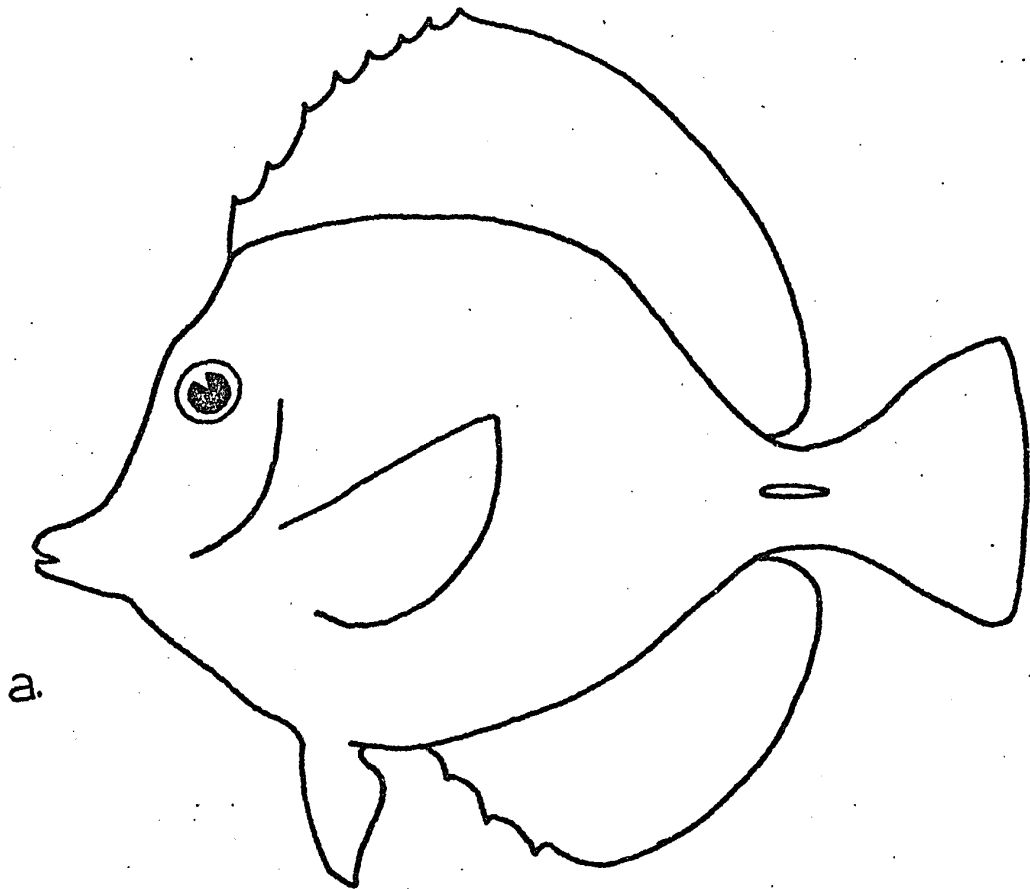
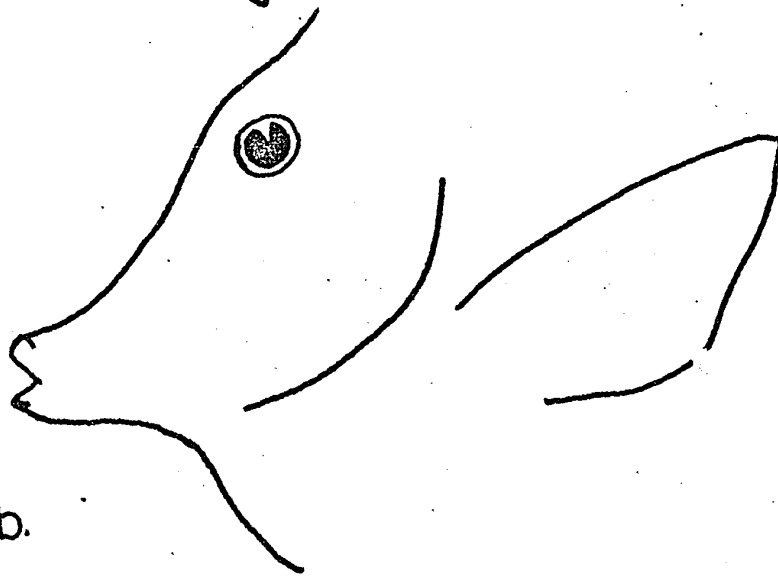


FIGURE 17. REPRESENTATIVE SPECIES OF ZEBRASOMA

a. Z. flavescens (After Jordan and Evermann, 1905), b. profile of Z. veliferum.



a.



b.

PROFILE OF THE HEAD: In comparing species of acanthurids differences in the profile of the head were noted. It is felt that the head profile and in particular the shape of the snout may have some bearing on the fish's "adaptations for" feeding.

Acanthurus dussumieri (Fig. 14e), A. mata, A. olivaceus, and A. xanthopterus all have quite rounded profiles that may be somewhat bulging above the mouth (Randall, 1956). The species of Ctenochaetus also have rounded profiles (Fig. 15), though this is not as well developed in C. hawaiiensis. The presence of this character in both genera suggests a possible relationship with the peculiar, almost vertical, feeding posture of the grazers (Chapter III).

In both Naso lituratus (Fig. 16d) and N. unicornis (Fig. 16e) the head profile is angular and the snout produced, providing possibly an effective feeding mechanism for getting at algae in restricted crevices. The head profile of N. brevirostris, is almost vertical. This species has a well developed horn in the adults while the juveniles have only a small protuberance (Figs. 16 a and b). In the adult the horn may protrude out beyond the snout.

Due to the produced snout, there may be a possible feeding disadvantage in this species restricting it to algae growing either quite tall or on flat or rounded surfaces, especially in the adults with the horn extending out well beyond the mouth. It would seem virtually impossible for the species to get the mouth down to the substratum due to interference from the horn (J. E. Randall, personal communication).

Food studies in Chapters III and IV show that Zebrasoma and the browsing Acanthurus eat very similar foods but the greatly produced snout of Zebrasoma (Fig. 17) might allow this genus to reach into cracks for algae not available to Acanthurus.

POSITION OF THE MOUTH: The position of the mouth may be important in terms of feeding behavior. In particular the location of the mouth relative to the eye would seem to be of significance for food gathering. Randall's (1961a) experiments on stimulus to feeding in A. sandvicensis indicated that this species selected food by sight and used olfactory senses for rejection of unsavory material. Field observations suggest that sight selection of food is important in most acanthurids.



Consequently, the distance from eye to mouth (snout length), the size of the eye, and the actual position of the mouth on the head relative to the eye are considered important.

Snout length: The proportional snout length is measured from the anterior edge of the orbit to the tip of the snout and divided into the standard length (Fig. 13 and Table XVIII).

Eye: The proportional size of the eye is measured as the width of the eye into the snout length (Fig. 13 and Table XVIII). A large eye is possibly important in animals that feed on small food particles.

Mouth angle: The position of the mouth relative to the eye is measured as an angle. Figure 13 shows the construction of this angle. The data are shown in Table XVIII. A small angle indicates that the mouth tends to be more in line with the eye and the horizontal plane and that the fish must look ahead for its food. A larger angle indicates that the mouth is located low on the head and that a fish must look down to see its food.

Acanthurus thompsoni, Naso hexacanthus, and N. brevirostris all have large eyes and short snouts. This

brings the eyes into close proximity with the mouth. The mouth is located high on the head and almost directly in front of the eye allowing for straight ahead pursuit in feeding. This would seem to be particularly advantageous to the zooplankton feeding Acanthurus thompsoni and Naso hexacanthus.

The small mouth angles in N. lituratus, N. unicornis and the Zebrasomas (Table XVIII) shows that the location of the mouth is high on the head more nearly in line with the eye and the horizontal plane of these animals than in other browsers. This may be indicative of an ability to select individual algal thalli. This is especially true of the Naso which characteristically feed on algal genera that are large and quite visible individually. In both Naso and Zebrasoma the alignment of the eye and the mouth seems advantageous for aiming the snout into crevices to reaching food growing there.

#### THE ALIMENTARY CANAL

##### MOUTH:

Projection of the Mouth: The mouths of the Acanthuridae are only slightly protrusile. Observations on feeding behavior and anatomy reveal some protrusibility of the

mouth in Ctenochaetus. Feeding observations suggest a very slight protrusion of the mouths of Acanthurus dussumieri, A. mata, A. olivaceus, and A. xanthopterus. In the above grazers there may be a need for a combination of a biting and sucking action to engulf a mouthful of the substratum upon which these fishes normally feed (Chapter III). Feeding observations show that both genera apply the mouth and lips close to the substratum when feeding. This seems to be necessary to provide a seal between the fish and the substratum that allows a suction pressure to build up. In the browsers, the lips are withdrawn from the teeth when algae is cropped from the substratum. Similarly, there does not appear to be a need as there is in the grazers, for great suction pressure coordinated with biting off of food.

Gape of the Mouth: The gape of the mouth is measured from rictus to rictus and then into the head length (Table XIX). In the majority of the Acanthuridae the mouth gape is moderate to large but in Acanthurus achilles, A. glaucopareius, A. thompsoni, all four of the Naso, and the Zebrasoma it is small. A small gape in Acanthurus thompsoni and Naso hexacanthus is not unexpected for fishes

FIGURE 18. ORIENTATION OF MOUTH GAPE MEASURED  
AS AN ANGLE

Line AB is drawn tangent to the open jaws, line CD is drawn parallel to the horizontal plane of the fish, angle ADE measures the direction in which the open mouth is pointed relative to the horizontal axis of the fish.

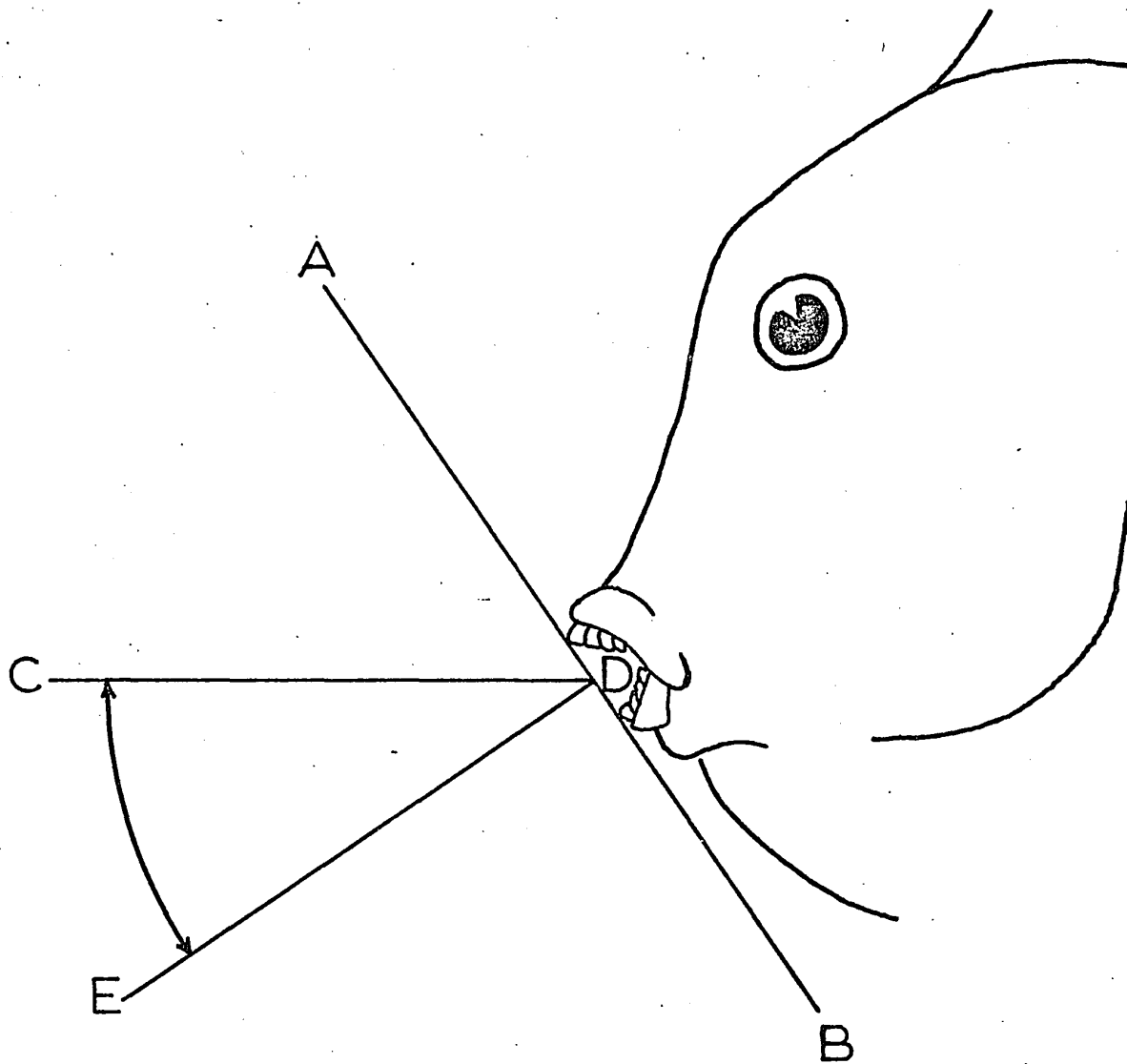


TABLE XIX. PROPORTIONAL MEASUREMENT WIDTH OF GAPE INTO HEAD, DIRECTION IN WHICH OPEN MOUTH POINTS (MEASURED AS AN ANGLE FIG. 16) AND MAXIMUM NUMBER OF TEETH IN THE UPPER AND LOWER JAWS FOR REPRESENTATIVE ACANTHURID SPECIES (TWO TO FIVE SPECIMENS OF EACH SPECIES WERE USED).

SPECIES	GAPE	DIRECTION OF MOUTH OPENING	MAXIMUM TEETH UPPER/LOWER <sup>1</sup>
<u>Acanthurus achilles</u>	6.2	25°	10/12
<u>A. glaucopareius</u>	4.9	25°	10/12
<u>A. guttatus</u>	3.7	60°	12/14
<u>A. leucopareius</u>	3.4	55°	16/20
<u>A. nigrofuscus</u>	X	35°	14/16
<u>A. nigroris</u>	X	50°	12/14
<u>A. sandvicensis</u>	3.5	50°	16/18
<u>A. dussumieri</u>	X	25°	20/22
<u>A. mata</u>	X	25°	20/20
<u>A. olivaceus</u>	4.0	30°	20/21
<u>A. xanthopterus</u>	X	25°	18/21
<u>A. thompsoni</u>	6.2	-10°	21/24
<u>Ctenochaetus strigosus</u>	4.1	20°	40/40
<u>Naso brevisrostris</u>	4.4	15°	50/40
<u>N. lituratus</u>	4.6	15°	35/30

TABLE XIX. (Continued) PROPORTIONAL MEASUREMENT OF WIDTH OF GAPE INTO HEAD, DIRECTION IN WHICH OPEN MOUTH POINTS (MEASURED AS AN ANGLE FIG.16) AND MAXIMUM NUMBER OF TEETH IN THE UPPER AND LOWER JAWS FOR REPRESENTATIVE ACANTHURID SPECIES (TWO TO FIVE SPECIMENS OF EACH SPECIES WERE USED) .

SPECIES	GAPE	DIRECTION OF MOUTH OPENING	MAXIMUM TEETH UPPER/ LOWER <sup>1</sup>
<u>N. unicornis</u>	4.7	15°	60/60
<u>N. hexacanthus</u>	5.6	0°	60/70
<u>Zebrasoma flavescens</u>	5.1	30°	18/22

<sup>1</sup>After Randall for Zebrasoma (1955c), for Ctenochaetus (1955d), for Acanthurus (1956), and after Smith (1966) for Naso.

feeding on individual zooplankters. The drawing out of the snouts and mouths in N. lituratus, N. unicornis, and the Zebrasoma species is perhaps an evolutionary modification done at the expense of a wide gape. Observations made in Chapter III and the foregoing sections of this chapter indicate that these fishes are able to be quite selective and feed on a variety of substrata from which most browsers are excluded. In Acanthurus achilles and A. glaucopareius the mouth (jaws) are laterally compressed and form a beak-like structure (Fig. 14a).

Direction of Gape: Another possible feature of adaptive significance in the Acanthuridae involves the direction in which the opened mouth is pointing relative to the fish's head. The mouth angle, calculated as shown in Fig. 18, is a measure of this. Data for representative species are found in Table XIX. A small or negative angle indicates that the mouth opens forward or up. A large angle means that the mouth opens down.

The mouth opens straight ahead in Naso hexacanthus and upward in Acanthurus thompsoni. These modifications are in agreement with those of Fryer (1959 a and b) and Keast (1966) for the zooplankton feeding fishes they studied.



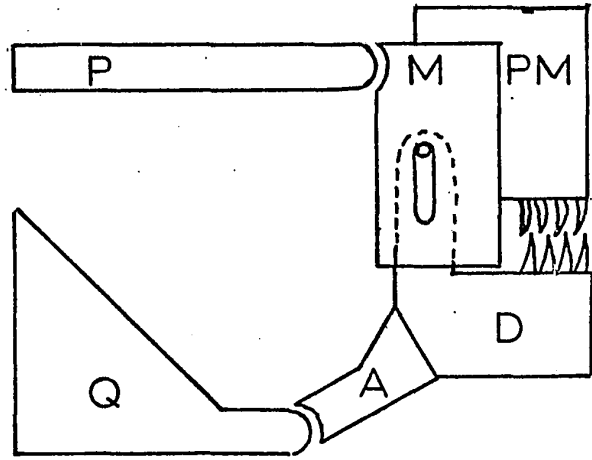
Food studies in Chapter III show that the remaining three Naso are quite selective in the food they eat. Possibly a mouth that opens only slightly downward, as it does in these species, aids in food selection. In the other browsing acanthurids the mouth opening points down considerably with the result that their browsing may be less efficient in terms of food selectivity.

Jaws: In the "typical" acanthurid, the jaws are opened by contraction of muscles attached to the mandible which pull back and down on the anteroventral part of the fused dentaries. The dentaries are bound tightly to the articulars by ligaments and these in turn pivot on the quadrates as the lower jaw opens and closes. The posterodorsal part of the lower jaw is connected by ligaments to the maxillary and premaxillary bones of the upper jaw. As the lower jaw is pulled down to open, these ligaments pull down and forward on the corners of the upper jaw, and it swings open on pivots between the maxillary and palatine bones (Fig. 19). There is an ascending process or pedicel on the premaxillary that rides into a cavity beneath the frontals and between the palatines when the mouth is opened. With little or no protrusibility of the mouth it

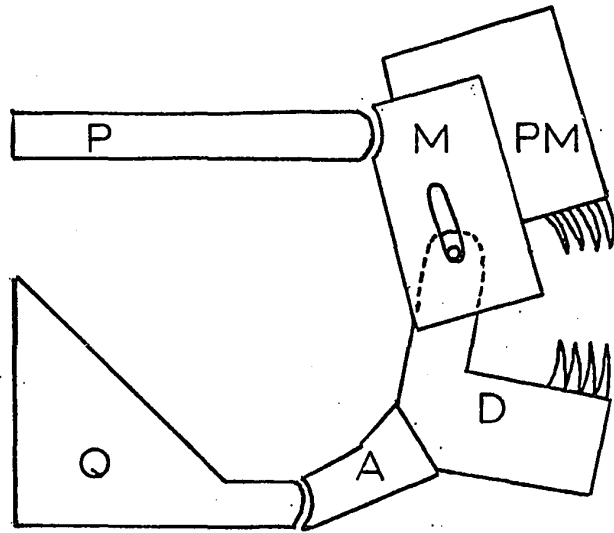
FIGURE 19. DIAGRAMMATIC SKETCH OF A "TYPICAL"  
ACANTHURID JAW

A-Articular  
D-Dentary  
M-Maxillary  
P-Palatine  
PM-Premaxillary  
Q-Quadrate

The cam operated opening of the upper jaw is  
analogous to the stretching of ligaments.



a.



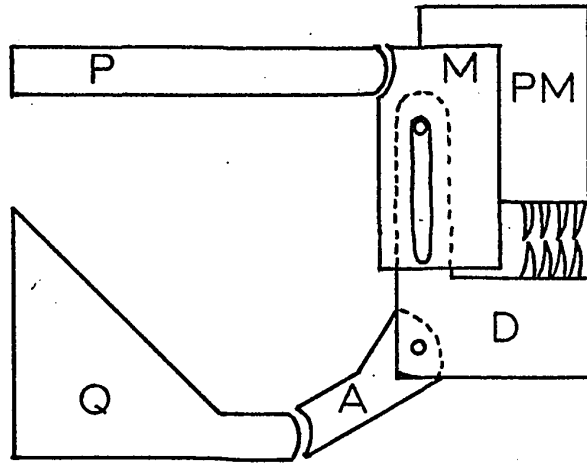
b.

is not surprising that this structure is poorly developed (Gosline, 1961). In the cheek on each side are two muscles, one that inserts on the maxillaries and premaxillaries of the upper jaw and one that inserts on the dentaries and articulars of the lower. These paired muscles close the jaws.

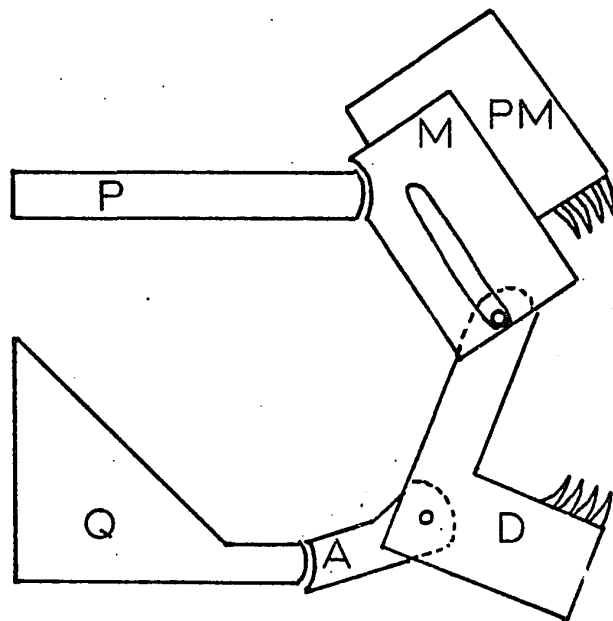
The greatest deviation occurs in jaws of Ctenochaetus. The dentary bones form a sharp V at their point of junction. The ascending process of the premaxillary is reduced to a bony knob. The jaws are less massive than the other acanthurids and hence are much lighter structures, poorly developed for biting. They are loosely bound and quite mobile. Much of this mobility is due to the fact that the articular is not tightly bound to the dentary and the lower jaw is essentially double-jointed for wider opening (Fig. 20 a and b). It seems likely that the joint between the articular and the dentary is involved in the function of opening the mouth but increased muscle contraction on the dentary causes a secondary rotation on the quadroarticular joint which in effect widens the gape as well as protruding the lower jaw.

This probably increases the efficiency of Ctenochaetus when feeding on diatoms and fine detritus. The mobility

FIGURE 20. DIAGRAMMATIC SKETCH OF THE DOUBLE  
JOINTED LOWER JAW OF CTENOCHAETUS (SEE  
FIG. 19 FOR DETAILED CAPTION AND ABBREVIATIONS)



a.



b.

and tremendous expansion of the open jaws may contribute toward an effective sucking mechanism.

Dentition: The teeth in most Acanthurus are small with denticulations on the margins (Fig. 21). They range from the quite large ones of A. guttatus (Fig. 21c) to the very fine ones of A. thompsoni (Fig. 21h). The largest numbers of teeth are found in A. thompsoni, A. dussumieri, A. mata, A. olivaceus, and A. xanthopterus (Table XIX). The greatest reduction in number of teeth occurs in the compressed beak-like jaws of A. achilles and A. glaucopareius.

The numerous, fine, and somewhat pointed teeth of A. thompsoni (Fig. 21h) are probably rarely used for cutting but serve only in grasping food. In the Acanthurus grazers the teeth are quite long, narrow, and rounded or somewhat pointed at the tips (Fig. 21 i-1). These teeth, rather than for biting or incising, seem to act more as a rake for grazing in loose sand. The denticulations on these teeth are small and may be holdovers from a point in evolutionary history when these species were entirely benthic algae feeders.

The less numerous and broader teeth of the browsers appear to be better for biting or incising filamentous

FIGURE 21. SKETCHES OF UPPER (LEFT) AND LOWER (RIGHT) TEETH OF SPECIES OF ACANTHURUS (AFTER RANDALL, 1956)

a. A. achilles (137mm), b. A. glaucopareius (143mm), c. A. guttatus (165 mm), d. A. leucopareius (156mm), e. A. triostegus (140mm, virtually identical to teeth of A. sandvicensis), f. A. nigrofuscus (81mm), g. A. nigroris (81mm) h. A. thompsoni (138mm), i. A. olivaceus (190mm), j. A. dussumieri (210mm), k. A. mata (228mm), i. A. xanthopterus (200mm).

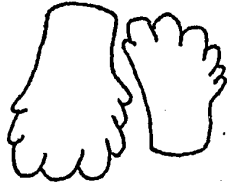




a.



b.



c.



d.



e.



f.



g.



h.



i.



j.



k.



l.

1mm

algae (Fig. 21 a-g). Filaments of algae caught between the cusps of the teeth are partly cut and partly snapped off by a quick jerk of the head.

Figures 21 and 22 demonstrate some differences between the teeth of Acanthurus and Zebrasoma. There is also a difference between the tooth structure of Z. flavescens and Z. veliferum (Fig. 22).

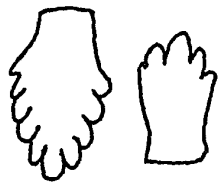
Except for Naso lituratus, the Naso have a large number of pointed teeth (Fig. 24 and Table XIX). The greatest number is found in the zooplankton feeding N. hexacanthus. In this species there are fine denticulations on the lateral margins of the teeth (Fig. 24b) which probably function in a similar manner to those of Acanthurus thompsoni (see above). The teeth are also finely serrate in Naso brevirostris (Fig. 24a) adults (Smith, 1966) and subadults. The young of N. unicornis have serrate teeth but the serrations are lost in the adults (Fig. 24c). The pointed teeth in N. brevirostris (at least in subadults) and N. unicornis are apparently quite effective in grasping and stripping off tough "leaves" from the thalli of Sargassum and for tearing off mouthfuls of the somewhat softer Dictyota (Chapter III). N. lituratus

FIGURE 22. SKETCHES OF UPPER AND LOWER TEETH OF  
ZEBRASOMA (AFTER RANDALL, 1955c)

a. Z. veliferum (171mm), b. Z. flavescens (100mm)

FIGURE 23. SKETCHES OF TEETH OF CTENOCHAETUS  
(AFTER RANDALL, 1955d)

a. C. striatus (141mm) not a Hawaiian species,  
b. C. strigosus (119mm), c. C. hawaiiensis (157mm)

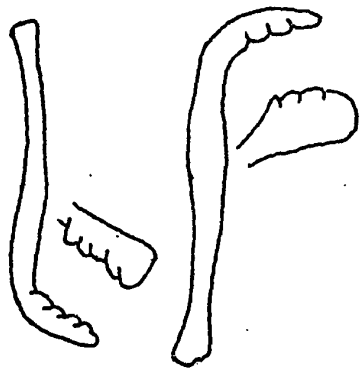


a.

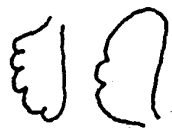


b.

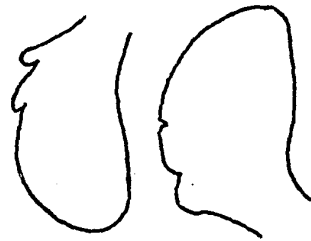
1 mm



a.



b.



c.

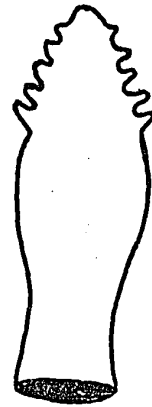
1 mm

FIGURE 24. SKETCHES OF LOWER TEETH OF NASO

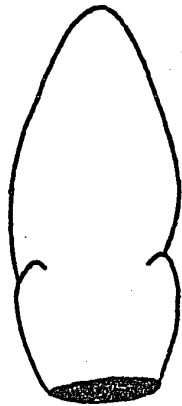
- a. N. brevirostris, b. N. hexacanthus,  
c. N. unicornis, d. N. lituratus



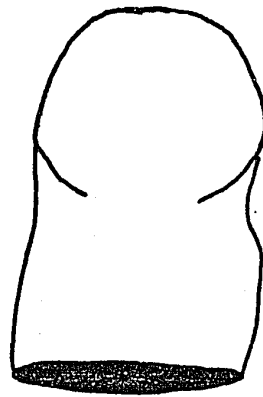
a.



b.



c.



d.

has fewer teeth than the other Naso. The adults of these fish have rounded or square cutting edges on the teeth (Fig. 24d) while in the juveniles they are pointed (Smith, 1966). The major food of this species, is Pocockiella (Chapter III). The texture of Pocockiella indicates that it might be of an abrasive nature. Once worn down the teeth of N. lituratus are more incisor-like. Pocockiella has a broad leaf-like structure that grows out from rock surfaces in a lichen-like manner. The thalli are quite brittle. Hence, grasping these thalli with pointed teeth might result in tearing away only small bits, doing little more than fraying the edges of the thallus. These small bits may be effective in nourishment of juveniles or subadults, but the larger N. lituratus would seem to require a more efficient feeding mechanism. A few closely set teeth, all equally squared off on their distal margins possibly provide a cutting edge that is more effective for handling this particular algal genus than pointed teeth.

In Ctenochaetus the teeth are long, flexible, and the ends spatula-like (Fig 23). Randall (1955d) found that in C. strigosus the number of teeth increased with increase in size of the fish. The teeth on the upper and lower jaws of

this genus seem to act like opposing brooms and the fishes appear to be "sweeping" and sucking up fine material from the reef. Fryer (1959b) noted that the mobile teeth of Psuedotropheus zebra, a Lake Nyasa cichlid, are able to fit and scrape irregular surfaces (i.e., a rock). The flexible teeth of Ctenochaetus seem capable of the same action. Similarly these flexible teeth may be effective in "combing" attached algal thalli to remove adhering detritus and diatoms.



## PHARYNGEAL REGION:

Number of Gill Rakers: Counts were made on both limbs of the first arch and combined (Fig. 25). The lowest counts are found in the genus Zebrasoma, and the highest in Acanthurus guttatus, A. nigrofuscus, A. nigroris, A. dussumieri, A. mata, A. olivaceus, A. xanthopterus, Ctenochaetus hawaiiensis, C. strigosus, and Naso hexacanthus.

Gill Arches and Pharyngeal Teeth: The entire gill arch and pharyngeal tooth apparatus was removed from each fish. The dorsal parts (including the infrapharyngobranchials and epibranchials) were separated from the ventral parts (including the basibranchials, hypobranchials, and ceratobranchials) at the cartilagenous junction between the epibranchials and ceratobranchials. Diagrammatic sketches are presented for representative species (Figs. 26-33). Where differences occur in these species, sketches are made of the parts or characters that differ.

There are four distinct gill arches in the Acanthuridae (Fig. 26). The remnants of the fifth arches occur as the lower pharyngeal tooth plates. There are bony tooth plates attached to infrapharyngobranchials two through four (Fig. 26b). The fourth gill arch has no bony basibranchial

FIGURE 25. FREQUENCY DIAGRAM SHOWING AVERAGE  
NUMBER OF GILL RAKERS (AFTER RANDALL,  
1955c,d and 1956 and SMITH, 1966)

10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30

Acanthurus  
achilles

\_\_\_\_\_

A. glaucopareius

\_\_\_\_\_

A. guttatus

\_\_\_\_\_

A. leucopareius

\_\_\_\_\_

A. nigrofuscus

\_\_\_\_\_

A. nigroris

\_\_\_\_\_

A. sandvicensis

\_\_\_\_\_

A. dussumieri

\_\_\_\_\_

A. mata

\_\_\_\_\_

A. olivaceus

\_\_\_\_\_

A. xanthopterus

\_\_\_\_\_

A. thompsoni

\_\_\_\_\_

Ctenochaetus  
hawaiiensis

\_\_\_\_\_

C. strigosus

\_\_\_\_\_

FIGURE 25. (Continued)

10 11 12 13 14 15 16 17 18 19 20 21 22 23 24 25 26 27 28 29 30

Naso

brevirostris

\_\_\_\_\_

N. lituratus

\_\_\_\_\_

N. unicornis

\_\_\_\_\_

N. hexacanthus

\_\_\_\_\_

Zebrasoma

flavescens

—

Z. veliferum

—

or hypobranchial elements but instead is directly connected through the ceratobranchials by a cartilagenous pad on the ventral midline.

In general, the pharyngeal apparatus becomes more complex from Naso through Ctenochaetus (Figs. 26-33).

In the species of Naso both N. lituratus (Fig. 26) and N. unicornis are essentially identical in the pharyngeal apparatus. The bony elements of the upper and lower pharyngeals are broad and armed with coarse, strong teeth arranged in rows (Fig. 26 a and b). The gill arches themselves are armed with blunt, coarse gill rakers that are studded with short strong teeth (Fig. 26 c). The pharyngeal apparatus of these species would seem to be ideal for handling the coarse algal material that they eat.

N. hexacanthus has a considerably different shape in the lower pharyngeals from the above species (Fig. 27 a). Teeth on the lower pharyngeals are less numerous but much longer than the other species. There is a slight reduction in size of the upper pharyngeal elements, particularly that of the third infrapharyngobranchial (Fig. 27 b). Tooth rows are not as well defined on the upper and lower pharyngeals as they are in N. lituratus (Fig. 26). The

FIGURE 26. PHARYNGEAL ELEMENTS OF NASO LITURATUS

a. Pharyngeal apparatus showing gill arches 1-4 and the lower pharyngeal bones, b. upper pharyngeal bones of the second through fourth infrapharyngobranchials (left side, ventral view), c. part of the fourth gill arch (diagrammatic sketches).

LOWER PHARYNGEALS

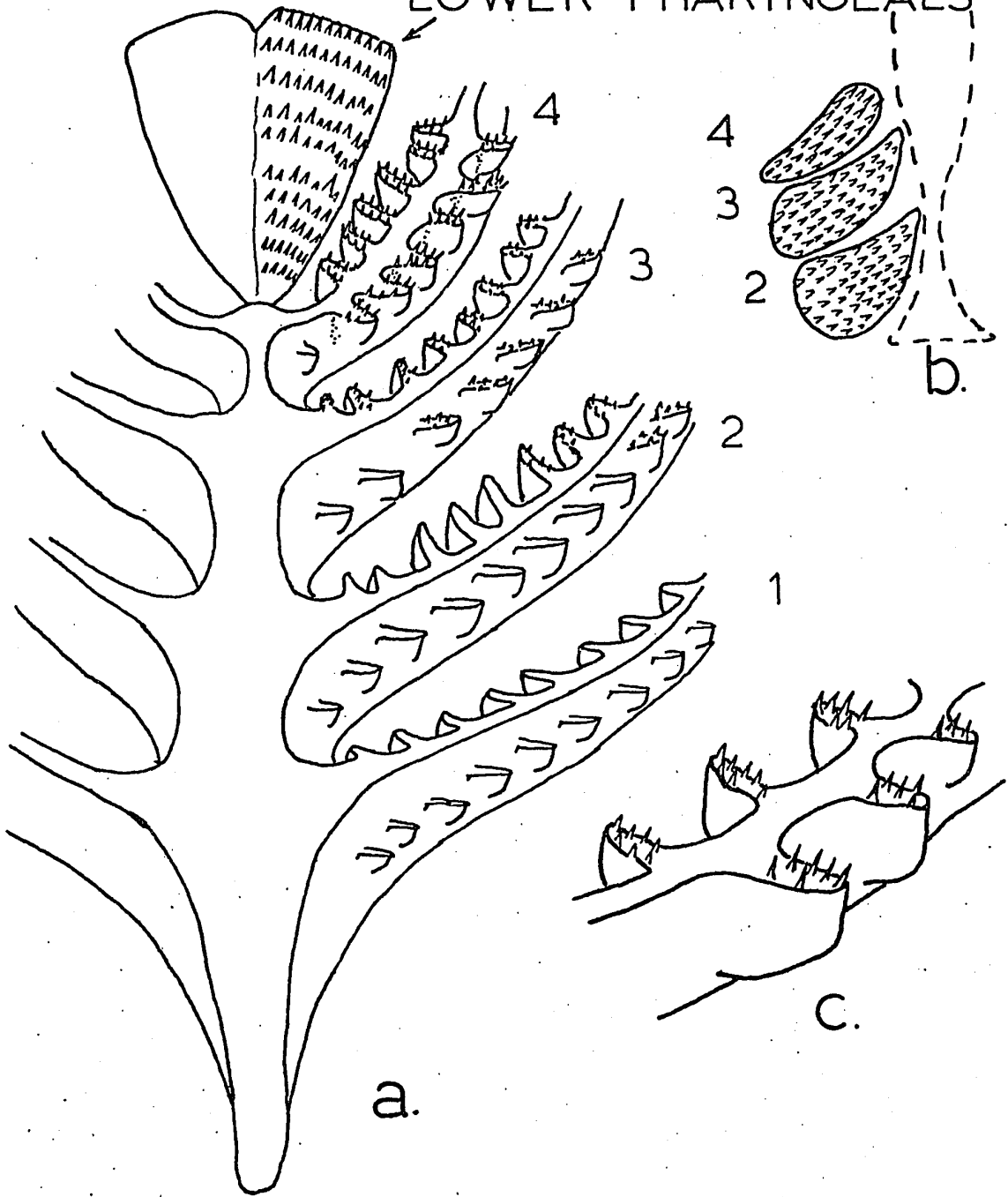


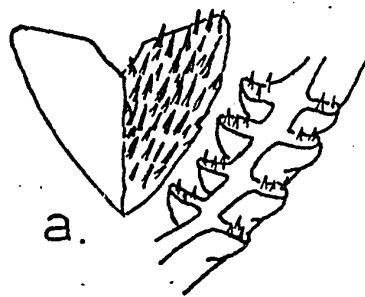
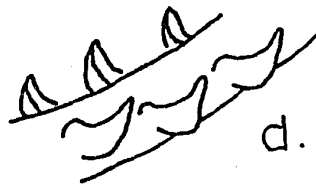
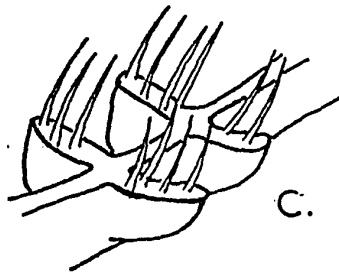
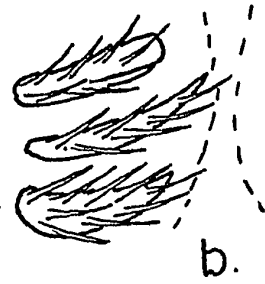
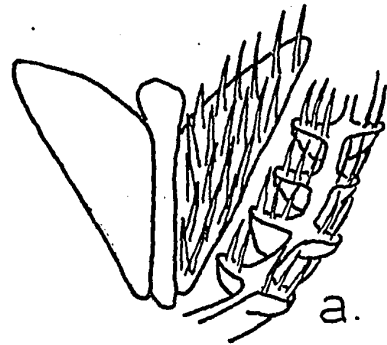


FIGURE 27. PHARYNGEAL ELEMENTS OF NASO HEXACANTHUS

a. Lower pharyngeals and arch four, b. upper pharyngeals, c. part of the fourth gill arch  
d. part of the first arch (diagrammatic sketches).

FIGURE 28. PHARYNGEAL ELEMENTS OF NASO BREVIROSTRIS

a. Lower pharyngeals and arch four, b. upper pharyngeals, c. part of the fourth gill arch (diagrammatic sketches).



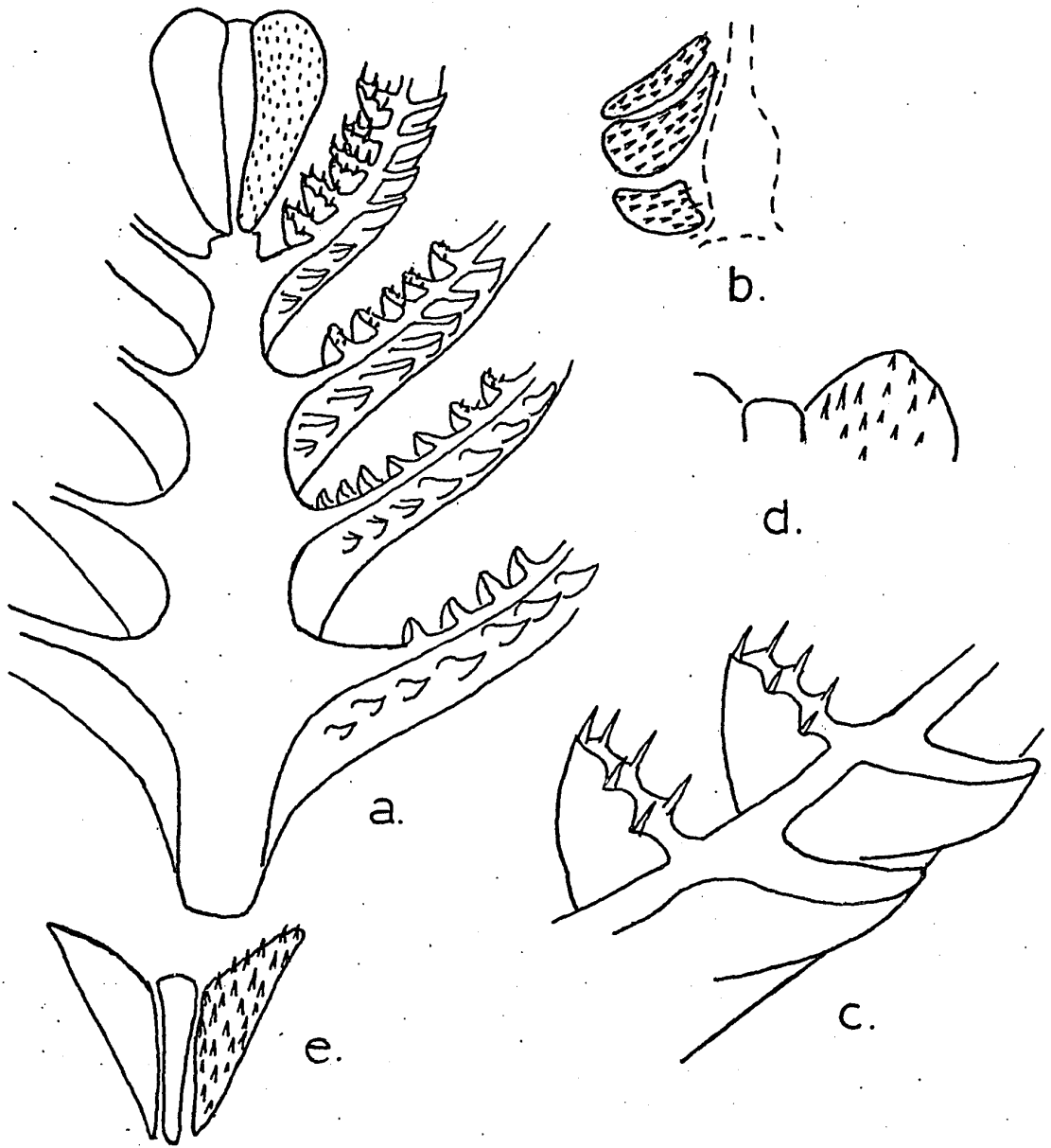
bristles on the gill rakers of N. hexacanthus, though less numerous, are considerably longer than the others (Fig. 27c). Gill rakers on the leading edges of the first and second arches are more elongate than in the other species of Naso (Fig. 27d). Gill rakers on the third and fourth arches form a sieve that probably directs zooplankton back onto the flexible teeth on the pharyngeals. It is a general consensus that in fishes movement of the pharyngeal bones "rakes" the prey (food) back into the esophagus.

N. brevirostris seems to be intermediate between N. lituratus and N.unicornis on the one hand and N. hexacanthus on the other (Fig. 28). This is true for the shape of the lower pharyngeals, reduction in number and increase in length of teeth on the pharyngeals and gill rakers, row formation of teeth on the pharyngeals and reduction of the upper pharyngeal tooth elements.

Figure 29a shows the ventral part of the pharyngeal apparatus of Zebrasoma flavescens. Z. flavescens (Fig. 29a) and Z. veliferum (Fig. 29e) are virtually identical except for differences in shape of the lower pharyngeal bones and size of teeth. The gill apparatus of Zebrasoma is somewhat intermediate between Naso and Acanthurus. Closest affinity

FIGURE 29. PHARYNGEAL ELEMENTS OF ZEBRASOMA

a. Pharyngeal apparatus of Z. flavescens showing gill arches 1-4 and the lower pharyngeal bones, b. upper pharyngeals, c. part of the fourth gill arch, d. part of the lower pharyngeals showing the armament, e. lower pharyngeals of Z. veliferum (diagrammatic sketches).

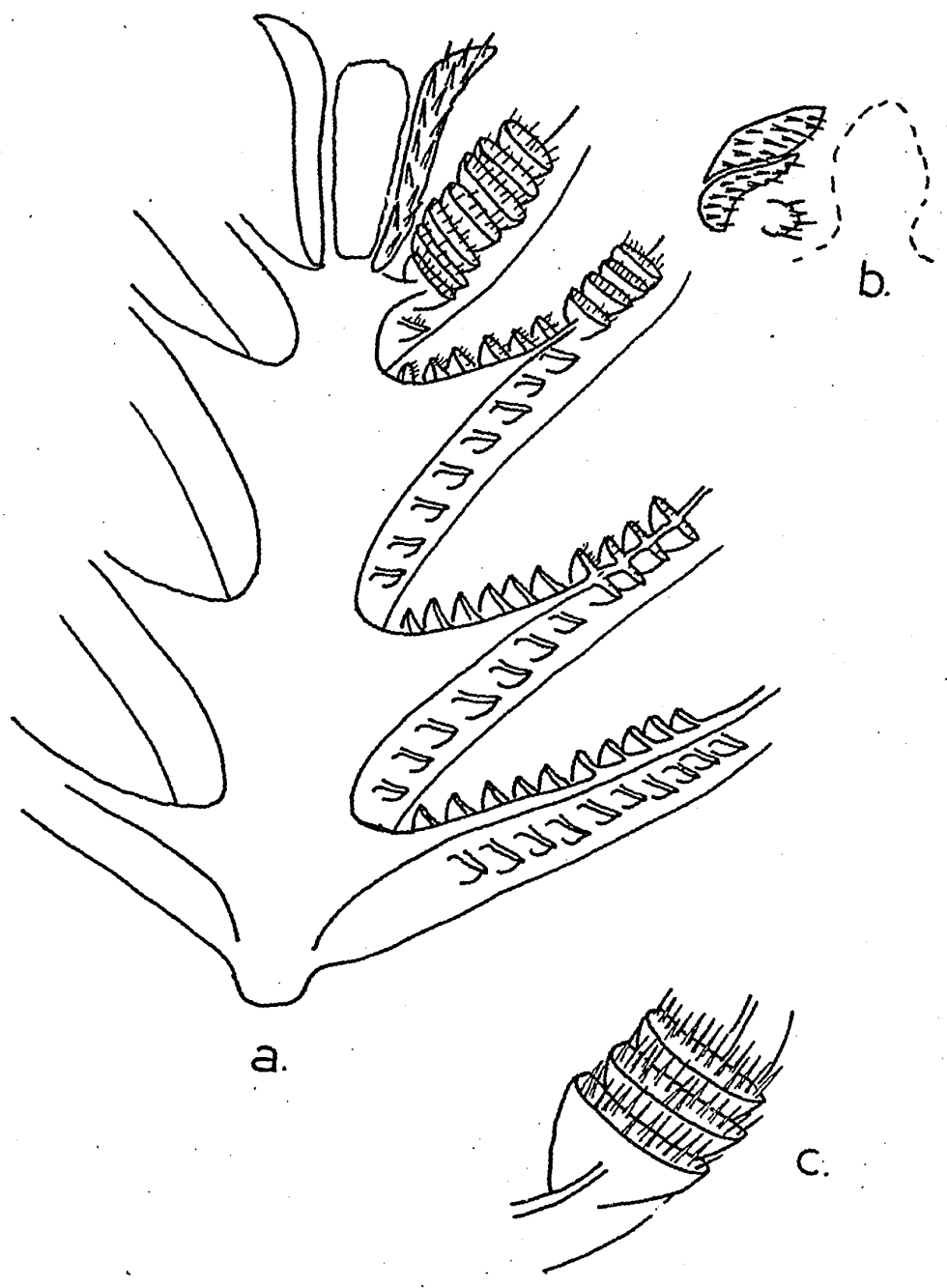


seems to be with Naso. This statement is based on the relatively broad pharyngeal tooth plates and low gill raker count. These two characters might suggest that Zebrasoma is capable of taking somewhat coarser material than the browsing Acanthurus, though food studies thus far have not shown this to be the case.

A sketch of the ventral part of the pharyngeal apparatus of Acanthurus nigroris (Fig. 30) serves to illustrate this genus. Basically A. guttatus, A. leucopareius, A. nigroris, A. dussumieri, A. mata, A. olivaceus, and A. xanthopterus are very similar in the pharyngeal apparatus. The lower pharyngeal plates are greatly reduced in size (Fig. 30a). The tooth plate of the second infrapharyngo-branchial is reduced to a very small patch of bone with about four to eight teeth (Fig. 30b). The upper pharyngeal elements have teeth arranged in an irregular manner. Teeth on the upper pharyngeals of the grazing Acanthurus tend to be stronger and less numerous than the other species of this genus. The ability of A. nigroris to feed occasionally on interstitial material may have some bearing on the resemblance of its pharyngeal apparatus to Acanthurus grazers. However the pharyngeal apparatus of the browsers

FIGURE 30. PHARYNGEAL ELEMENTS OF ACANTHURUS NIGRORIS

a. Pharyngeal apparatus showing gill arches 1-4 and the lower pharyngeal bones, b. upper pharyngeals, c. part of the fourth gill arch (diagrammatic sketches).





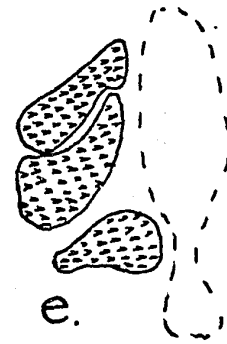
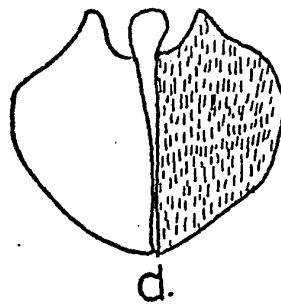
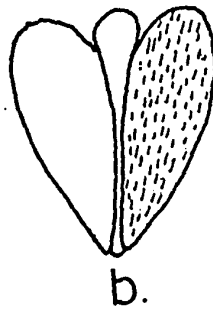
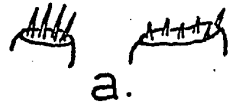
A. guttatus and A. leucopareius is also of the "grazing type".

A. nigrofuscus bears considerable similarity with the above group in reduction of the lower pharyngeal bones but the second infrapharyngobranchials are slightly better developed (Fig. 31a). This species tends to be somewhat intermediate between the above group and the following one.

A. achilles and A. glaucopareius are essentially identical. There is much better development in the lower pharyngeal tooth plates than in the above species (Fig. 31b). There is an extremely dense pattern of very fine teeth on the plates. The second and third infrapharyngobranchials are better developed in these species than in the foregoing (Fig. 31c). Teeth on the upper pharyngeals are in distinct rows. A. sandvicensis has an enormous expansion of the lower pharyngeals (Fig. 31d). They are larger even than those of Naso lituratus and N. unicornis. Like Acanthurus achilles and A. glaucopareius these plates are armed with a dense pattern of extremely fine teeth. The second and third infrapharyngobranchial plates are well developed and all three upper pharyngeal

FIGURE 31. PHARYNGEAL ELEMENTS FROM REPRESENTATIVE SPECIES OF ACANTHURUS

a. Comparison of development in the second infra-pharyngobranchial tooth plates, that of A. nigroris (left) is poorly developed, that of A. nigrofuscus (right) shows moderate development. b-c lower and upper pharyngeals of A. achilles, d-e lower and upper pharyngeals of A. sandvicensis (diagrammatic sketches).



tooth plates have the teeth in distinct rows. (Fig. 31e). It seems likely that this expansion of the tooth plates and associated fine teeth would possibly make these species more effective browsers on fine filamentous algae.

A. thompsoni has moderately well developed lower pharyngeal tooth plates (Fig. 32a). All three elements of the uppers are well developed though somewhat smaller and differently shaped than the above three species (Fig. 32b). The main difference between A. thompsoni and the other species of Acanthurus is the formation of extremely long and flexible bristle-like teeth on the upper and lower pharyngeals. The same is true of the bristles on the gill rakers of the third and fourth gill arch. It is much like Naso hexacanthus in this respect. The gill rakers of the first arch tend to be more elongate than those of the other Acanthurus. Another difference is that there are several well-developed gill rakers on the cartilaginous base of the fourth gill arch (Fig. 32a). The function of the gill apparatus of this animal probably approximates that proposed for another zooplankton feeder, Naso hexacanthus.

Figure 33 is a sketch of the pharyngeal apparatus of Ctenochaetus strigosus. C. strigosus and C. hawaiiensis

FIGURE 32. PHARYNGEAL ELEMENTS OF ACANTHURUS THOMPSONI

a. Lower pharyngeals and arches 3-4, b. upper pharyngeals (diagrammatic sketches).

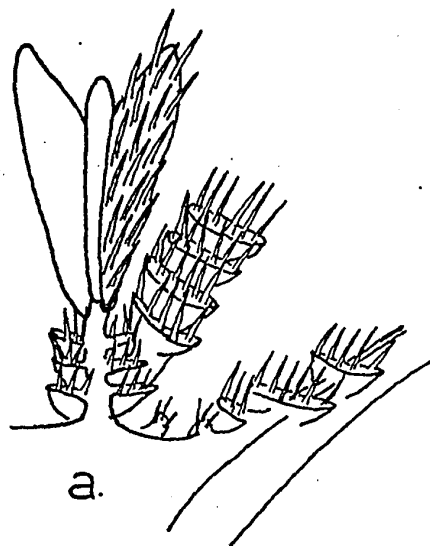
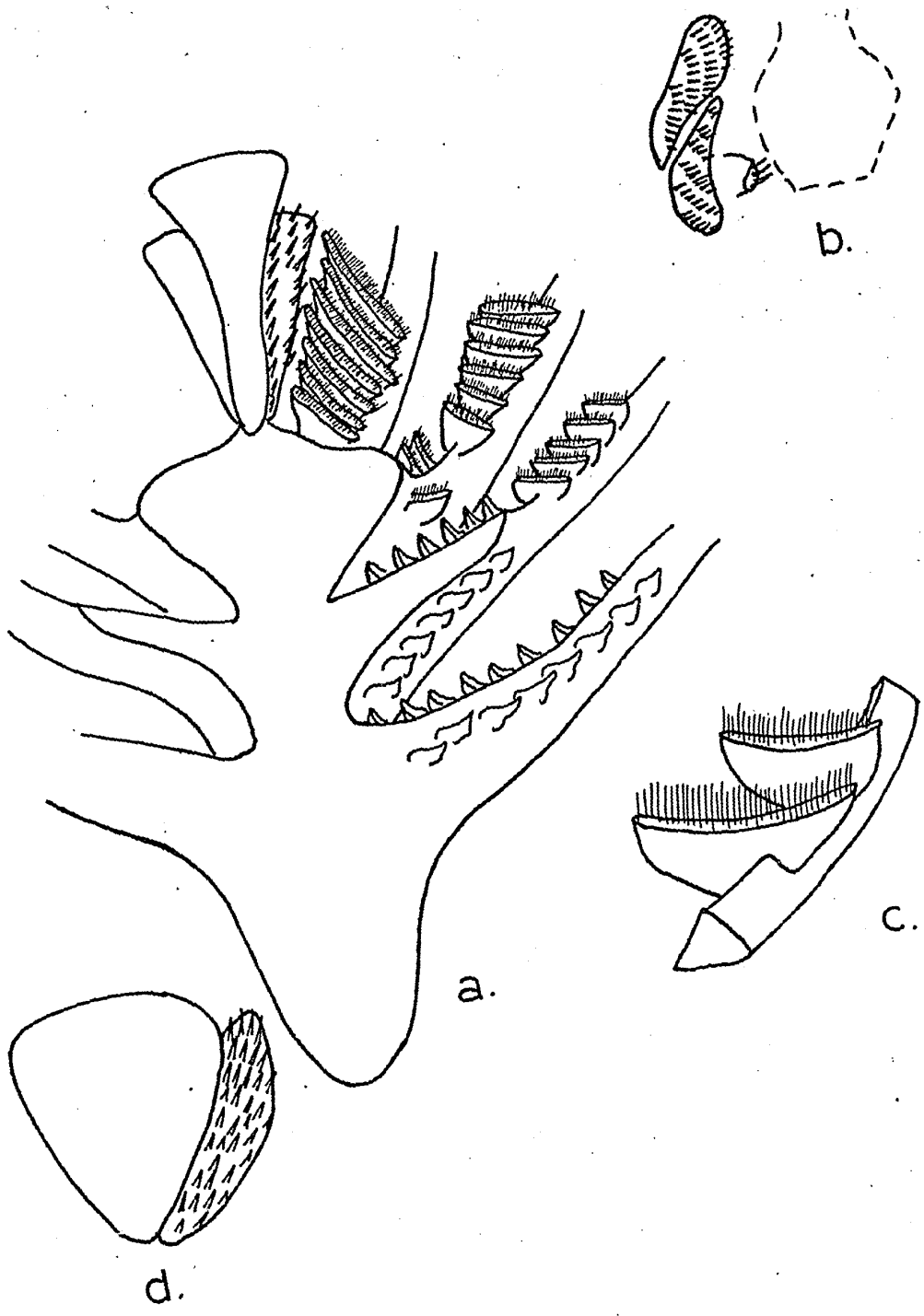


FIGURE 33. PHARYNGEAL ELEMENTS OF CTENOCHAETUS

a. Pharyngeal apparatus of C. strigosus showing gill arches 1-4 and the lower pharyngeal bones, b. upper pharyngeals, c. part of the fourth gill arch, d. lower pharyngeals of C. hawaiiensis (diagrammatic sketches).

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are virtually identical except for the somewhat larger and more widely spaced lower pharyngeal tooth plates in C. hawaiiensis (Fig. 33 a and d). C. hawaiiensis also has more teeth on the lower pharyngeals. C. strigosus has two complete rows on the sides and one incomplete row down the center of the lower pharyngeal bones. Both have finer bristles on the gill rakers than any other genus and the fused gill rakers of the fourth arch are much wider (Fig. 33 a and c) than the others. The second infrapharyngobranchial is poorly developed and has three to six teeth. The third and fourth are well-developed and have distinct curving rows of very fine teeth (Fig. 33b). The pharyngeal apparatus of this genus would seem to be quite effective in handling of the fine particulate matter ingested.

## SOFT ANATOMY (GUT) :

The soft anatomy of the alimentary canal was studied next. The anatomy of some acanthurid alimentary canals has been dealt with briefly by Al-Hussaini (1947), Breder and Clark (1947), Hiatt and Strasburg (1960), and Randall (1956, 1961a).

Dissections were made on each species to investigate the length of the alimentary canal, its pattern of coiling, and the gross structure and lining of the stomach and esophagus. Representative species were chosen from each genus. Where differences occurred among species sketches were provided to emphasize these differences.

It was known previously (Randall, 1956 and Hiatt and Strasburg, 1960) that there is a variation in stomach type within the genus Acanthurus (thin vs. thick-walled pylorus). Hence two species were chosen to represent Acanthurus. Species chosen are A. nigrofuscus to represent the group with the thin-walled stomach (which also includes A. achilles, A. glaucopareius, A. guttatus, A. leucopareius, A. nigroris, and A. sandvicensis) and A. dussumieri to represent the group with a gizzard-like stomach (which also includes A. mata, A. olivaceus, and A. xanthopterus). Considerable modification in the gut of A. thompsoni made

it necessary to deal separately with this species. The other genera are represented by Ctenochaetus strigosus, Zebrasoma flavescens, and Naso lituratus.

Two to five specimens of each species were examined. For each specimen, dissection began on the left side of the animal. Skin, muscle, ribs, and the pectoral fin elements were removed. The mesentery of the component organs was teased apart to expose the type and position of the stomach, position and number of pyloric caeca, entry of the bile duct, and pattern of intestinal coils. These organs were sketched as dissection proceeded. The alimentary canal of the right side was similarly exposed and sketches made. Primary interest on this side is in the intestinal coil pattern and the structure and position of the rectum relative to other parts of the intestine.

The gut was carefully unwound and its length measured from esophagus to anus. The gut of preserved fishes was measured and the data are presented in Table XX. Measurement of the gut length in most animals is difficult. The major problem is to avoid stretching it beyond its normal length. Some error may result from this but the data were roughly reproducible in several specimens of each species

and it is felt that the error is less than one-half of the standard length.

The final step was to excise the stomach in a section from the anterior end of the esophagus to a point just below the pyloric caeca. This was done to permit a more detailed study of the apparatus.

The esophagus and stomach were split open to inspect their lining. The pyloric stomachs of one animal with a "gizzard" and one with a "thin wall" were dissected to show transverse and vertical aspects (Fig. 34).

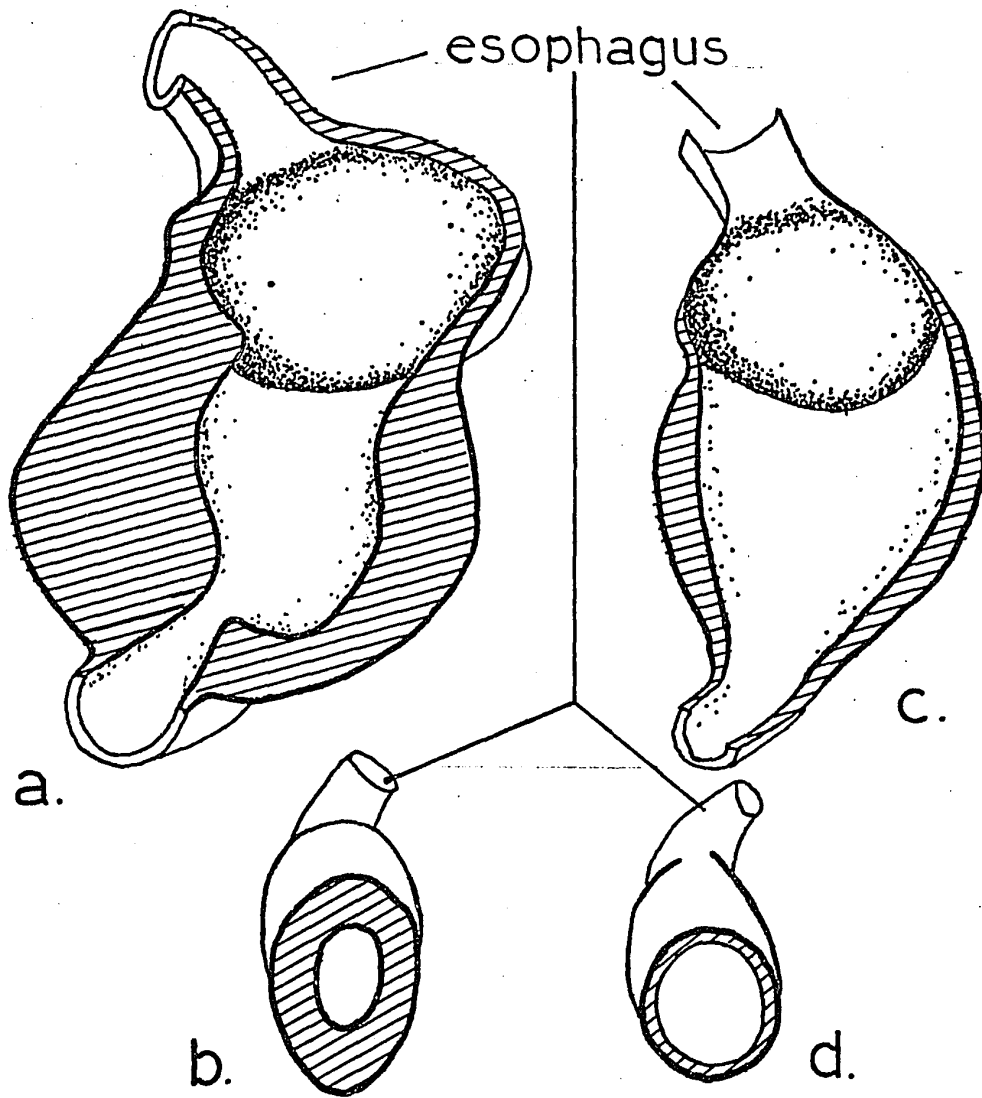
Figures 35 to 40 present the anatomy of the species studied far better than a detailed verbal description. But it is necessary to give a few general observations and make some brief remarks about the individual species.

Genera of the family Acanthuridae show marked similarity in the arrangement of the alimentary canal and its component parts. Major differences are most likely to occur in different lengths of the gut, coiling of the intestine, and as a modification of the pyloric region of the stomach as a grinding organ.

In all genera the number of pyloric caeca is typically five. The alimentary canal has constrictions between the

FIGURE 34. DIAGRAMMATIC COMPARISON OF THE GIZZARD-  
LIKE STOMACH VS. THE THIN WALLED STOMACH

a-b. Longitudinal and transverse aspects of  
the "gizzard" type, c-d. longitudinal trans-  
verse aspects of the thin walled type.



cardiac and pyloric regions of the stomach, the pyloric region and the duodenum (pyloric valve), and at the recto-intestinal junction.

The left side of the body cavity shows extraordinary likeness in all genera. On this side and somewhat medially is found the stomach and pyloric caeca. The largest part of the liver and a characteristic loop of the intestine occurs lateral to the stomach. The latter is found in every species and forms a semi-circle around the viscera that lie along the dorsal, ventral, and posterior margins of the body cavity. Naso hexacanthus is an exception. The loop is present but does not coil anteriorly and dorsally over the stomach (Fig. 40b).

The right side of the animal contains the majority of the intestine, usually in complicated coils, a small lobe of the liver, and the gall bladder. The bile duct leads to the opposite side of the body where it connects to one of the pyloric caeca.

Table XX shows data on gut length. It becomes evident from these data that certain species fall into groups. Acanthurus leucopareius has the greatest gut to standard length ratio (6-7) with A. sandvicensis next (5-6). One

TABLE XX. PROPORTIONAL LENGTH OF THE GASTRO-  
 INTESTINAL TRACT (LENGTH DIVIDED BY STANDARD  
 LENGTH) IN EACH SPECIES MEASURED FROM  
 ESOPHAGUS TO ANUS (THREE TO FIVE SPECIMENS  
 WERE USED FOR EACH MEASUREMENT) .

SPECIES	LENGTH OF GI. TRACT
<u>Acanthurus</u> <u>achilles</u>	5.2
<u>A. glaucopareius</u>	4.9
<u>A. guttatus</u>	4.6
<u>A. leucopareius</u>	6.9
<u>A. nigrofuscus</u>	4.0
<u>A. nigroris</u>	4.4
<u>A. sandvicensis</u>	5.8
<u>A. dussumieri</u>	3.0
<u>A. mata</u>	3.8
<u>A. olivaceus</u>	3.4
<u>A. xanthopterus</u>	?
<u>A. thompsoni</u>	3.1
<u>Ctenochaetus</u> <u>hawaiiensis</u>	3.5
<u>C. strigosus</u>	3.5
<u>Naso</u> <u>brevirostris</u>	2.2



TABLE XX. (Continued) PROPORTIONAL LENGTH OF THE GASTROINTESTINAL TRACT (LENGTH DIVIDED BY STANDARD LENGTH) IN EACH SPECIES MEASURED FROM ESOPHAGUS TO ANUS (THREE TO FIVE SPECIMENS WERE USED FOR EACH MEASUREMENT).

SPECIES	LENGTH OF GI. TRACT
<u>N. lituratus</u>	3.2
<u>N. unicornis</u>	3.2
<u>N. hexacanthus</u>	1.8
<u>Zebrasoma flavescens</u>	3.7
<u>Z. veliferum</u>	3.7

group with a moderately long gut (4-5 times the standard length) consists of A. achilles, A. glaucopareius, A. guttatus, A. nigrofuscus, and A. nigroris. The largest group, with moderately short gut length (3-4), comprises A. thompsoni, A. dussumieri, A. mata, A. olivaceus, A. xanthopterus, Ctenochaetus hawaiiensis, C. strigosus, Zebrasoma flavescens, Z. veliferum, Naso lituratus, and N. unicornis. The shortest gut lengths are present in N. brevirostris and N. hexacanthus (about 2). Acanthurus nigrofuscus -- when working with A. sandvicensis, Randall (1961a) found that the digestive anatomy of the species was identical to that of A. coeruleus, described by Breder and Clark (1947). These descriptions hold true for A. nigrofuscus and the other members of the group. The illustration (Fig. 35) gives the basic structure typical for most members of the genus. The cardiac region of the stomach is thin-walled and quite distensible, the pyloric region is muscular but not thick walled and specialized for grinding (Fig. 35b).

The center of the coil on the right side of these animals is usually made up of an S shaped loop (Fig. 35). Basically the intestine from the region of the pyloric caeca

FIGURE 35. GASTROINTESTINAL TRACT OF ACANTHURUS  
NIGROFUSCUS

a. left side, b. stomach, c. right side

BD-bile duct

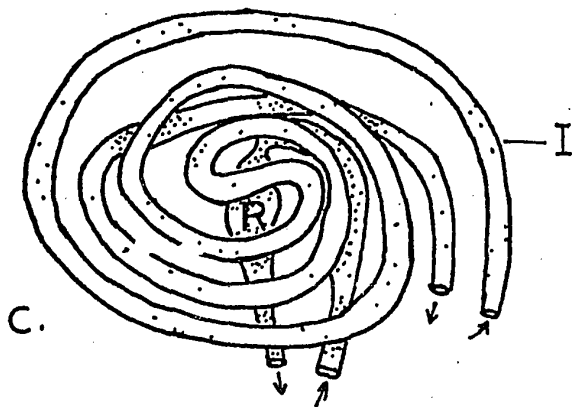
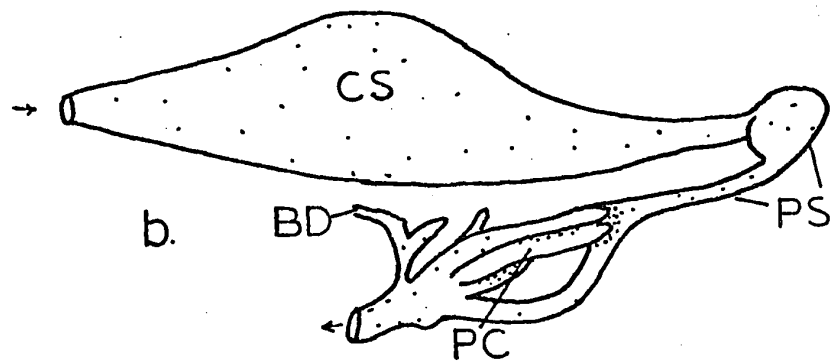
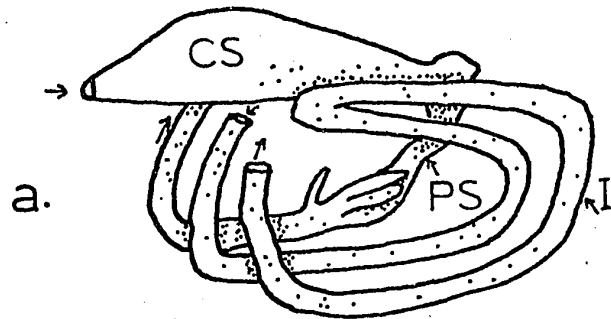
CS-cardiac region of the stomach

I -intestine

PC-pyloric caeca

PS-pyloric region of the stomach

R -rectum



crosses from the left to right side of the body whereupon it makes two complete counterclockwise turns before entering the lower limb of the S. The intestine emerges at the upper limb of the S, makes another complete turn clockwise then passes back to the left side where it enters the lower limb of the characteristic U-shaped loop. The other end of this loop returns the intestine to the right side where it enters the U-shaped rectum. The bottom of the U is dorsal and its posterior limb turns ventrally to terminate at the anus. This situation is identical in all the thin walled stomach group except A. leucopareius and A. guttatus. In A. leucopareius the intestine on the right side makes three counterclockwise turns instead of two before entering the lower limb of the S.

This is true of adults and specimens down to 80 mm. The additional turn accounts for the much greater length of the gut in A. leucopareius. The coil pattern of A. guttatus is more like that of the thick-walled Acanthurus described in the next group (Fig. 36c). No differences are found between the coiling of the intestine of A. nigrofuscus and A. sandvicensis even though the latter has a slightly longer intestine than the rest of the thin-walled

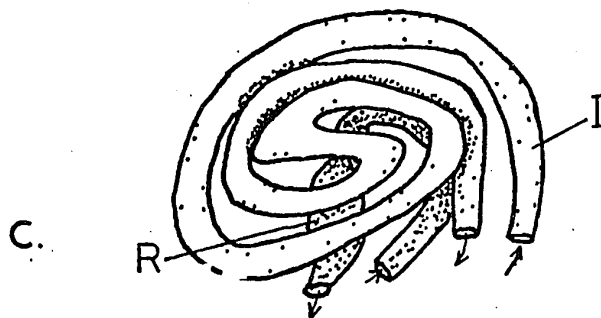
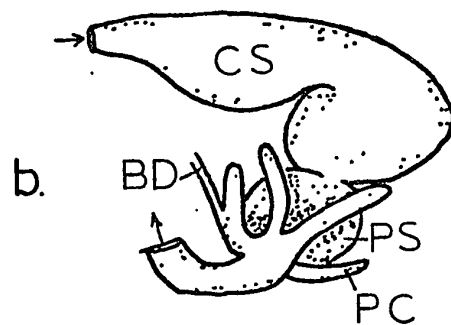
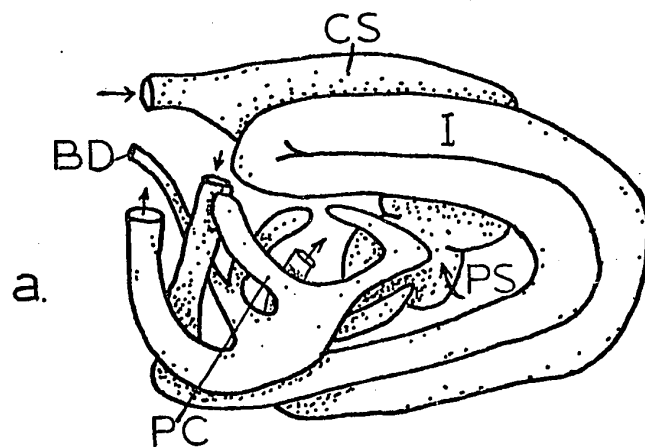
group (except A. leucopareius). The difference in length may be accounted for by tightness of intestinal packing or size of the body cavity. It should be pointed out here that though it is included with the thin-walled stomach group, A. nigroris has a stomach that tends to be of somewhat intermediate thickness but closer to the thin-walled group.

The much longer intestine of the surge zone dwelling A. leucopareius might be perhaps advantageous for increasing the area of absorption. Similarly the intestine of the sub-surge reef dwelling A. sandvicensis, though shorter than A. leucopareius, is longer than the other species.

Acanthurus dussumieri -- This species represents the "atypical" members of the genus Acanthurus which have the pyloric region of the stomach modified as a grinding organ or gizzard (Fig. 36 a and b) and have the shortest intestine (except for A. thompsoni). The coils of the intestine also differ from the thin-walled group (except A. guttatus). The intestine passes from the region of the pyloric caeca to the right side of the body where it makes one complete counterclockwise turn and enters the upper limb of an S coil (Fig. 36c). The intestine passes from the lower

FIGURE 36. GASTROINTESTINAL TRACT OF ACANTHURUS  
DUSSUMIERI

a. left side, b. stomach, c. right side  
(see Fig. 35 for abbreviations)





limb of this coil into one clockwise turn and continues on exactly as the intestine in the thin-walled group. This simplification results in the shorter intestine. No variation was noted among the species of this group.

It would seem that the most obvious feature in common among the grazers, including Ctenochaetus (discussed below) is the gizzard-like pyloric stomach. Muqil cephalus, the gray mullet, also has a gizzard-like stomach and frequently feeds on diatoms. Al-Hussaini (1947) reported a similar situation in the red mullet, Muqil auratus. It is the general consensus that these are triturating organs that grind up and crush the frustules of diatoms. Visual observations of diatoms in the gut, anterior to the pylorus of the acanthurid grazers show that most of the frustules are intact. Posterior to the pylorus, a great majority of the frustules are broken.

There are no major differences among the grazers in the coiling of the intestine. The length of the gut of grazing Acanthurus is shorter than the browsing ones. This might suggest a more "easily" digestible food material than that available to some of the multicellular benthic algae feeders.

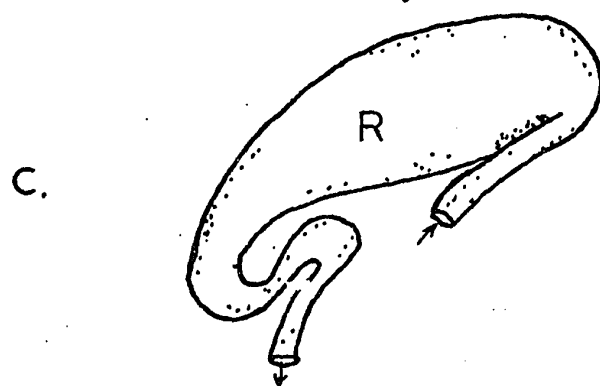
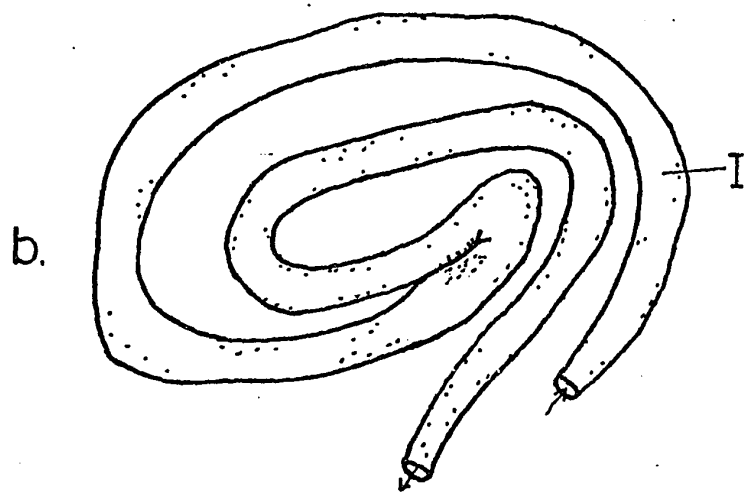
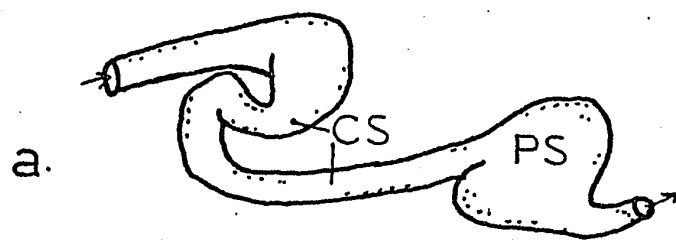
All Acanthurus (except A. thompsoni) have the "longitudinal irregular scalloped folds on the inner surface" of the esophagus and cardiac stomach described by Randall (1961a) for A. sandvicensis.

Though A. thompsoni is a thin-walled species it is different enough from the other species to be described separately. The cardiac stomach is long and doubled back on itself (Fig. 37a). The pyloric stomach is a large thin balloon-like sac much larger than the pylorus of the other thin-walled species. Instead of the longitudinal folds in the lining of the esophagus and cardiac stomach, A. thompsoni has regular rows of thorn like papillae. The intestinal coil differs from all other Acanthurus in that like the thick-walled group the intestine makes only one turn before entering the S coil, but like the thin-walled group it enters the lower, not the upper, limb of the S then makes only a half turn clockwise before passing into the loop on the left side (Fig. 37b). The rectum of this species is much larger than the foregoing and has a small extra U-shaped coil (Fig. 37c).

The large balloon-like pylorus of A. thompsoni specimens was always distended with plankton. The species has,

FIGURE 37. GASTROINTESTINAL TRACT OF ACANTHURUS  
THOMPSONI

a. stomach, b. intestine, c. rectum  
(see Fig. 35 for abbreviations)

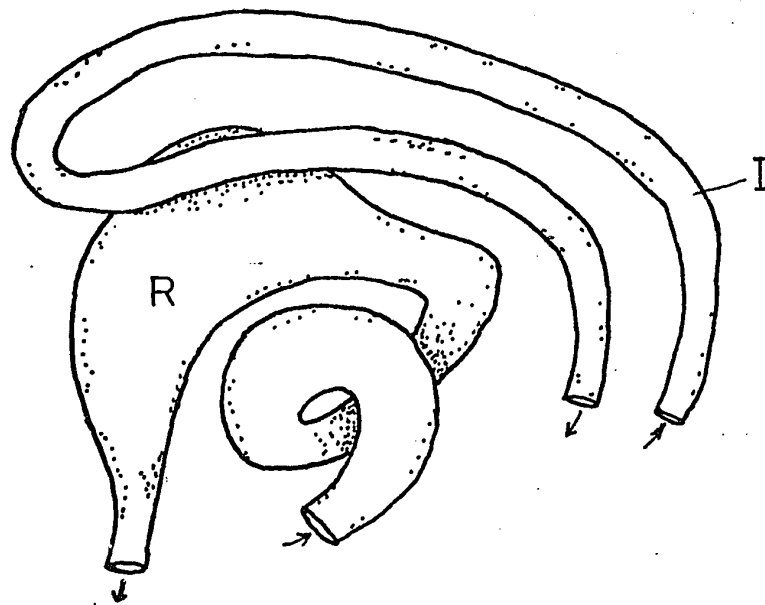


as expected, a shorter gut than the herbivorous Acanthurus.

Ctenochaetus strigosus -- the grinding organ in this genus may or may not have evolved independently from that in the genus Acanthurus, but its gross structure is similar to that of A. dussumieri. The intestinal walls are exceedingly thin, noticeably more so than the other acanthurid species. Otherwise, the gut of this species is like that of A. dussumieri in both structure and probably function.

Zebrasoma flavescens -- The left side of this species is essentially the same as that for the other species. There is, however, a marked difference on the right side primarily manifested as a reduction in number of intestinal loops (Fig. 38). This simplification results in a short intestine. Figure 38 shows a greater complexity at the posterior end of the intestine and the rectum than that found in the other acanthurids. The linings of the esophagus and stomach have longitudinal folds. The pyloric stomach is not especially well developed. The gut is shorter than that of the species of Acanthurus, that browse, as this one does, on fine filamentous algae. The physiological significance of the above characters is not known, but they certainly separate morphologically the alimentary

FIGURE 38. SOME OF THE GASTROINTESTINAL ELEMENTS  
OF ZEBRASOMA FLAVESCENS, RIGHT SIDE INTESTINE  
AND RECTUM



canal systems of the browsing Acanthurus from Zebrasoma.

Naso lituratus -- The most distinctive character in this species is the bulbous outpouching of the ventral wall of the cardiac region of the stomach (Fig. 39). This feature was also reported for Naseus (=Naso) unicornis by Al-Hussaini (1947) and has been verified here.

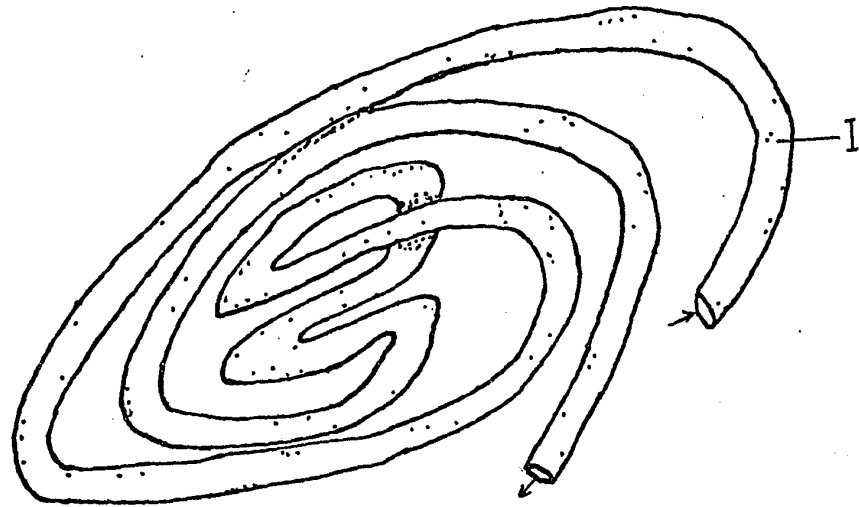
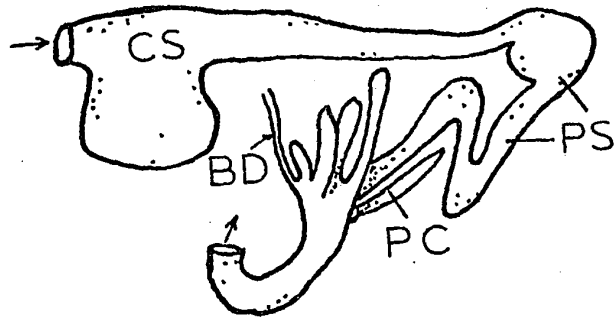
Both N. brevirostris and N. hexacanthus lack this ventral pouch. They have just a suggestion of a downward curve at this point. Coiling of the intestine in N. lituratus, N. unicornis, and N. brevirostris are identical with the thick-walled stomach Acanthurus. Figure 40a shows the somewhat more complicated coiling of the intestine of N. hexacanthus. As previously mentioned the latter species has the characteristic loop on the left side shortened (Fig. 40b). In N. lituratus and N. unicornis the esophagus and stomach (and its ventral pouch) are lined with longitudinal folds like the majority of the foregoing. But N. hexacanthus has the rows of papillae like A. thompsoni. Surprisingly enough, in the consistently intermediate N. brevirostris the anterior part of the esophagus and the cardiac stomach have papillae, and the posterior part of the cardiac stomach has longitudinal folds. There are no



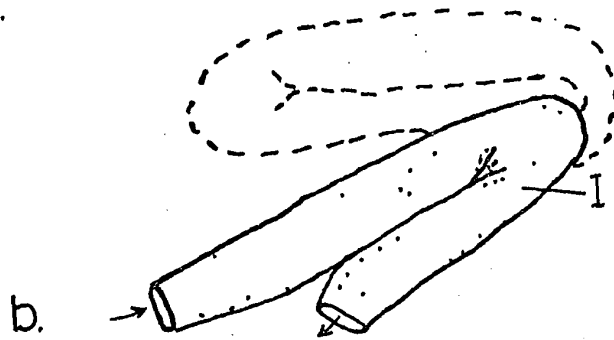
FIGURE 39. STOMACH OF NASO LITURATUS

FIGURE 40. GASTROINTESTINAL ELEMENTS OF NASO  
HEXACANTHUS

a. right side intestine, b. left  
side intestine (dashed line is the  
normal condition in other acanthurids).



a.



b.

extensive modifications of the pyloric stomachs in these four species.

The gut of all three browsing species of Naso is shorter than any of the browsing acanthurids (except Zebrasoma flavescens). Naso brevirostris has the shortest gut of the three species and its length is quite close to the zooplankton feeding N. hexacanthus. The significance of shortening of the gut of N. lituratus and N. unicornis is not clear unless the digestive enzyme system of these animals is more efficient than the Acanthurus browsers or that the algae fed upon are more easily digested.

## CHAPTER VI

### OTHER FACTORS OF POSSIBLE SIGNIFICANCE IN ECOLOGICAL SEPARATION

#### GENERAL

It would be foolish to think that this study of habitat, foraging methods, digestive morphology, and food habits has unfolded all the secrets of ecological separation in the Acanthuridae. Many of the factors studied here which are postulated to be instrumental in ecological separation may indeed be valid. Yet no ecosystem could be so uncomplicated.

It is a well known fact in population ecology that there are frequently factors which operate to keep populations of species below the level of interspecific competition (Crombie, 1947). Species cannot be in competition if their populations remain at levels such that the resource(s) for which they might compete are not in short supply.

Two such possibly controlling phenomena are reproductive efficiency and predation. To these many ecologists add parasitism, disease, climate, etc. as means by which populations of animals remain within non-competing bounds. Some cursory observations made on the first two warrant discussion. Others that are not discussed may also be present.

REPRODUCTION: Very little is known about reproduction in the Acanthuridae. It is widely assumed, and probably correctly so that all species reproduce in reef areas but produce pelagic eggs and larvae.

Randall (1961 a&b) is the only author who has observed spawning in the Acanthuridae. He observed spawning in Acanthurus triostegus, Ctenochaetus striatus, and Zebrasoma scopas. The three species had several things in common in their reproductive behavior. First, they all formed aggregations from which spawning individuals would rush rapidly toward the surface of the water several feet above them, release gametes, and return to the aggregation with equal speed. Second, spawning occurred in the late afternoon and third, all three spawned in reef channels where strong currents were setting to open sea.

Aside from surgeonfishes the upward rush in spawning has also been seen by Randall and Randall (1963) for five West Indian parrotfishes (Scaridae), one wrasse (Labridae), and a goatfish (Mullidae). Hence this may prove to be a common method of spawning among many reef fishes.

Randall (1961b) postulated that this upward rush has the primary function of expulsion of gametes by the rapidly

expanding airbladder. Flexure of the bodies of these fishes as they turned and started back down probably also assisted in the release of gametes. This seems to be an entirely satisfactory explanation of the upward rush. Yet there might be still another perhaps secondary advantage that has come about as a result of the purely functional side. Randall himself had first thought that the rush to the surface possibly confused predators. He abandoned this idea in favor of the primary hypothesis. There is reason to believe that he was not entirely wrong in his first observation. On the reef the majority of possible predators on the eggs are fishes that normally feed along or near the substratum (e.g., chaetodonts, pomacentrids, labrids, cirrhitids, etc.). By releasing gametes near the surface the acanthurids are effectively placing the eggs out of reach of many of the bottom dwelling predators. One only has to observe the voracious attacks by many reef fishes on the demersal eggs of Abudefduf abdominalis to see the damage these animals are capable of inflicting on an unguarded nest. Helfrich (1958) regarded predation on the eggs in A. abdominalis nests to be a primary factor in mortality. Along the same line of reasoning are the facts

that the acanthurid eggs are released just before dark and in areas where currents might take them clear of the reef before daylight.

The above factors would seem to result in reduced predation on the eggs and hence increased egg survival.

There is unfortunately another aspect. Eggs swept out to sea might not return. The same thing would be applicable to the weak-swimming larvae that are subsequently hatched. Gosline and Brock (1960) pointed out that in Hawaii unfavorable currents could result in the loss of many young of reef fishes with pelagic stages in their life histories. Randall (1961a) remarked that the maintenance of populations of Acanthurus sandvicensis might be a considerable problem around small islands, such as Johnston Island, where strong currents sweep in one direction. There must, however, be factors involved in the hydrography of long shore currents which result in eddy patterns that assist in maintenance of seed populations (Randall, 1961a). Boden (1952) discussed certain hydrographic phenomena based on temperature, salinity, and sigma t. that tend to conserve insular plankton. His work was done at Bermuda but might possibly be equally applicable, particularly to Johnston Island fishes.

Chamberlain (in Moberly, 1963) pointed out that the seasonal and annual shifting of sand along Hawaiian coasts is the result of "some force" doing work. One of the energy sources for this work is unidirectional water movement. There is a general drift pattern of currents set up by the Northeast Trades. This current sets to the West and is known as the North Equatorial Current. Local currents around the Hawaiian Islands are primarily eddies created by the effects of the Hawaiian Islands on the North Equatorial Currents as well as the effect of tidal currents. The latter are particularly conspicuous in the shallower shelf areas and the former in deeper waters. These currents are considered a part of what Chamberlain calls the "Coastal Current System".

Inshore areas inside the reef and along beaches are affected by the "Near Shore Current System". This system is mainly the result of mass water transport due to wave action. Tidal currents also affect this system but to a lesser degree than wave action.

It is the Near Shore Current System that acts first on newly released acanthurid eggs. Chamberlain noted (Moberly, 1963) that the inshore system is derived from



mass transport of water onshore, the along shore transport, and the return flow seaward or rip currents. These movements depending on local conditions are capable of moving sediment on shore, along shore and offshore. Eggs would tend to be moved similarly. Due to positive buoyancy of the eggs versus the negative buoyancy of sand the similarity is not complete. Eggs would continue to drift in currents too weak to move sand grains. Certainly some of the eggs must be kept near shore by eddies of the Near Shore Current System but what of those that enter the Coastal Current System? No doubt many of these eggs or larvae are returned and exchanged by eddying of the Coastal System into the Near Shore System, but even so an enormous number must be lost.

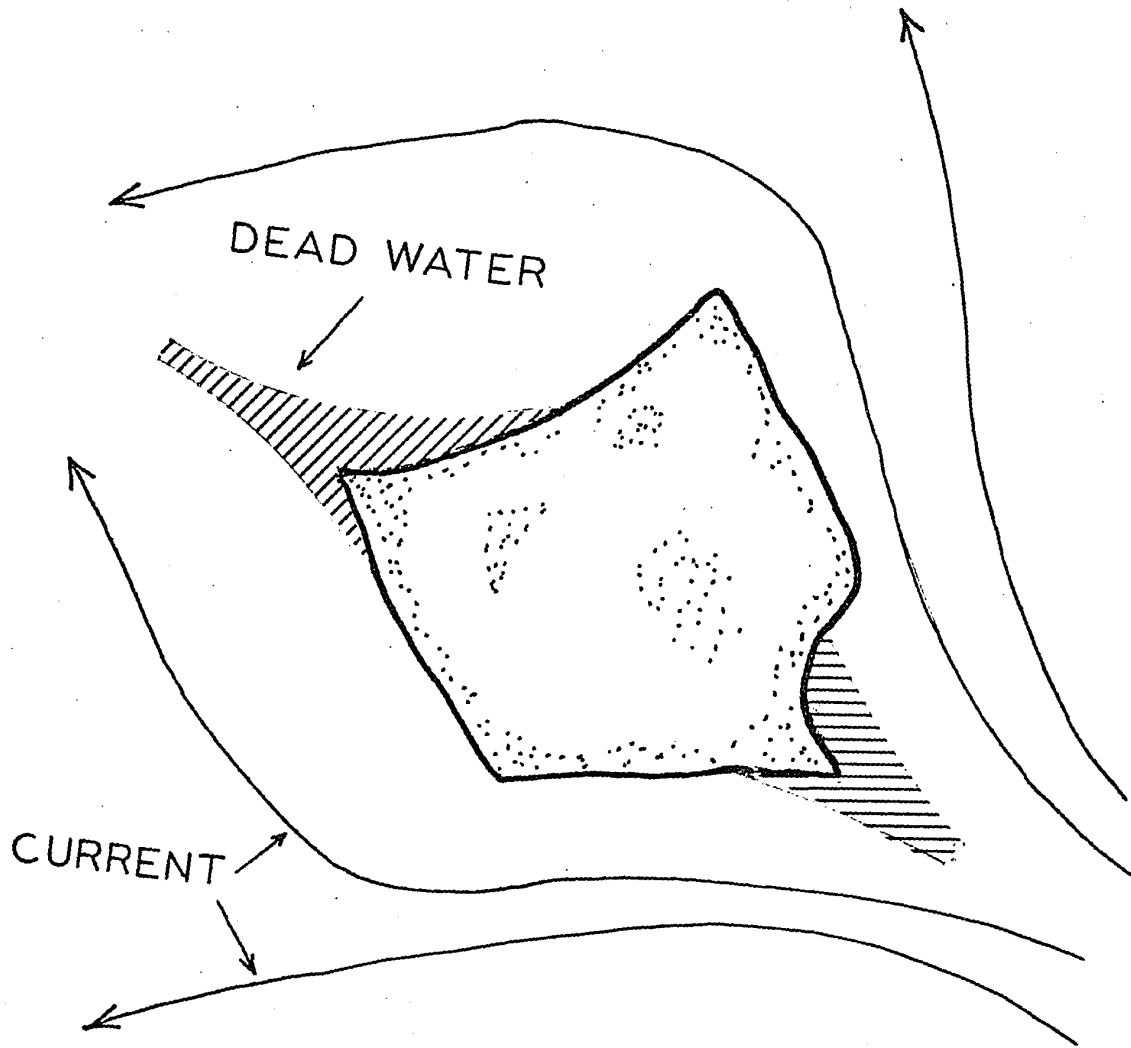
Barkley (personal communication) indicated that large gyres tend to form in the lee of the Island of Hawaii. As the gyres "mature" they move off in a northwesterly direction along the Hawaiian Chain. Eggs released by acanthurids on the Kona Coast of Hawaii and entering one of these gyres could conceivably contribute to acanthurid populations on Maui, Lanai, Molokai, Oahu, and Kauai.

Barkley also pointed out that there are frequently

"dead water areas" to windward and leeward of islands (Fig. 41). The dead spots, which vary with the shape of the island, could serve as traps for eggs and larval populations.

Barkley et al. (1964) found that the current systems near the Hawaiian Islands vary seasonally in strength but that the general drift is six to eleven nautical miles per day. Randall (1961a) found that it took about two and one half months for A. sandvicensis to metamorphose. E. C. Jones (personal communications) who has done considerable work on plankton populations in the Central Pacific felt that this estimate might be the minimum physiological time required for metamorphosis and that without proper stimuli these animals might remain in the larval condition for a much longer period. The stimulus or stimuli for transformation is or are not known but presumably would be associated with inshore reef substrata. Both R. Gooding and B. Higgins (personal communications) remarked that they had captured larval acanthurids and goatfishes several hundred miles from the nearest land. Frequently these fishes when placed in buckets of sea water completely transformed to juveniles within a few hours. Thus if acanthurid eggs or

FIGURE 41. DIAGRAMMATIC REPRESENTATION OF CURRENT FLOW AROUND AN ISLAND. NATURAL TRAPS FOR EGGS AND LARVAE OCCUR ON BOTH THE UP CURRENT AND DOWN CURRENT SIDES OF THE ISLAND.



larvae enter the Coastal Current System and then the North Equatorial Current there is a strong likelihood that these animals will be lost to the Hawaiian populations.

Acanthurid larvae were found in the stomachs of pelagic fishes by Reintjes and King (1953) in the yellowfin tuna (Thunnus albacares) and Rothschild et al. (MS) in the skipjack tuna (Katsuwonus pelamis). These examples plus the foregoing observations would seem to indicate that many acanthurid eggs and larvae are indeed swept out to open sea.

This evidence brings up two points of considerable significance. First, the reproductive efficiency of the Acanthuridae may be greatly impaired by larval loss from Island ecosystems, This might then serve to keep local populations from reaching levels of severe competition. The second point is that if delayed metamorphosis is possible then this would be an important adaptation for dispersal of the species.

While speaking of reproductive behavior it might be of interest to point out that Acanthurus sandvicensis, probably the most numerous of the Hawaiian acanthurids, transforms and passes a part of its juvenile existence in tide pools (Randall 1961a). It leads a relatively "sheltered life" in a habitat not used significantly by other

acanthurids. Though larval A. sandvicensis are presumably subjected to the same probabilities of larval loss as the other surgeon fishes, the relatively "sheltered" existence in the tide pools at the very least preserves the early juveniles from competition with other acanthurids.

PREDATION: Predation by pelagic fishes on larval acanthurids has already been pointed out in the work of Reintjes and King (1953) and Rothschild et al. (MS). If however, these young animals had already been swept away from their "home" Islands then predation is irrelevant.

Randall (1961a) noted that predation on A. sandvicensis was probably most severe in early life stages. He found juvenile A. sandvicensis in moray eels (Muraenidae) and has observed predation on them by lizardfishes (Synodontidae), frogfishes (Antennaridae) and jacks (Carangidae). Randall and Brock (1960) working in the Society Islands found young surgeonfishes in the stomachs of several species of groupers and snappers. Helfrich et al. (MS) found similar results in the Line Islands. In contrast, Bardach (1959) found none of the atlantic acanthurids in Bermudan carnivores. Randall (1961a) suggested that in Hawaii juvenile A. sandvicensis might be preyed upon by

holocentrids, scorpaenids, cirrhitids, and spyraenids. He suggested that, where there are no well developed lutjanid and serranid populations, that A. sandvicensis once reaching the adult stage is practically immune to predation. His observations on A. sandvicensis would seem to be applicable to other species as well. During an extensive period of diving in the Hawaiian Islands I have not yet observed predation on adult acanthurids. On several occasions I have seen adult surgeonfishes swimming and feeding around holes in the reef in which large moray eels were living. These fishes seemed to swim about with immunity, though practically touching the heads of the eels. Yet many times I have speared one of these same fishes and had the eel instantly snatch it from the end of the spear and retreat into the hole. It is obvious then that moray eels are capable of swallowing adults. Bardach et al. (1959) found that at least one Atlantic moray feeds at night and preys primarily on fishes in a state of torpor. Since many of the Acanthuridae do "sleep", some nocturnal predation by eels and other predators might occur. Helfrich (1967) suggested that nocturnal predation is a major cause of adult mortality in fishes studied at Christmas Island.

While diving off Molokini Island two large (5-6 feet) gray sharks (Carcharhinus sp.) were seen to swim repeatedly through a large school of Naso unicornis. The individual N. unicornis moved just far enough out of the way to allow the sharks to pass through the school. At no time did the sharks attempt to feed on the Naso and at no time did the Naso seem "disturbed" by their presence.

Even if predation was restricted to the young it could possibly be great enough such that there is less likelihood of any species reaching a point where competition for food becomes limiting.



## CHAPTER VII

### DISCUSSION AND CONCLUSIONS

#### GENERAL

In the Hawaiian and Johnston Island environments there is a large number of closely related species of the family Acanthuridae that appear to be coexisting. This observation seems to be in conflict with Gause's Principle (Odum, 1953) which has been interpreted as saying that no two species can coexist in the same ecological niche.

Lack's (1947) work on Darwin's Finches, and Hardin's (1960) general review of the "competitive exclusion principle" noted that seemingly trivial differences in such things as food habits, adaptations for feeding, and habitat differences are enough to allow two species to coexist. DaCunha et al. (1951) point out that competition between sympatric species for a limited variety of habitats leads to natural selection for adaptations that reduce this competition. For marine gastropods, Kohn (1959, p. 87) suggested that "the number of ecologically closely related species which may occupy a habitat is proportional to the amount of fractionation into microhabitats, which may

overlap but are sufficiently distinct that severe interspecific competition is precluded".

DaCunha (1957) found considerably more niche diversification in the tropics than in temperate areas. Larkin (1956), Myers (1960), and Johannes and Larkin (1961) have pointed out the tendency for temperate fish faunas to show a low degree of specialization and tropical aquatic systems a high one. It is therefore justifiable to presume that coral reefs provide heterogeneous environments. This in turn leads to the assumption that the Acanthuridae dwell in an environment with considerable potential for niche diversification.

It was pointed out in Chapter VI that there are a multitude of factors which may operate to regulate animal populations (see Crombie, 1947, for an extensive review of competition, population regulatory devices, and associated literature). Attention in this study, however, is focused primarily on habitat specialization, foraging methods, food eaten, and morphological specialization for feeding.

Physical separation of species in the environment has been found for a variety of organisms; e.g., Beachamp et al.

(1932) for freshwater triclads, Hairston (1951) for salamanders, Barkman (1955) and Bakker (1959) for marine snails, Cooper and Dobzhansky (1956) for Drosophila, and Fryer (1959) a and b) for fishes.

The early work of Grinnel (1904) is noteworthy for demonstration that the methods for getting food might vary enough to allow two species to coexist. Since that time considerable literature has amassed evidence providing for the separation of fishes in the environment by foraging method or the way in which they gather their food. Workers on fishes include Fryer ( 1959 a and b), Hiatt and Strasburg (1960), and Keast (1966).

Where the method by which food is obtained may indicate ecological separation; ecological separation based on food ingested is rare, and particularly so in fishes (Larkin, 1956). Some of the more successful researchers in this endeavor have been Daiber (1956), Fryer (1959 a and b), and Keast (1965). Most have found, as did Hartly (1948), that the major ecological differences lay in the proportion of food eaten and not the kind. Furthermore, these authors all found considerable overlap in the foods eaten.

Foraging methods apparently are a more important isolating mechanism than the specific materials ingested, provided that food is of the same general nature. If this be so, then one is led to the conclusion that morphological specialization in food gathering must also likely ensue. Perkins (1903) found that variations in bill structure of the Hawaiian Drepanidae allowed them to coexist. Lack's (1947) work on Darwin's finches showed that bill specialization and size of the bird is important in ecological separation. Similarly, Fryer (1959 a and b) and Keast (1966) pointed out a number of morphological adaptations that separated, ecologically, the fishes they studied,

FACTORS WHICH SEPARATED SPECIES OF  
HAWAIIAN AND JOHNSTON ISLAND ACANTHURIDAE

Acanthurus thompsoni and Naso hexacanthus may be considered as isolated from the other acanthurids by virtue of their mid-water habitat. There is additional isolation in that they seem "adapted for" and feed on zooplankton. There is a possibility that adult N. brevirostris might also occupy this habitat and feed on zooplankton but no evidence in support of this view, is available at this time.

It is predicted here that Acanthurus bleekeri and A. nubilis, two central Pacific forms not found in Hawaii, may also be zooplankton feeders. This prediction is based primarily on mouth structure, internal anatomy, and body shape from illustrations and descriptions by Randall (1956). He noted that the stomach of A. bleekeri is lined with rows of large thorn-like papillae. These sound much like the same structures found in A. thompsoni. The figures of A. nubilis appear to show the same upturned mouth of the plankton feeders; but in addition it also has a general body shape much like the zooplankton feeding Chromis (Pomacentridae). This speculation may be carried further when one considers the species included by Smith (1966) in the subgenus Atulonotus. Naso hexacanthus is a member of this subgenus. The complex also includes N.A. lopezi, N.A. vomer, N.A. tapeinosoma, and N.A. thorpei. The illustrations, descriptive morphology, and habitat notes suggest that these species may also be zooplankton feeders.

The sand patch habitat, presence of fine teeth, large numbers of gill rakers, the grinding organ of the stomach, and diet all operate to separate Acanthurus dussumieri, A. mata, A. olivaceus, and A. xanthopterus from most other

acanthurids. Items in the diet and the presence of the <sup>211</sup>  
gizzard make these similar to Ctenochaetus, but the latter  
genus occupies a different habitat.

Commercial fishing indicated that the grazing  
Acanthurus species might be somewhat separated from one  
another by depth. Even if zonation is incomplete, the  
author considers it unlikely that these four Acanthurids  
are competing for a food source that is in short supply.

Ctenochaetus hawaiiensis and C. strigosus, with  
extremely mobile jaws, flexible teeth, and reef habitat,  
are separated from the foregoing sand feeding Acanthurus.  
The same morphological adaptations for feeding plus diet  
are adequate to separate them from the other reef dwelling  
species. Any competition for food must exist between the  
two species. The rarity of Ctenochaetus hawaiiensis seems  
to infer that it poses no serious competition with C.  
strigosus. If this species arrived before C. strigosus  
or is an endemic (Randall, 1955d) and derived from another  
now absent Ctenochaetus, then its rather marginal existence  
in the southern-most Islands of the Hawaiian Chain (Lanai  
and Hawaii) could be explained by calling it a relict  
species in its last foothold against the extremely success-  
ful C. strigosus.

The enormous number of C. strigosus in the Hawaiian environment is ample testimony to the success of the species. Randall (1955d) noted that C. strigosus was abundant in Hawaii but rather scarce in other parts of the Indo-Pacific. He postulated that this might be due to the presence of C. striatus in great numbers in the Indo-Pacific. The absence of this species in Hawaii might then account for the success of C. strigosus. Similarly strigosus may be gradually excluding C. hawaiiensis.

Small differences in head profile, size of the eye, snout length and pharyngeal apparatus might be enough to ecologically separate these fishes in feeding behavior where diet does not.

Subadult Naso brevirostris, N. lituratus, and N. unicornis differ from other reef dwelling acanthurids in that they browse primarily on large leafy or fleshy algae. The other reef dwelling acanthurids eat smaller, more typically filamentous algae. N. lituratus and N. unicornis differ from N. brevirostris by having produced snouts, well developed and well armed pharyngeal tooth plates, longer intestines, longitudinal folds lining the esophagus and cardiac stomach, and a distinct ventral outpouching of

of the cardiac stomach. In N. brevirostris, it is seen that in addition to these differences, the anterior end of the esophagus and cardiac stomach are lined with papillae like the zooplankton feeders while the posterior end of the cardiac stomach has longitudinal folds.

The diets of N. unicornis and subadult N. brevirostris are similar in that they take large amounts of Sargassum and Dictyota. N. unicornis is by far the more successful of the two in Hawaii. Subadult N. brevirostris were rare and the adults were not seen. If competition exists between these two species then N. unicornis seems to be dominant. If the adult N. brevirostris is found to be a zooplankton feeder, the successful coexistence of these species might be explained.

N. lituratus differs from the above by having fewer teeth, the teeth are incisor-like, and it has a different diet. The species ingests primarily Pocockiella. This algal genus is not commonly eaten by the other two species.

The remaining species are reef dwelling members of the genera Zebrasoma and Acanthurus. The Zebrasoma species differed from all others in having the greatest production of the snout, fewest gill rakers, simple intestine, and



large rectum with several folds. They differ from most of the reef dwelling Acanthurus in having broad, well armed pharyngeal tooth plates, and a much shorter intestine. It is quite possible that in the absence of filamentous algae this genus could exist on coarser algae similar to that eaten by the Naso. The produced snout seems well adapted for foraging where filamentous algae feeding Acanthurus could not reach. The success of the genus might well depend on this feeding advantage.

No way was found to ecologically separate the subadults of Zebrasoma veliferum from Z. flavescens. The adult Z. veliferum however, was most frequently encountered in the surge zone where Z. flavescens is not normally found. Z. veliferum was the rarer of the two and possibly the less successful competitor.

The last seven Acanthurus were divided in part by their selection of habitat. Acanthurus achilles, A. guttatus, A. leucopareius, and A. glaucopareius are found in surge areas. There seems to be some zonation of these species. When all four are present (which is rare) A. guttatus is found in the area of greatest surge intensity. This is a rather uncommon species. If, as its protective

coloration seems to suggest, it is restricted to white water areas then its population numbers might be controlled by the density-independent scarcity of suitable habitat. Normally the white water areas constitute a rather thin white line of breakers along the windward shores of islands.

A. achilles is found most frequently in the surge zone at the edge of the white water areas. At Johnston Island, where A. guttatus is extremely rare, A. achilles also enters the white water areas. This species and its near relative A. glaucopareius with their beak-like mouths would seem to be "adapted for" feeding on a wide variety of substrata. Both A. achilles and A. glaucopareius seem capable of reaching into depressions on the reef that neither A. guttatus or A. leucopareius could reach.

A. leucopareius occupies the next zone seaward, and observations suggest that it is kept there in part by the aggressive nature of A. achilles. The considerably longer intestines of A. leucopareius might be considered advantageous under certain conditions. Increase in absorptive surface and possibly an associated increase in length of time for the material to pass through the gut could conceivably allow this species to feed for a shorter time or in an area where algal foods are reduced in quantity.

The fish might possibly be a more efficient converter of energy requiring less food than the other species with shorter intestines and lower absorption efficiency. When the two species are found together, A. achilles tended to occupy areas with a dense coral or coralline algal growth while A. leucopareius occupy in areas where coral growth is low and there is considerable exposed basalt surface. The occurrence of A. leucopareius only on high, relatively recent, basalt islands with limited coral growth (Hawaiian, Marcus, and Easter Islands) might suggest as Randall (1956) postulated that it is a relict species. A. achilles is much more common in coral rich Oceania as well as the relatively coral rich habitats in Hawaii and Johnston Island. It is postulated here that though both species have what appear to be morphological adaptations for more effective feeding, A. achilles would tend to replace the relict A. leucopareius as coral succession advances in the Hawaiian environment.

A. glaucopareius occupies a zone between the surge zone and subsurge reef areas. This may not be the typical habitat for the species in Oceania. In the absence of, or a reduction in population size of A. achilles, it seems to

get into the part of the surge zone normally occupied by A. achilles. The aggressive behavior of A. achilles dominates this species. A. glaucopareius would seem to fit the definition of a fugitive species (as defined by Hutchinson, 1951). It appears to be a sibling species with A. achillies. The latter species when they occur together is decidedly more abundant and A. glaucopareius is probably the rarest of the Hawaiian acanthurids (Randall, 1956). Yet its dispersal mechanism seems to be quite effective; it is found all over Oceania and is one of the three Indo-Pacific acanthurids that has crossed the East Pacific Barrier (Ekman, 1953) to the islands off the West coast of Mexico.

The remaining three Acanthurus to be discussed are the subsurge reef dwelling A. nigrofuscus, A. nigroris, and A. sandvicensis. If field observations are correct and A. nigrofuscus does defend a feeding territory, this could be an important mechanism for the survival of the species. Time after time, A. nigrofuscus was seen to drive away much larger fishes than itself including both acanthurids and scarids. The greatest number of aggressive encounters was between this species and A. nigroris and A. sandvicensis.

It seemed significant that the aggressive behavior of both A. nigrofuscus and A. achilles was almost always directed toward other browsers on filamentous algae and rarely against grazers or feeders on leafy or large fleshy algae.

The position of A. nigroris in the community would seem to be quite favorable, since the evidence at hand indicates that this species is capable of feeding either as a browser or grazer. Even though it does not have the gizzard of the normal grazer it is possible that it could subsist in part on interstitial material, particularly detritus. In direct competition with the more efficient grazers it might stand little chance of survival, but by being in a position to switch back and forth it would have the advantage of avoiding overspecialization.

Acanthurus sandvicensis has what may be a much more effective pharyngeal apparatus for dealing with filamentous algae than any other browsing Acanthurus. It has a longer intestine than any of the subsurge reef dwellers. This would seem to be an advantage similar to that enjoyed by A. leucopareius in the surge zone. Above all the schooling behavior of this animal seems to be one of the better adaptations for feeding. By adopting this method

of feeding, the animal covers a greater portion of the reef and seems to be "guaranteed" a higher percentage of feeding time per individual by reducing attacks from more aggressive species.

#### COMPETITION FOR FOOD

A study of the food habits of Acanthurus achilles, A. glaucopareius, A. leucopareius, A. nigrofuscus, A. nigroris, A. sandvicensis, and Zebrasoma flavescens showed considerable overlap of food genera, a wide variety of food eaten, and a distinct inconsistency of proportion and composition of food eaten by species from different localities.

Many workers have suggested that because fish species may be eating the same foods is not a just cause for assuming that they are competing (Hartly, 1948; Larkin, 1956; Johannes and Larkin, 1961; and others). It is in fact not uncommon to find the same food organisms in different species of fish (Larkin, 1956). It would seem that the acceptance of a wide variety of foods and in varying proportions (Hartly, 1948) would be advantageous

to the species in avoiding overspecialization and would divide the effect of competition among several foods. Figure 42 shows a hypothetical graph of the phenomenon. No one algal genus would be subjected to constant removal from the environment. If all species ate only Polysiphonia, it might soon become exhausted, but dividing the browsing pressure among several algal genera results in less pressure on any one genus. Hence, though Polysiphonia was found in all the specimens and all species it was never found alone.

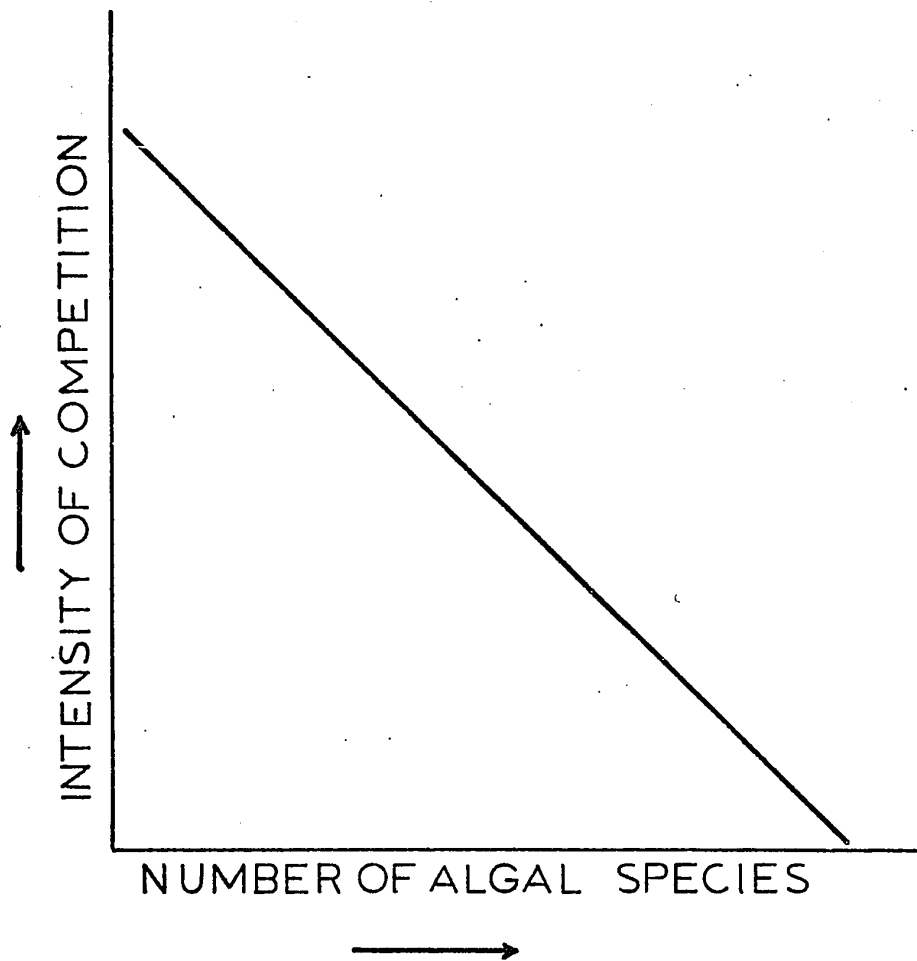
A problem arises as a result of failure to distinguish between algal species. Differentiation in food could occur at the species and not the generic level.

Another significant factor could be the fact that 100 percent overlap of primary food was never found in these fishes. It is, in fact, quite impossible to tell just what percent overlap would be necessary for competition to occur. The fact that overlap varied from station to station further complicated the problem.

It would be of great interest to know what factors are important in the selection of food genera. It was pointed out in Chapter III that the acanthurids probably

FIGURE 42. A HYPOTHETICAL SITUATION TO SHOW THE POSSIBLE EFFECT OF A VARIED DIET ON COMPETITION. AS THE NUMBER OF AVAILABLE FOOD SPECIES INCREASES, THE INTENSITY OF COMPETITION SHOULD BE REDUCED.





depend primarily on sight selection of their food. It seems likely that the fishes are greatly influenced by the organisms in their immediate environment and therefore would, as the data in Chapter IV indicate, take different foods in different localities. This might imply the existence of some sort of searching image (Clark, 1962 and Gibb, 1962). Even before the term searching image was introduced into animal behavior, Reighard (1908) found that the gray snapper Lutjanus griseus could be conditioned to eat baitfish that were dyed blue. When red dyed baitfish were introduced they were ignored for a time but eventually the snappers became conditioned to accept them. Reintroduction of the blue fish required reconditioning. Randall (1961a) found that Acanthurus sandvicensis could be conditioned to eat certain algae. When other algae were introduced it was several hours before the fish would begin to eat the new addition. Hence acanthurids may become conditioned to eat algae in their immediate locality. If searching image is involved then they would be expected to contain in largest proportion those algal genera that are both palatable and common. The species would, because of their searching image, tend to overlook

less frequent algae. If species are examined from another locality where the algal community is different they might be conditioned to eat an entirely different group of genera depending upon their palatability and frequency in the locality. The only inherited preference involved seems to be that one (or those) that tends to reduce variability in diet between individuals of the same species in one locality. Thus any two A. sandvicensis in a particular locality both eat similar proportions of the same algal genera. Though the consistency of composition and proportion eaten probably has a genetic basis, the actual choice of food depends on the structure of the algal community.

It might also be considered that the dominant food organisms in an animal's stomach are not the preferred foods. Instead, the foods taken in smaller proportions are the ones the animal searches for in the environment. It is conceivable that they may be uncommon in the algal community; and though preferred by the animal, they are uncommon in its stomach. The food in greatest proportion might then be the most common palatable food in the environment. Even though the food is not the preferred

one it is the one most readily available to satisfy a feeding "drive". This "drive" could possibly overcome food preference.

Three major trends in food habits by the species at each station are shown in Figures 6 - 12. They are: fishes that eat a large variety of primary food and have a small secondary food category, fishes that eat a reduced variety and small amounts of primary food but have a large secondary resource, and fishes that eat a small variety of, but large amounts of primary food and hence have a reduction of the secondary food reserve. None of the species consistently were found to fit any one of these trends over all the stations. Animals that fit the first one would show the least amount of specialization and hence have considerable flexibility of food habits. Fishes that fit this trend included A. nigroris, A. sandvicensis, and Zebrasoma flavescens. Fishes with a large secondary food reserve were only slightly more specialized than the above and again contained Acanthurus sandvicensis and Zebrasoma flavescens. The third trend represents considerable specialization and a great reduction in flexibility of food habits. The most consistent species

in this category was Acanthurus achilles.

It seems that the greatest amount of food specialization occurred in A. achilles and the least in A. sandvicensis and Zebrasoma flavescens. Acanthurus glaucopareius, A. leucopareius, and A. nigrofuscus were not collected at enough stations to notice any trend. It will be recalled that A. achilles is a highly aggressive fish of the surge zone and that A. sandvicensis is a subsurge reef animal with a wide ranging feeding behavior and low aggressive tendencies. Zebrasoma flavescens was restricted to dense coral areas and was able to feed on part of the algal community inaccessible to the other browsers.

For competition to operate at least one algal genus must be required by two species in excess of the immediate supply. The work of Randall (1961b) and of Stephenson and Searles (1960) suggested that browsing animals tended to keep algal turf grazed exceedingly short. This might imply that food is indeed limited in the reef environment. Bardach (1959) discovered that some of the reef fishes in Bermuda had an "unrealized growth potential". Some of these fishes (groupers) were found to gain 300 percent of their initial weight on unlimited food in the laboratory.

Randall's (1956) observation that several acanthurid species vary in size from various localities might suggest that inter-or intraspecific competition for food in some localities restricts the size of the animals. Many examples of stunted growth are found among "crowded" centrarchid fishes in freshwater environments (Larkin, 1956).

Acanthurus nigrofuscus is larger in Hawaii than in other places (Randall, 1956) studied in the central Pacific. Even in Hawaii, I have noted populations in some localities to be composed of larger individuals than in others. One such locality was in an area off Kewalo Basin where the largest A. nigrofuscus were seen. The most striking thing about this area is that other acanthurids are practically non-existent. Aggregations of this species appear to defend feeding territories and might thereby restrict themselves to too small a feeding area. Although they may as a group successfully defend the area against other acanthurids, they must undoubtedly be faced with strong intraspecific competition in a limited feeding space. The largest of the Acanthurus are the four grazing species which would seem to have a superabundance of food. Genetic variation between species and populations should not of

course be ignored and could invalidate the above suggestions.

Hayne and Ball (1956) studied two similar ponds in southern Michigan. They removed all fishes from one pond and noted changes in the benthic fauna between the ponds. In the pond without fishes they found that the rate of production of benthic organisms was quite low though the standing crop was slightly above that of the pond with fishes. The rate of production in the pond with fishes was 17 times the standing crop during the production season. It is conceivable that the experiments of Randall (1961b) and Stephenson and Searles (1960) measured the standing crop of algae growing in the wire enclosures but did not take into account a possibly higher rate of production in the browsed algae. Indeed, Stephenson and Searles (1960) found that in some of their enclosures algae grew rapidly and formed "unstable" mats that later became bare patches.

Regardless of the status of competition and availability of food, the fact remains that I did not find any individual of any species of the family Acanthuridae (out of several hundred) that did not have a gorged stomach

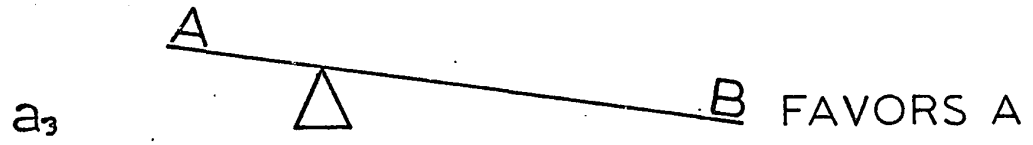
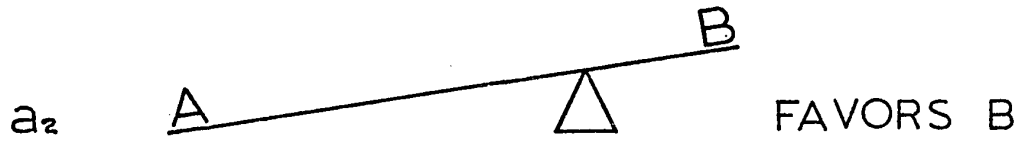
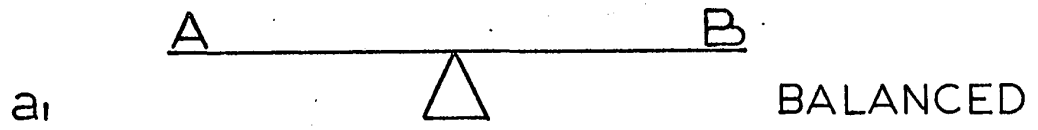
and intestine. It should also be pointed out that no consideration has been given in this study regarding time-dependent factors. Just because none of the fishes had empty stomachs during sampling periods does not mean that there could not be times during the year when food is less abundant. A more frequent series of sampling intervals than was carried out here would counter this bias.

Figure 43 shows a hypothetical set of situations regarding competition for food between species A and B, two browsing herbivores. The two species are balanced on a board representing the environment (Fig. 43 a.1). The fulcrum, on which the board and the weight of the two populations of species is balanced, represents the algal community that species A and B feed upon. The left-right displacement of the fulcrum changes the generic composition and biomass of each genus of the algal community. The algal community (fulcrum) may shift to favor either species depending on the direction of shift (Fig. 43 a.2) and a.3). The amount of imbalance also depends on the population biomass of species A and B. In Figure 43 b the algal community favors species A but the resultant increase in biomass of A's population and the corresponding decrease in B's allow B to continue to exist. A sudden



FIGURE 43. HYPOTHETICAL EFFECT OF COMPETITION  
ON TWO BROWSING SPECIES

- a. Populations of species A and B are of about equal size. A left-right shift of the composition and biomass of the algal community (fulcrum) tends to favor one species over the other and results in community imbalance.
- b. Imbalance caused by shift of the algal community toward A is countered by an increase in the population of A and a corresponding decrease in that of B.



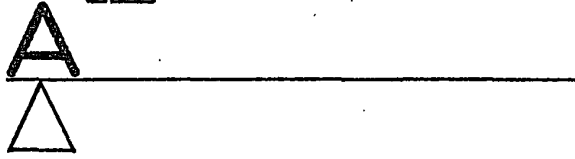
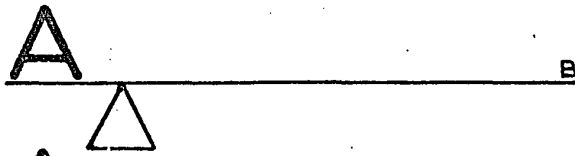
a.



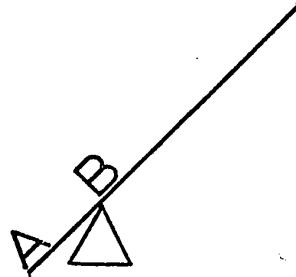
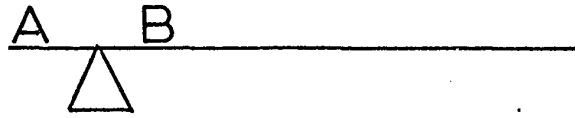
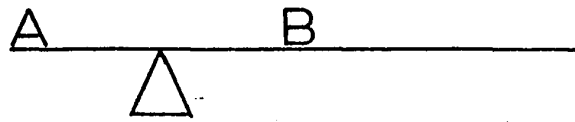
b.

## FIGURE 43. (Continued)

c. The situation at b. may be continued until the algal community favors A only and B is gradually eliminated. d. In another situation B itself may move toward the algal community by adaptations through natural selection on food habits and balance is restored or else B moves closer to the algal community than A and a new imbalance is set up.



C.



d.

shift in the algal community back toward species B might leave species A with an oversized population and thus result in heavy mortality if not extinction. A more gradual shift in the algal community might eventually put the fulcrum directly under species A which would result in the gradual elimination of species B (Fig. 43c). It is also possible for either species to become through natural selection, better adapted to a particular algal community and thus itself move toward the fulcrum (Fig. 43d).

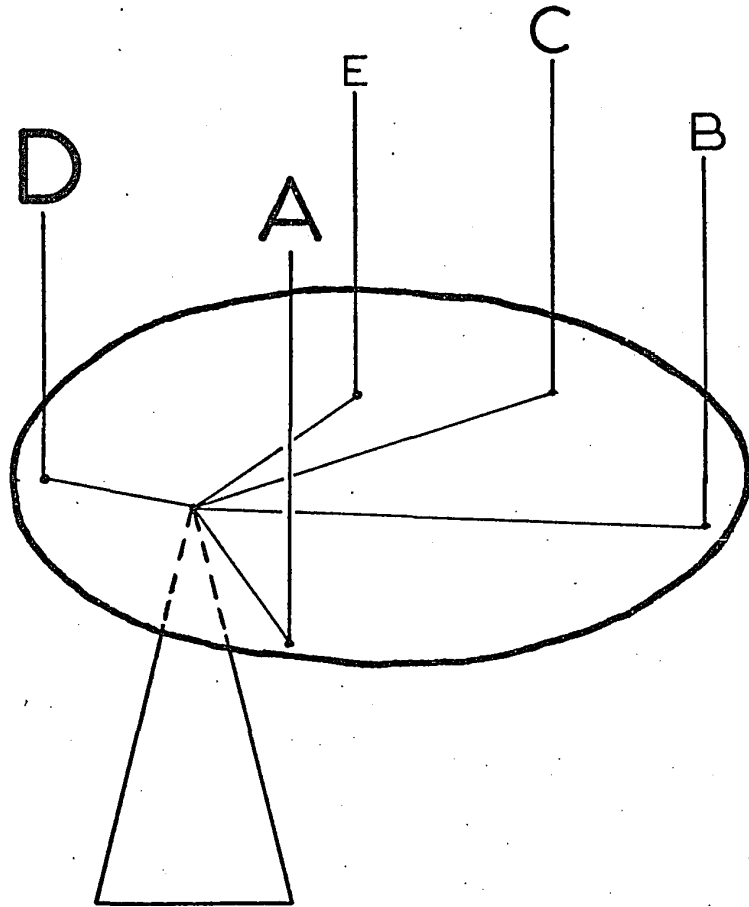
In a more complex and certainly more typical situation, we might expect to find that instead of a board, the environment might be better represented by a large disc on the radii of which are located all the competing species of browsers in the community. In this case the interaction of species position and biomass on the disc and the location of the algal community (fulcrum) under the disc would be a more realistic picture of the community ecosystem (Fig. 44).

#### CONCLUSIONS

There are then two major points to be made regarding the coexistence of Hawaiian and Johnston Island Acanthuridae.

FIGURE 44. HYPOTHETICAL RELATIONSHIP BETWEEN  
COMPETING SPECIES OF A COMMUNITY

The acanthurid community is represented by the disc. Each species position in the community is represented by a point on the disc. The relative size of the letter designating each species indicates the population size of that species. The length of the line from a species position to the apex of the fulcrum (algal community) is an indication of how favorable that algal community is to that species in terms of food. The algal community may change through physical changes in the environment and move to favor certain species. On the other hand, the species may change through natural selection and move toward the fulcrum. Resultant changes must occur in the other species for the community balance to be maintained. A and D are nearest the fulcrum, are most favored by the algal community and hence maintain large populations. B and C are progressively farther away and have smaller populations. E's proximity to the fulcrum suggests that it should be larger than it is but other factors (e.g., predation, disease, etc.) may possibly be keeping the population down.



First, it is evident that there are several possible methods operating that provide for ecological separation of the species. There are four groups of species that are separated from each other by selection of different habitats (mid-water, sand patch, subsurge reef, and surge zone). There are three different ways in which acanthurid species forage (zooplankton feeders, grazers, browsers). In terms of food eaten, there are at least four major categories (zooplankton, interstitial material, coarse algae, and filamentous algae). At the species level there are numerous modifications of the alimentary canal that suggest that many of the species are able to handle food in a different manner from other species.

Secondly, there is no clear evidence to suggest that food was a limited resource during this study. Why then are these animals found in different habitats, foraging in different ways and on several different categories of food, and why do they differ in the morphology of the alimentary canal?

It seems likely that competition for food is rarely severe in the environment. Yet at these rare times, extreme pressure in the form of natural selection may be



brought to bear. Thus selection may have occurred in the past at times when food was limited. In the present, we may possibly be looking at species which have ample common food supplies yet have a "standby condition" which provides them with potential means for survival should food again become limited.

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