Ecological Relationships in Hawaiian and Johnston Island Acanthuridae (Surgeonfishes)[1]

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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 specializations 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 zone dwellers. These habitats are defined in terms of acanthurid species composition and general physiography.

With regard to foraging methods and food eaten, the Acanthuridae comprise zooplankton feeders, grazers, and browsers. The zooplankton feeders actively pursue and capture copepods, crustacean larvae, and the pelagic eggs of numerous marine 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 the size and morphology of the algae.

At the species level several modifications in the morphology of the digestive tract are found which suggest that many of these fishes are able to handle their food in a different manner from other species.

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.

In the geographic areas considered there are four genera and twenty species of this family 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).

The author has undertaken an investigation 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 works of Randall (1955 a-d, 1956, 1961 a-c, 1965); Dawson, *et al.* (1955); Hiatt and Strasburg (1960); and Bakus (1967).

The primary emphasis of this paper is on ecological separation by habitat, foraging methods, and major food types eaten. In addition, comparative studies of the gross morphology of the alimentary canals of the species have been undertaken as a relevant part of a study of feeding habits. Morphological differences might suggest possible adaptations in the feeding mechanisms of the species.

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

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 (1955 a-d), Hiatt and Strasburg (1960), and Gosline (1965).

It should be pointed out 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 zone habitat, moving about in a reef-protected or subsurge area. This does not alter the fact that there are habitats in the Hawaiian and Johnston Island environments where one can predict the presence of particular acanthurid species. Randall (1961 a) 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 somewhat obscured when 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).
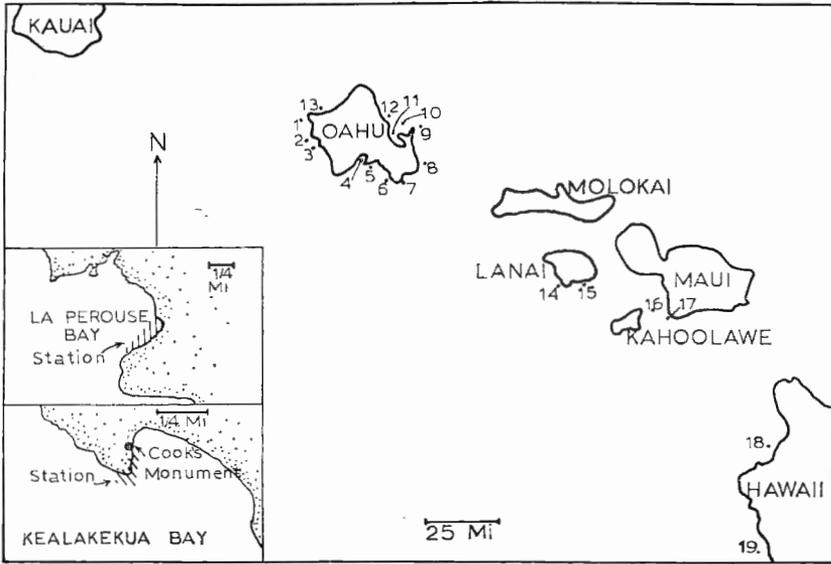
Fig. 1. Chart of Hawaiian Island Stations

1—Kaena Pt.	2—Makaha	3—Waianae Artifical Reef
4—Kewalo Basin	5—Maunalua Bay	6—Koko Head
7—Hanauma Bay	8—Makapuu Pt.	9—Moku Manu
10—Kaneohe, Outer Reef	11—Kaneohe Bay	12—Kuloa Pt.
13—Puuiki	14—Palaoa Pt.	15—Puupehe Rock (Manele Bay)
16—Molokini	17—La Perouse Bay	18—Honokaope Bay
19—Kelakekua Bay		
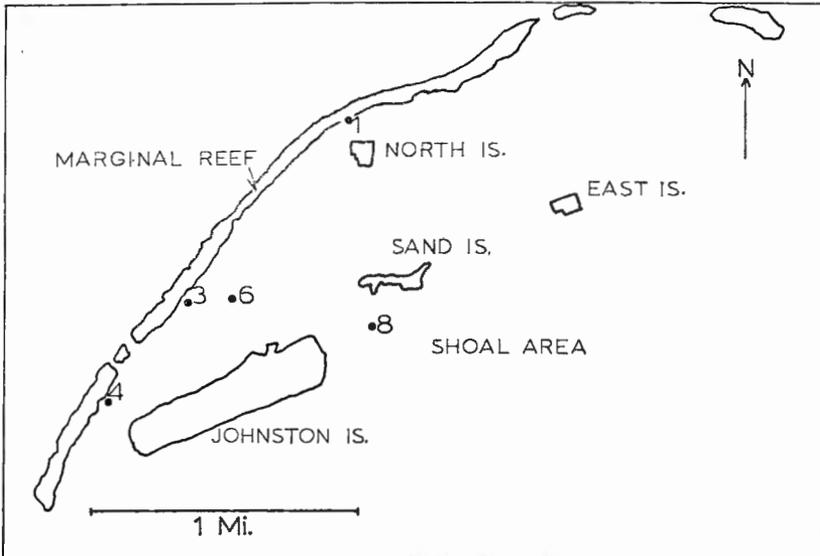
Fig. 2. Chart of Johnston Island Stations

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 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 term "shoal" seems more applicable to Johnston Island than "atoll." It differs from the "typical" atoll in lacking a deep central lagoon and a raised leeward reef. Though not exceedingly rich when compared with other central Pacific faunal areas, Johnston Island boasts a more prolific coral growth than Hawaii.

All of the Acanthuridae found at Johnston Island are also found in Hawaii, except *Ctenochaetus cynaoguttatus*. The Hawaiian acanthurids that are as yet unrecorded from Johnston Island are *Acanthurus dussumieri, A. leucopareius, A. nigrofuscus, A. thompsoni, A. xanthopterus, Naso brevirostris,* and *N. hexacanthus.*

Table I includes a list of all of the acanthurids considered in this paper.

MID-WATER HABITAT

The mid-water habitat is a subsurge part of the Hawaiian marine environment (Fig. 3A). This habitat may be found near shore but is usually seaward of surge or breaker zones. Its boundaries may encompass considerable depths along submerged island slopes. Unlike the majority of acanthurids studied, those found in this habitat are associated with the water column itself rather than the bottom community.

Frequently there is a steep slope of dark basalt nearby. The substratum beneath the water column normally consists of broken basalt, covered with patches of corals as *Pocillopora damicornis* and *Porites compressa.*

The acanthurid species most characteristic of this habitat are *Acanthurus thompsoni* and *Naso hexacanthus* (Table I). 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 most ubiquitous fish indicators.

The mid-water habitat with the associated species was encountered in the following areas (Fig. 1). On Oahu it was studied off Koko Head, in Hanauma Bay, off Moku Manu Island, and over the artificial reefs located at Maunalua Bay (automobile bodies) and on the Waianae Coast (concrete sewer pipes). 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 Kealakekua Bay (see insert, Fig. 1). The mid-water habitat with its particular association of fishes was not observed at Johnston Island.

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 both mid-water species make use of open water for rapid maneuvering to avoid capture. In addition, both species show a range

Table I. Summary of Habitats, Foraging Methods, and Major Food Types
Eaten by the Acanthurids Studied

Abbreviations denote:	Habitats	Foraging Methods	Food Types
	MW—Mid-water	B—Browser	DD—Diatoms & detritus
	SZ—Surge zone	G—Grazer	FA—Filamentous algae
	SP—Sand patch	PF—Plankton feeder	L/F—Leafy and fleshy algae
	SSR—Subsurge reef		P—Plankton

Species	Habitat	Foraging Method	Food Type
Acanthurus achilles Shaw	SZ	B	FA
" *dussumieri* Cuvier & Valenciennes	SP	G(B*)	DD(FA)
" *glaucopareius* Cuvier	SZ	B	FA
" *guttatus* Bloch & Schneider	SZ	B	FA
" *leucopareius* (Jenkins)	SZ	B	FA
" *mata* (Cuvier)	SP	G	DD
" *nigrofuscus* (Forskal)	SSR	B	FA
" *nigroris* Cuvier & Valenciennes	SSR	B(G)	FA(DD)
" *olivaceus* Bloch & Schneider	SP	G	DD
" *sandvicensis* Streets	SSR	B	FA
" *thompsoni* (Fowler)	MW	PF	P
" *xanthopterus* Cuvier & Valenciennes	SP	G	DD
Ctenochatus hawaiiensis Randall	SSR	G	DD
" *strigosus* (Bennett)	SSR	G	DD
Naso brevirostris Cuvier & Valenciennes	SSR	B	L/F
" *hexacanthus* (Bleeker)	MW	PF	P
" *lituratus* Bloch & Schneider	SSR	B	L/F
" *unicornis* (Forskal)	SSR	B	L/F
Zebrasoma flavescens (Bennett)	SSR	B	FA
" *veliferum* (Bloch)	SSR(SZ)	B	FA

* Some fishes were observed feeding alternately in different categories.   The least common methods are in parentheses.

of background color from dark gray to black.   Their frequent association with vertical basalt structures may render them virtually invisible to potential pelagic predators.

Data on the limits of the habitat are based on the limits observed for the above fishes.   The habitat ranges from six to at least 137 m.   The maximum depth is based on 14 research submarine ("Asherah") dives made by Strasburg, *et al.* (1968).   They observed *Naso hexacanthus* on all 14 dives off the Waianae Coast to a depth of 137 m. (Table II).   It seems reasonable to speculate that the lower limit of the mid-water habitat is even greater.

SAND PATCH HABITAT

In the Hawaiian Islands these areas are found inside fringing reefs, bays, or in the deeper waters of the subsurge zone.   They are found in the Johnston Island "shoal" environments.   The habitat includes moderate to extensive sandy

areas with interspersed coral or basalt structures (Fig. 3B).

Acanthurids characteristic of the sand patch habitat are *Acanthurus dussumieri*, *A. mata*, *A. olivaceus*, and *A. xanthopterus* (Table I).

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.

The observed vertical limits of this habitat based on the fishes that characterize it were between four and 128 m. (Table II, for maximum depth).

Table II. Observations on Fishes Made by Strasburg, Jones, and Iversen (1968) from the Research Submarine "Asherah" on the Waianae Coast of Oahu

Species observed	Number of dives on which observations were made	Depth range in meters
Acanthurus glaucopareius	2	49–67
A. leucopareius	1	85
A. sandvicensis	1	30–46
A. dussumieri	4	30–128
A. olivaceus	5	34–46
A. xanthopterus	7	46–91
Ctenochaetus strigosus	1	30–46
Zebrasoma flavescens	1	30–46
Naso brevirostris	1	30–46
N. lituratus	2	49–61
N. hexacanthus	14	15–137

SUBSURGE REEF HABITAT

Basically this is the area pictured 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" at Johnston Island.

In this habitat are found a great number of fish species representing a large biomass. 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 lituratus* Smith, 1966), *N. unicornis*, *Zebrasoma flavescens*, and sub-adult *Z. veliferum* (Table I).

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

The fishes defining the limits of this habitat are most commonly observed from depths of a few centimeters to about 30 m. Although several of these species were reported at greater depths (Table II), these depths are considered to be below the limits of active coral growth and not within the normal habitat.

SURGE ZONE HABITAT

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 a
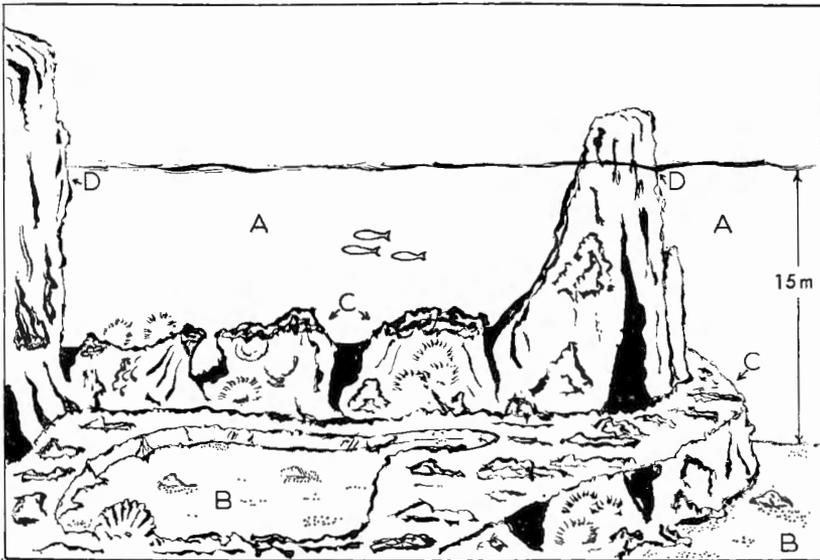
Fig. 3.   Habitats are Illustrated in the Sketch.   Open Sea is to the Right, There is an Offshore Rock and Sea Cliff Against Which Incoming Waves Break.

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

high density 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.

The acanthurids most characteristic of this habitat are *Acanthurus achilles, A. glaucopareius, A. guttatus,* and *A. leucopareius* (Table I).   On occasion the large adults of *Zebrasoma veliferum* were observed in this habitat.   Other acanthurids were seldom seen here except at times of flat calm seas or when passing rapidly 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.

This habitat is usually honeycombed with numerous cracks and caves.   At least one of the species, *Acanthurus guttatus,* seemed to use the most turbulent part of the surge for cover.   Randall (1955d.) noted that the white spots on the flanks of this species may render it virtually invisible in white water.

This habitat is of course restricted to the heavy surge areas of the reef and is by nature quite shallow.   Most of the characteristic species are limited to about six meters.   Some of the observations of Strasburg, *et al.* (1968) (Table II) indicated that a few of these species were found, though infrequently, at considerable depths.   Again such observations are negligible when compared to the main population concentrations along the surge areas.

ANALYSIS OF FORAGING METHODS AND FEEDING HABITS

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

ZOOPLANKTON FEEDERS

This category includes two species that actively pursue and capture individual zooplankters. The two species 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* (Table I). 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*. Smith (1966) points out that certain species of the acanthurid subfamily Nasinae have "predatory" food habits. No other reference to carnivorous acanthurids was found 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 (page 312). 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. The negative pressure produced by opening the mouth probably draws in these small food organisms. *Naso hexacanthus* differs from this only in that it occurs in transient schools, breaking up occasionally to feed, then re-forming the school.

Both species contained mostly crustacean remains. This material was basically derived from copepods, crab zoeae and megalops, and mysids. In addition, they contained pelagic eggs and nematocysts. One small cephalopod was found in *Acanthurus thompsoni*. No attempt was made to further 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, *et al.* (1968) at considerable depths (Table II).

On one occasion, two or three thalli of the red alga genus, *Polysiphonia*, and several sponge spicules were found 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.) On the other hand such items more likely represent accidental ingestions.

GRAZERS

Fishes that purposely pick up large quantities 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 this group include the sand patch-feeding *Acanthurus dussumieri*, *A. mata*, *A. olivaceus*, and *A. xanthopterus*, and the reef-dwelling *Ctenochaetus hawai-*

iensis and *C. strigosus* (Table I).

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 action.

The *Acanthurus* are commonly seen moving over the bottom in small to medium sized schools (4-20) picking up mouthfuls of sand. Periodically they stop to feed on and around rock and reef structures, but these structures on closer inspection are found to be covered with a layer of sand and detrital material.

Species of *Ctenochaetus* feed over rocks and dead corals. This genus was never observed feeding in the sand patch area. 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 that 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 generally avoided but if picked up was "forcefully ejected."

Randall (1956:162) 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 (1960:91) 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, 1960:248) 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 foraminiferans were also found. They felt that the gastropods and foraminiferans were inadvertently pick up. They reported 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" (p. 91).

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 the coralline alga *Porolithon*. Hiatt and Strasburg (1960) found short algal filaments, much sand, and some hydrozoan remains in *A. xanthopterus* from Eniwetok. 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 material discussed below.

The major difference most readily seen between the grazing *Acanthurus* and *Ctenochaetus* gut contents is the particle size of the sediment. It is coarse and grainy in *Acanthurus* and fine and silty 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 of 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, while *Ctenochaetus* get theirs from a much finer calcareous matrix on the rock and dead corals of reefs. (Fox, *et al.* 1953, referred to the detrital material as leptopel.)

The upper layer of sand or epipsammon of the Hawaiian environment in subsurge areas is often bound together by blue green algae, particularly *Microcoleus cthonoplastes*. This along with the interstitial organisms, forms a thin layer that may be somewhat mucoid in texture. Detritus and diatoms are 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 surmised 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 (1965:343) noted at Eniwetok "that organic matter including aggregates, transported in suspension from the reefs to mid-atoll areas may constiue 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) reported this for some salarine blennies; and Whipple, (1966) for littorine snails. Johannes (1967) reported *Spratelloides delicatulus* and *Chromis* sp. feeding on suspended aggregates. Though no data are at hand for the former species, the genus *Chromis* is often a mid-water plankton feeder. There is frequently however a mucoid mass associated with the plankton in the stomachs of plankton feeders which may indicate that these fishes feed on both aggregates and plankton.

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 the 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 at the time. The Maunalua Bay group had only a small amount of sand in the gut. These fish obviously had been feeding on the benthic 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 fragments of algae.

Table III. Summary of Algae Eaten by the Herbivorous Genera of Acanthurids

Symbol		*Acanthurus*	*Zebrasoma*	*Naso*	
D—Dominant		84–93%[1]	84–100%[2]	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%	

			Fish genera:	*Acanthurus*	*Zebrasoma*	*Naso*
Algal divisions	Algal orders	Algal genera	No. of Specimens:	N=197	N=37	N=62
Phaeophyta	Dictyotales	*Pocockiella*		P	—	D
"	"	*Dictyota*		R	R	A
"	"	*Padina*		R	—	P
"	"	*Dictyopteris*		—	R	R
"	Ectocarpales	*Ectocarpus*		D	D	R
"	Sphacelariales	*Sphacelaria*		D	D	R
"	Fucales	*Sargassum*		—	—	A
"	"	*Turbinaria*		—	—	R
"	Dictyosiphonales	*Chnoospora*		—	—	R
Chlorophyta	Cladophorales	*Cladophora*		A	A	—
"	"	*Rhizoclonium*		—	—	P
"	Siphonocladales	*Cladophoropsis*		—	—	R
"	"	*Dictyosphaeria*		R	R	C
"	"	*Microdictyon*		—	R	C
"	Ulvales	*Enteromorpha*		C	C	—
"	"	*Ulva*		—	—	P
"	Siphonales	*Caulerpa*		P	R	R
"	"	*Codium*		R	P	—
"	"	*Udotea*		R	—	R
"	Dasycladales	*Acetabularia*		R	—	R
Rhodophyta	Ceramiales	*Acanthophora*		R	—	P
"	"	*Acrochaetium*		P	A	—
"	"	*Alsidium*		R	R	—
"	"	*Centroceras*		A	D	—
"	"	*Ceramium*		A	D	—
"	"	*Champia*		R	P	P
"	"	*Chondria*		R	P	—
"	"	*Griffthsia*		R	P	—
"	"	*Laurencia*		P	R	C
"	"	*Polysiphonia*		D	D	R
"	"	*Spyridia*		R	—	R
"	"	*Tolypiocladia*		R	—	—
"	Cryptonemiales	*Jania*		C	P	—
"	Gelidiales	*Gelidium*		D	D	—
"	Gigartinales	*Hypnea*		R	P	C
Cyanophyta	Oscillatoriales	*Anabaena*		R	—	—
"	"	*Calothrix*		P	R	—
"	"	*Hydrocoleum*		R	—	—
"	"	*Lyngbya*		D	D	—
"	"	*Microcoleus*		R	—	—

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

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

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 *Lyngbya*. It seems most likely that these algal genera are accidentally ingested, while the preceeding group were selected.

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 *et al.* (1968) (Table II), who found many of these species at considerable depths. Brooks (1950) found that benthic algae in Lake Baikal dropped out at 5 m but he collected benthic diatoms 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 a larger size than any other species of the genus. Both the *Acanthurus* and *Ctenochaetus* species 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 grazing *Acanthurus* species is due to nutrition alone. It is 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 are attached to basalt or coral surfaces. Hence the fishes themselves are 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 I).

Table III gives a general summary of the algae eaten by the herbivirous genera.

The most significant observation from this table is the size of food ingested rather than specific items. For example *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 each algal division. In cases where there is overlap between the *Acanthurus/Zebrasoma* group and the *Naso* group, the former tend to eat much smaller or immature members of the fleshy algae.

It is also of interest to note that of the 160 odd algal genera available to the browsing Acanthuridae in Hawaii, only 40 were found in fish stomachs during this study. Omitting those algae which were so rare as to be most likely accidentals (i. e., *Dictyopteris*, *Turbinaria*, *Chnoospora*, *Udotea*, *Acetabularia*, *Anabaena*, *Hydrocoleum*, and *Microcoleus*) the number is reduced to 32 which

represents only 20 percent of the algal genera 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 (1961 a: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 (Jones, MS) 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, localitites, 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 any 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 *Cymodocea*. Similarly, the finding of large fleshy algae in *A. dussumieri* would be additional proof since the small teeth of this grazing species seem less adapted for biting the larger algae than are those of the true browsers (See page 333). Randall's (1961 a) feeding experiments showed that when they have no choice, *A. sandvicensis* could 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 (Table I): *Naso lituratus* and *N. unicornis* show considerable similarity in their foraging. 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. Considerably less information 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* obtained 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 five to 15 m of water. Strasburg, *et al.* (1968) reported them on one dive down to 46 m (Table II). Both *N. lituratus* and *N. unicornis* were observed feeding in waters of one to 15 m.

The preferred food of *N. lituratus* was *Pocockiella*; it was found in all of the 37 fish examined and in 25 of the 37 it made up 100 percent of the stomach contents (Table IV).

The nearly equal amounts of *Pocockiella*, *Sargassum*, and *Dictyota* in La Perouse Bay (Fig. 1, see insert) 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.

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
Dictyota		35%	20–30%	0	0
Sargassum		30%	5%	0	0
Pocockiella		35%	60%	100%	50–70%
Dictyosphaeria		0	0	0	10–20%
Miscellaneous		0	0	0	10–20%

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). Though *Pocockiella* is by far the preferred food, the La Perouse and Station 8 samples serve to adequately demonstrate that when confronted with a poorly developed *Pocockiella* population, the fish can and will vary the diet somewhat.

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 (Fig. 1), differed considerably in the ranking and generic composition of food (Table V).

Table V. Composition and Proportion of Algal Genera Eaten by *Naso unicornis*
Based on Percent Wet Weight

Locality:		Hawaii				Johnston Is.
Stations:		La Perouse Bay	Kealakekua Bay	Kuloa pt.	Puuiki	4
Algal genera	No. of Specimens:	N=2	N=1	N=5	N=5	N=1
Dictyota		59%	30%	0	21%	0
Sargassum		32%	50%	20%	74%	0
Pocockiella		9%	0	0	0	100%
Padina		0	10%	4%	0	0
Acanthophora		0	0	28%	0	0
Laurencia		0	0	13%	2%	0
Hypnea		0	0	18%	0	0
Champia		0	10%	5%	0	0
Microdictyon		0	0	6%	0	0
Miscellaneous		0	0	6%	3%	0

Though there is some variability depending on locality, Table V 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*, a situation that does not exist in Hawaii.

Though the data at hand for *N. brevirostris* was inadequate, those 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) specimens had large amounts of *Sargassum* in their stomach. A collection of *N. brevirostris* from La Perouse Bay, Maui, contained about 90 percent by volume of *Sargassum* and about 10 percent *Tolypiocladia*.

Browsers—Feeding of filamentous and small fleshy algea: Fishes of the group include *Acanthurus achilles*, *A. glaucopareius*, *A. guttatus*, *A. leucopareius*, *A. nigroris*, *A. sandvicensis*, *Zebrasoma flavescens*, and *Z. veliferum* (Table I).

Table III 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 would be required to show any 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 the section on habitats 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 leaving *Acanthurus achilles*, *A. glaucopareius*, *A. guttatus*, *A. leucopareius*, and the larger individuals 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 cease 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 cease 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*). Bakus (1967:137) reports that *A. guttatus* at Eniwetok is a grazer and ingests "significant quantities of coral fragments along with benthic algae." It seems possible that this would either be 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 (1955 a) found calcareous material and several types of fine algae with *Jania* and *Calothrix* predominating in *A. guttatus* from the Gilberts.

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. Similar observations have been made on *A. triostegus* by Randall (1961 a:263) in the Tuamotu archipelago, Eibl-Eibesfeldt (1962:171-173) at Addu Atoll and by Helfrich, *et al.* (1968;355) in the Line Islands. 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 (Fig. 8) 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.

COMPARATIVE GROSS MORPHOLOGY

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
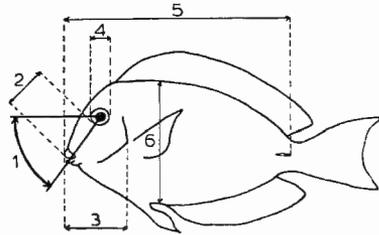
Fig. 4. A Generalized Acanthurid Showing Some of the Measurements Used in Discussion of Morphological Adaptations for Feeding
1—Eye/Mouth Angle   2—Snout length
3—Head length   4—Diameter of the eye
5—Standard length   6—Body depth
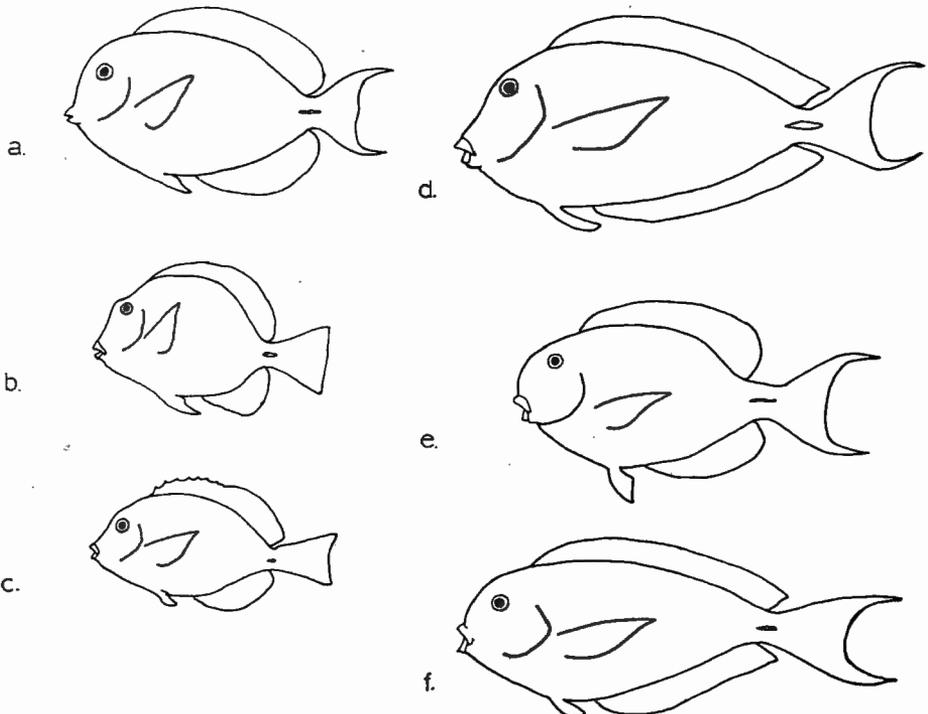
Fig. 5. Representative Species of *Acanthurus*
a. *A. achilles*, b. *A. guttatus*, c. *A. sandvicensis* (After Randall, 1956), d. *A. nigrofuscus* (profile retouched), e. *A. dussumieri*, f. *A. thompsoni* (d and f after Randall, 1956).

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, 1959b and Keast, *et al.* 1966). Body depth into standard length was used as an indication of general body shape (Fig. 4 and Table VI).

The mid-water dwellers, *Acanthurus thompsoni* (Fig. 5f) and *Naso hexacanthus* (Fig. 7c) are among the most elongate species of their respective genera (Table VI). 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. 5e; *A. mata*; *A. olivaceus*; and *A. xanthopterus*) are usually more elongate than most of the remaining members of this genus (Table VI).

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. 5a), *A. glaucopareius*, *A. guttatus* (Fig. 5b), *A. leucopareius*, *A. nigroris*, *A. sandvicensis* (Fig. 5c), *Ctenochaetus hawaiiensis* (Fig. 6a), *C. strigosus* (Fig. 6b), *Zebrasoma flavescens* (Fig.
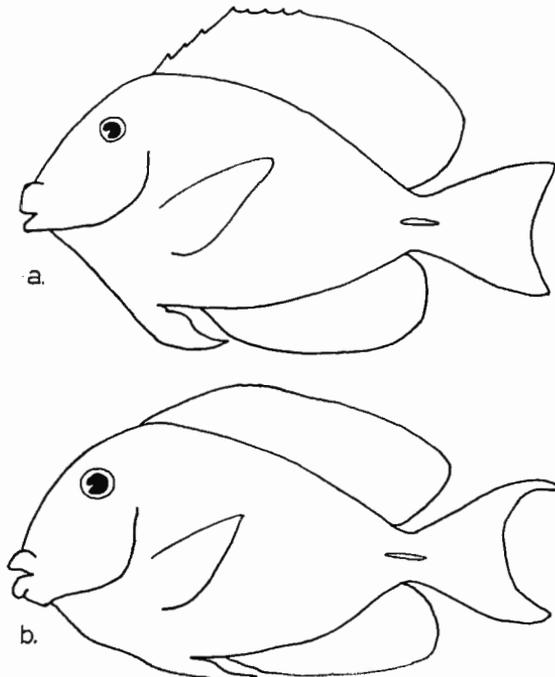
Fig. 6. Representative Species of *Ctenochaetus*
a. *C. hawaiiensis*,   b. *C. strigosus* (After Randall, 1955d).
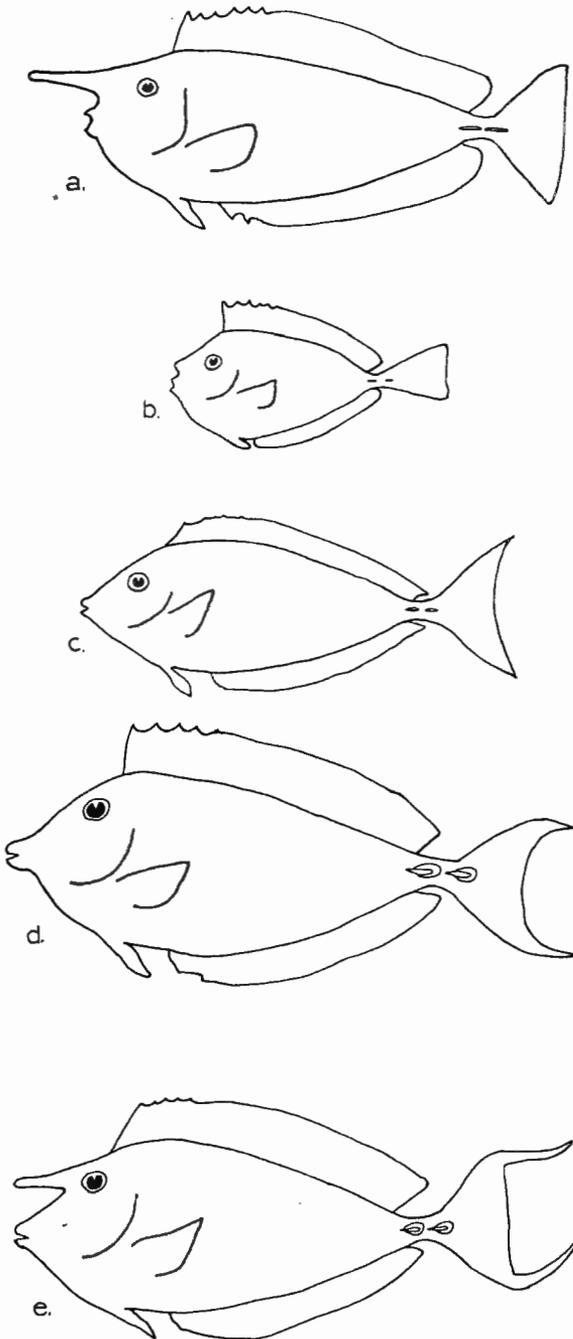
Fig. 7.　Representative Species of *Naso*

a.　*N. brevirostris* adult (556 mm),　b.　subadult (140 mm),　c.　*N. hexacanthus* (400 mm) (After Smith, 1966),　d.　*N. lituratus* (604 mm),　e.　*N. unicornis* (604 mm) (After Smith, 1966, Caudal filaments eliminated in d.).

8a), and *Z. veliferum*. Note, however, the exception found in the reef-dwelling *Acanthurus nigrofuscus*. (Fig. 5d) This species is very nearly as elongate as the mid-water form, *A. thompsoni* (Fig. 5f).

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. 5e), *A. mata*, *A. olivaceus*, and *A. xanthopterus* all have a characteristically rounded profile that may be somewhat bulging above the mouth (Randall, 1956). The species of *Ctenochaetus* also have rounded profiles (Fig. 6), 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 (p. 317).

In both *Naso lituratus* (Fig. 7d) and *N. unicornis* (Fig. 7e) the head profile is angular and the snout produced, providing possibly an effective feeding mechanism for getting algae in restricted crevices. By contrast, 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 (Fig. 7 a and b). In the adult the horn protrudes out beyond the snout and there may be a possible feeding disadvantage in this species. It would seem virtually impossible for the
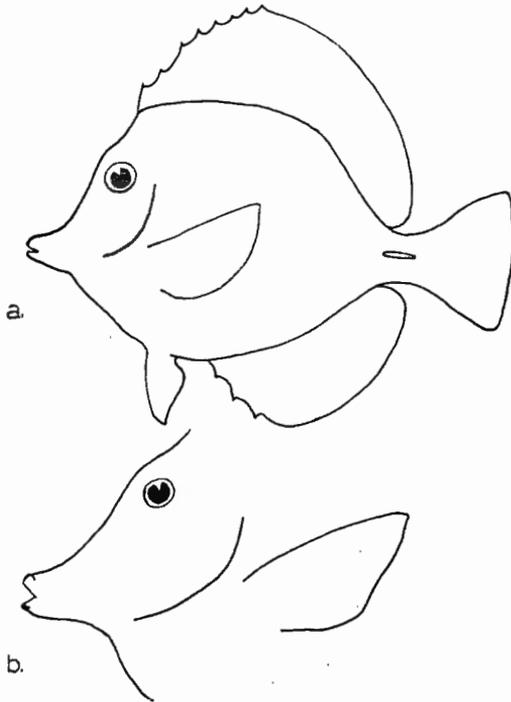
Fig. 8.   Representative Species of *Zebrasoma*
a. *Z. flavescens* (After Jordan and Evermann, 1905),   b. profile of
Z. veliferum.

adults to get the mouth down to the substratum due to interference from the horn (J. E. Randall, personal communication).

Food studies (Table III) show that *Zebrasoma* and the browsing *Acanthurus* eat very similar foods but the greatly produced snout of *Zebrasoma* (Fig. 8) might allow this genus to reach into cracks for algae not available to *Acanthurus*.

Position of mouth, size of eye, and snout length: Randall's (1961a) experiments on stimulus to feeding in *A. sandvicensis* indicated that the 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 (Fig. 4, Table VI).

The position of the mouth relative to the eye is measured as an angle. Figure 4 shows the construction of this angle. 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

Table VI. Proportional Measurements and Angles of Possible Significance in Feeding
(see Fig. 4): 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)

Species	BD	SNT	EYE	EYE/MOUTH
Acanthurus thompsoni	2.3	8.0	1.7	48°
A. achilles	1.8	4.0	3.2	62°
A. glaucopareius	1.8	4.1	2.8	62°
A. guttatus	1.6	3.9	3.8	62°
A. leucopareius	1.8	4.2	3.0	62°
A. nigrofuscus	2.2	4.6	2.6	56°
A. nigroris	1.9	4.2	3.2	58°
A. sandvicensis	1.9	4.8	2.7	55°
A. dussumieri	2.0	4.4	3.4	50°
A. mata	2.0	4.4	3.2	50°
A. olivaceus	2.4	4.7	3.2	50°
A. xanthopterus	2.1	4.9	3.2	52°
Ctenochaetus hawaiiensis	1.8	3.7	3.8	50°
C. strigosus	1.9	4.6	3.2	55°
Naso brevirostris	2.8	6.0	2.0	33°
N. hexacanthus	3.0	6.6	2.0	27°
N. lituratus	2.7	4.3	3.1	33°
N. unicornis	2.8	4.4	3.3	38°
Zebrasoma flavescens	1.7	4.3	3.1	47°
Z. veliferum	1.8	4.6	3.3	45°

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 *Zebrasoma* species (Table VI) show 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 also to be advantageous for aiming the snout into crevices to reach food growing there.

THE ALIMENTARY CANAL

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 the combination of a biting and sucking action to engulf a mouthful of the substratum upon which these fishes normally feed (p. 317). Observations show that both grazing 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. 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 VII). 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 feeding on individual zooplankters. The drawing out of the snouts 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 the foregoing sections of this paper indicate that these fishes are able to be quite selective and feed on a variety of substrata (depressions and cracks) from which other browsers are excluded. In *Acanthurus achilles* and *A. glaucopareius* the mouth (jaws) are laterally compressed and form a beaklike structure (Fig. 5a).

Orientation of Gape: Another possible feature of adaptive significance in the Acanthuridae involves the direction in which the opened mouth is oriented relative to the fish's head. This orientation is calculated as shown in Fig. 9. Data for representative species are found in Table VII. A small or negative angle indicates that the open mouth faces forward or up. A large angle means that the open mouth faces 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
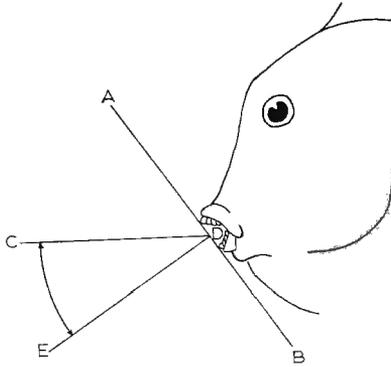
Fig. 9.   Orientation of Mouth Gape Measured as an Angle
    Line AB is drawn tangent to the open jaws, line CD
is drawn parallel to the horizontal plane of the fish, angle
ADE measures the direction in which the open mouth is
pointed relative to the horizontal axis of the fish.
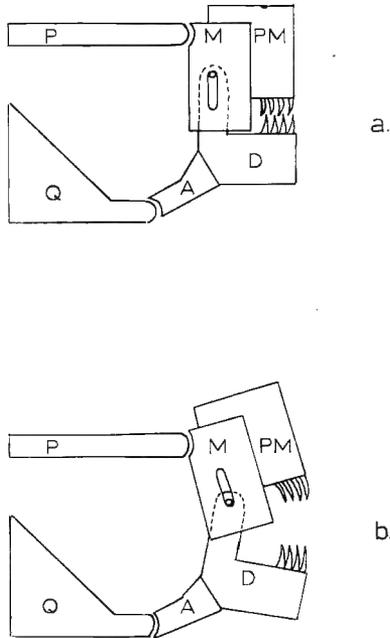
Fig. 10.   Diagrammatic Sketch of a "Typical" Acanthurid Jaw
            A—Articular   D—Dentary
            M—Maxillary   P—Palatine
            PM—Premaxillary
    The cam operated opening of the upper jaw is analagous
to the stretching of ligaments.

b) and Keast *et al.* (1966) for the zooplankton feeding fishes they studied.

Food studies in previous sections show that the remaining three *Naso* species 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. On the other hand, their ability to see an approaching predator while they are feeding may be enhanced.

Jaws: In the "typical" acanthurid, the jaws are opened by contraction of muscles attached to the mandible which pull posteriorly and ventrally 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. 10). There is a short 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 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
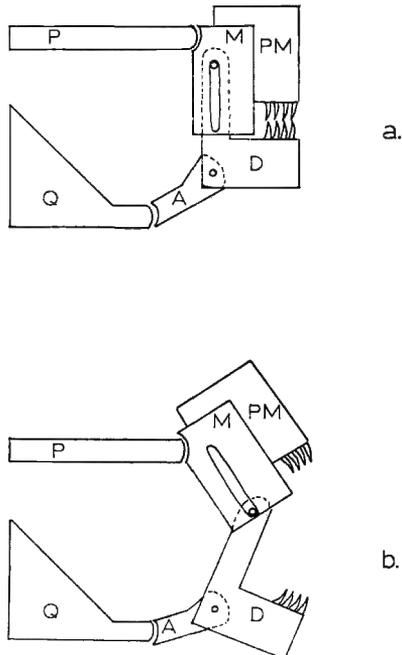
Fig. 11. Diagrammatic Sketch of the Double Jointed Lower Jaw of
Ctenochaetus (see Fig. 10 for Detailed Caption of Abbreviations)

articulars of the lower. These paired muscles close the jaws.

The greatest deviation from this pattern 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. 11 a and b). It seems likely that the quadroarticular joint is involved in the function of opening the mouth but increased muscle contraction on the dentary causes a secondary rotation on the joint between the articular and the dentary which in effect widens the mouth opening as well as protruding the lower jaw.

This probably increases the efficiency of *Ctenochaetus* when feeding on diatoms and fine detritus. The mobility 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. 12). They range from the relatively large ones of *A. guttatus* (Fig. 12c) to the very fine ones of *A. thompsoni* (Fig. 12b). The largest numbers of teeth are found in *A. thompsoni*, *A. dussumieri*, *A. mata*, *A. olivaceus*, and *A. xanthopterus* (Table VII). The greatest reduction in number of teeth occurs in the compressed beak-like jaws of *A. achilles* and *A. glaucopareius*.
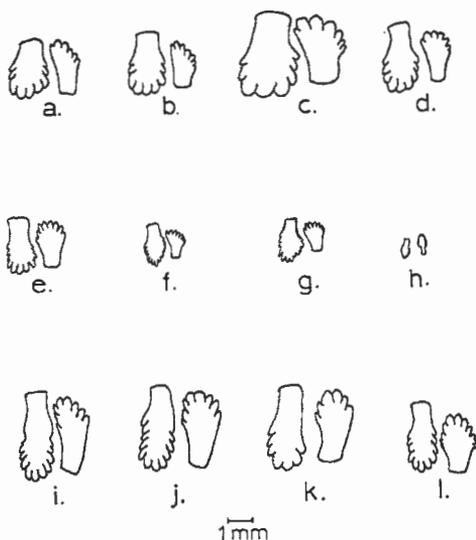
Fig. 12. Sketches of Upper (Left) and Lower (Right) Teeth of Species of *Acanthurus* (After Randall, 1956)

a. *A. achilles* (137 mm), b. *A. glaucopareius* (143 mm), c. *A. guttatus* (165 mm), d. *A. leucopareius* (156 mm), e. *A. triostegus* (140 mm, virtually identical to teeth of *A. sandvicensis*), f. *A. nigrofuscus* (18 mm), g. *A. nigroris* (81 mm), h. *A. thompsoni* (138 mm), i. *A. olivaceus*, j. *A. dussumieri* (210 mm), k. *A. mata* (228 mm), l. *A. xanthopterus* (200 mm).

1 mm
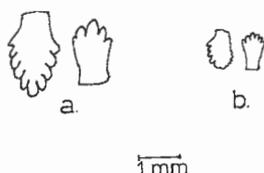
Fig. 13. Sketches of Upper and Lower Teeth of *Zebrasoma*
(After Randall, 1955 c)
a. *Z. veliferum* (171 mm),   b. *Z. flavescens* (100 mm)

The numerous, fine and somewhat pointed teeth of *A. thompsoni* (Fig. 12h)
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. 12 i-l). These teeth, rather than for biting or incising,
seem to act more as a rake for grazing in loose sand. The denticulations on the
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 algae (Fig. 12 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 12 and 13 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. 13).

Except for *Naso lituratus*, the *Naso* have a large number of pointed teeth
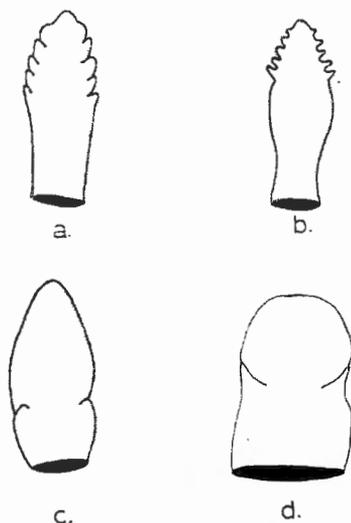
Fig. 14. Sketches of Lower Teeth of *Naso*
a. *N. brevirostris*,   b. *N. hexacanthus*,   c. *N. unicornis*,
d. *N. lituratus*

(Fig. 14 and Table VII). 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. 14b) which probably function in a similar manner to those of *Acanthurus thompsoni* (see above). The teeth are also finely serrate in *Naso brevirostris* (Fig. 14a) adults (Smith, 1966) and subadults. The young of *N. unicornis* have serrate teeth but the serrations are lost in the adults (Fig. 14c). 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* (Table V). *N. lituratus* has fewer teeth than the other *Naso*. The adults of these fish have rounded or square cutting edges on the teeth (Fig. 14d) while in the juveniles they are pointed (Smith, 1966). The major food of this species, is *Pocockiella* (Table IV). The texture of *Pockockiella* 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 fan-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 pieces 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. 15). Randall (1955d) found that in *C. strigosus* the number of teeth increased with increase in size of the fish. Table VII shows the approximate number of teeth in adult *Ctenochaetus*. The teeth on the upper and lower jaws of this genus seem
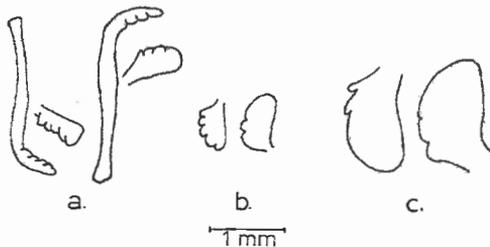
Fig. 15. Sketches of Teeth of *Ctenochaetus* (After Randall, 1955 d)
a. *C. striatus* (141 mm) not a Hawaiian species, b. *C. strigosus* (119 mm), c. *C. hawaiiensis* (157 mm)

to function as 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 over and scrape irregular surfaces (i. e., a rock). The flexible teeth of *Ctenochaetus* seem capable of the same action over the irregular rock surfaces they feed upon. Similarly these flexible teeth may be effective in "combing" attached algal thalli to remove adhering detritus and diatoms.

Table VII. Width of Gape Into Head, Orientation of Gape (Measured as an
Angle Fig. 9), and Maximum Number of Teeth in the Upper and
Lower Jaws for Representative Acanthurid Species

Species	Gape	Direction of mouth opening	Maximum teeth Upper/Lower[1]
Acanthurus achilles	6.2	25°	10/12
A. glaucopareius	4.9	25°	10/12
A. guttatus	3.7	60°	12/14
A. leucopareius	3.4	55°	16/20
A. nigrofuscus	×	35°	14/16
A. nigroris	×	50°	12/14
A. sandvicensis	3.5	50°	16/18
A. dussumieri	×	25°	20/22
A. mata	×	25°	20/20
A. olivaceus	4.0	30°	20/21
A. xanthopterus	×	25°	18/21
A. thompsoni	6.2	−10°	21/24
Ctenochaetus strigosus	4.1	20°	40/40
Naso brevirostris	4.4	15°	50/40
N. lituratus	4.6	15°	35/30
N. unicornis	4.7	15°	60/60
N. hexacanthus	5.6	0°	60/70
Zebrasoma flavescens	5.1	30°	18/22

[1] After Randall for *Zebrasoma* (1955 c), for *Ctenochaetus* (1955 d), for *Acanthurus*
(1956), and after Smith (1966) for *Naso*.

Gill Arches and Pharyngeal Teeth: The entire gill arch and pharyngeal
tooth apparatus was removed from each fish. The dorsal parts (including the
infrapharygobranchials and epibranchials) were separated from the ventral parts
(including the basibranchials, hypobranchials, and ceratobranchials) at the carti-
lagenous junction between the epibranchials and ceratobranchials. Diagrammatic
sketches are presented for representative species (Figs. 16-22). Where differences
occur in these species, sketches are made of the parts or characters that differ.
In addition, gill raker counts were made on both limbs of the first arch and
combined (Table VIII).

There are four distinct gill arches in the Acanthuridae (Fig. 16a). 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.
16b). The fourth gill arch has no bony basibranchial 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. 16-22).

In the species of *Naso* both *N. lituratus* (Fig. 16) 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

Table VIII. Frequency Diagram Showing Average Number of Gill Rakers
(After Randall, 1955 c, 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. sandvicensis	
A. dussumieri	
A. mata	
A. olivaceus	
A. xanthopterus	
A. thompsoni	
Ctenochaetus hawaiiensis	
C. strigosus	
Naso brevirostris	
N. lituratus	
N. unicornis	
N. hexacanthus	
Zebrasoma flavescens	
Z. veliferum	
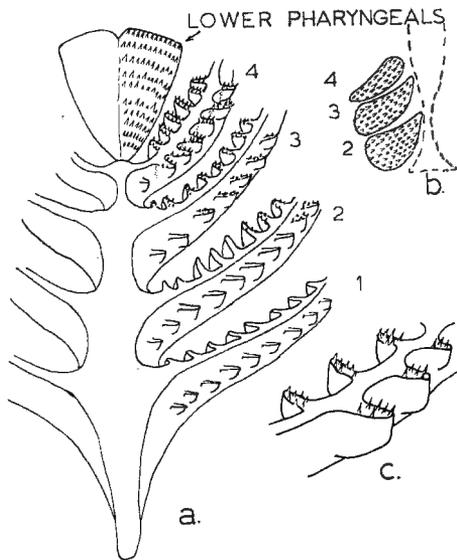
Fig. 16. Pharyngeal Elements of *Naso lituratus*
a. Pharyngeal apparatus showing gill arches 1-4 and the lower pharyngeal bones, b. upper pharyngeal bones of the second through fourth infrapharynbranchials (left side, ventral view), c. part of the fourth gill arch (diagrammatic sketches).

rows (Fig. 16 a and b). The gill arches themselves are armed with blunt, coarse gill rakers that are studded with short strong teeth (Fig. 16c). 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. 17a). 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 infra-pharyngobranchial (Fig. 17b). Tooth rows are not as well defined on the upper and lower pharyngeals as they are in *N. lituratus* (Fig. 16). The bristles on the gill rakers of *N. hexacanthus*, though less numerous, are considerably longer than the others (Fig. 17c). Gill rakers on the leading edges of the first and second arches are more elongate than in the other species of *Naso* (Fig. 17d). 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 (Fig. 18) seems to be intermediate between *N. lituratus* and *N.*
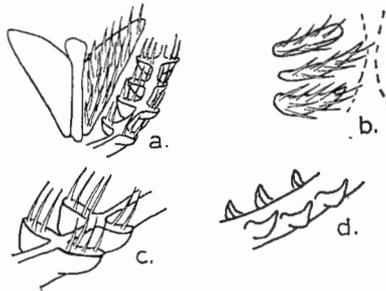
Fig. 17.   Pharyngeal Elements of *Naso hexacanthus*
a. Lower pharyngeals and arch four,   b. upper pharyngeals,
c. part of the fourth gill arch,   d. part of the first arch (diagram-
matic sketches).
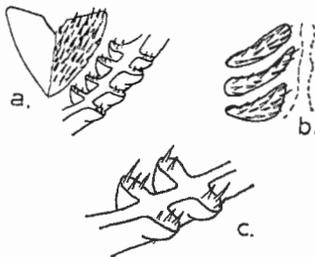
Fig. 18.   Pharyngeal Elements of *Naso brevirostris*
a. Lower pharyngeal and arch four,   b. upper pharyngeals,
c. part of the fourth gill arch (diagrammatic sketches).

unicornis on the one hand and *N. hexacanthus* on the other. 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 pharynge- als and reduction of the upper pharyngeal tooth elements.

Figure 19a shows the ventral part of the pharyngeal apparatus of *Zebrasoma flavescens*. *Z. flavescens* (Fig. 19a) and *Z. veliferum* (Fig. 19e) 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 seems to be with *Naso*. This conclusion is based on the relatively broad pharyngeal tooth plates and low gill raker count. These two characters 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.
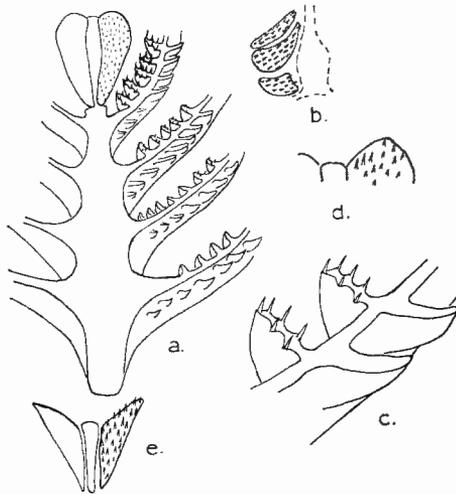
Fig. 19. Pharyngeal Elements of *Zebrasoma*
a. Pharyngeal apparatus of *Z. flavescens* showing gill arches 1-4 and the lower pharyngeal bones, b. upper pharyngeals, c. part of the fourth gill arch, d. part of the lower pharyngeals showing the armament, e. lower pharyngeals of *Z. veliferum* (diagrammatic sketches).

A sketch of the ventral part of the pharyngeal apparatus of *Acanthurus nigroris* (Fig. 20) 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. 20 a). The tooth plate of the second infrapharyngobranchial is reduced to a very small patch of bone with four to eight teeth (Fig. 20b). 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 have some bearing on the resem-
blance of its pharyngeal apparatus to *Acanthurus* grazers. However the pharyngeal
apparatus of the browsers *A. guttatus* and *A. leucopareius* would also have to be
classified as the "grazing type."
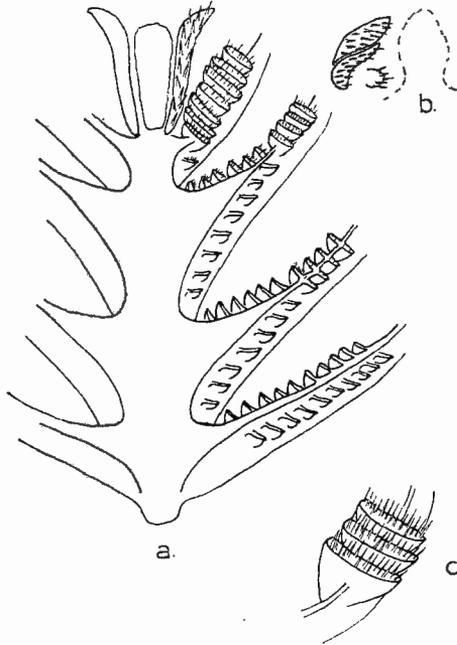
Fig. 20.   Pharyngeal Elements of *Acanthurus nigroris*
a. Pharyngeal apparatus showing gill arches 1-4 and the lower
pharyngeal bones,   b. upper pharyngeals,   c. part of the fourth gill arch
(diagrammatic sketches).

A. nigrofuscus bears considerable similarity with the above group in reduction
of the lower pharyngeal bones but the second infrapharyngobranchials are slightly
better developed (Fig. 21a). 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.
21b). 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. 21c). Teeth on the upper pharyngeals are in distinct
rows. *A. sandvicensis* has an enormous expansion of the lower pharyngeals (Fig.
21d). They are proportionately 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 infrapharyngo-
branchial plates are well developed and all upper pharyngeal tooth plates have the
teeth in distinct rows. (Fig. 21e). It seems likely that this expansion of the tooth
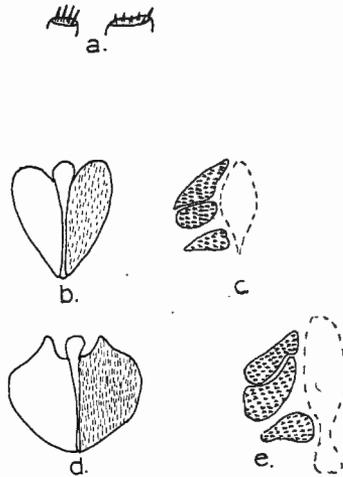
Fig. 21. Pharyngeal Elements from Representative Species of *Acanthurus*
a. Comparison of development in the second infrapharyngobranchial tooth plates, that of *A. nigroris* (left) is poorly developed, that of *A. nigrofuscus* (right) shows moderate development. b-c lower and upper pharyngeals of *A. achilles*, d-e lower and upper pharyngeals of *A. sandvicensis* (diagrammatic sketches).
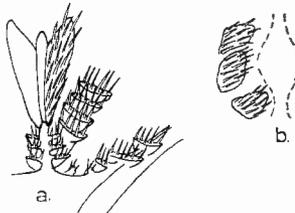
Fig. 22. Pharyngeal Elements of *Acanthurus thompsoni*
a. Lower pharyngeals and arches 3-4, b. upper pharyngeals (diagrammatic sketches).

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. 22a). All three elements of the uppers are well developed though somewhat smaller and differently shaped than the above three species (Fig. 22b). 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 arches. 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 striking difference is the presence of well-developed gill rakers on the

cartilaginous base of the fourth gill arch (Fig. 22a). The function of the gill apparatus of this animal probably approximates that proposed for the other zooplankton feeder, *Naso hexacanthus*.

Figure 23a is a sketch of the pharyngeal apparatus of *Ctenochaetus strigosus*. *C. strigosus* and *C. hawaiiensis* are virtually identical except for the somewhat larger and more widely spaced lower pharyngeal tooth plates in *C. hawaiiensis* (Fig. 23d). *C. hawaiiensis* also has considerably more teeth on the lower pharyngeals. *C. strigosus* has only 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. 23a 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. 23b). The pharyngeal apparatus of this genus would seem to be most effective in handling of the fine particulate matter ingested.
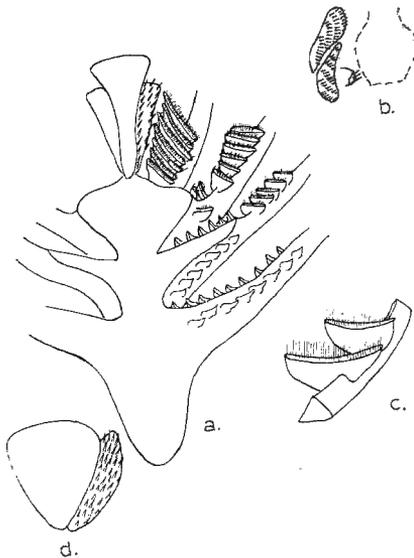
Fig. 23. Pharyngeal Elements of *Ctenochaetus*
a. Pharyngeal apparatus of *C. strigosus* showing gill arches 1-4 and the lower pharyngeal bones, b. upper pharyngeals, c. part of the fourth gill gill arch, d. lower pharyngeals of *C. hawaiiensis* (diagrammatic sketches).

Soft Anatomy (Gut): 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 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 occur among species, sketches are 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 pyloris). 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.* Three to five specimens of each species were examined.

The gut was carefully unwound and its length measured from esophagus to anus. The data are presented in Table IX.

The esophagus and stomach were split open to inspect their lining. The pyloric stomachs of two animals, one with a "gizzard" and one with a "thin wall," were dissected to show transverse and vertical aspects (Fig. 24).
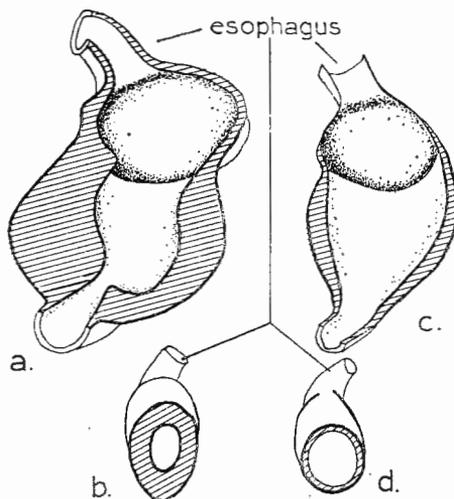
Fig. 24. Diagrammatic Comparison of the Gizzard-Like VS. The thin Walled Stomach
a-b. Longitudinal and transverse aspects of the "gizzard" type,
c-d. longitudinal transverse aspects of the thin walled type.

Figures 25 to 30 present the anatomy of the species studied.

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 cardiac and pyloric regions of the stomach, the pyloric region and the duodenum (pyloric valve), and at the rectointestinal

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 semicircle around the viscera that borders the dorsal, ventral, and posterior margins of the body cavity (Fig. 25a). *Naso hexacanthus* is an exception, the loop is present in this species but does not coil anteriorly and dorsally over the stomach (Fig. 30b).

The right side of the acanthurids 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.

From the data on gut length in Table IX it becomes evident that species fall into groups. *Acanthurus leucopareius* has the greatest gut to standard length ratio (range 6-7 times the standard length) with *A. sandvicensis* next (range 5-6). A second group with a moderately long gut (range 4-5) consists of *A. achilles*, *A. glaucopareius*, *A. guttatus*, *A. nigrofuscus*, and *A. nigroris*. The largest group has a moderately short gut length (range 3-4) and comprises *A. thompsoni*, *A. dussumieri*, *A. mata*, *A. olivaceus*, *A. xanthopterus*, *Ctenochaetus hawaiiensis*, *C. strigosus*, *Zebrasoma*

Table IX. Proportional Length of the Gastrointestinal Tract (Length Divided by Strandard Length) in Each Species Measured from Esophagus to Anus (Three to Five Specimens Were Used for Each Measurement)

Species	Length of GI. Tract
Acanthurs achilles	5.2
A. glaucopareius	4.9
A. guttatus	4.6
A. leucopareius	6.9
A. nigrofuscus	4.0
A. nigroris	4.4
A. sandvicensis	5.8
A. dussumieri	3.0
A. mata	3.8
A. olivaceus	3.4
A. xanthopterus	?
A. thompsoni	3.1
Ctenochaetus hawaiiensis	3.5
C. strigosus	3.5
Naso brovirostris	2.2
N. lituratus	3.2
N. unicornis	3.2
N. hexacanthus	1.8
Zebrasoma flavescens	3.7
Z. veliferum	3.7

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. Figure 25 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 as a triturating organ (Fig. 25b).

The center of the coil on the right side of these animals is usually made up of an S-shaped loop (Fig. 25c). Basically the intestine from the region of the pyloric caeca 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 one complete turn clockwise and 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.
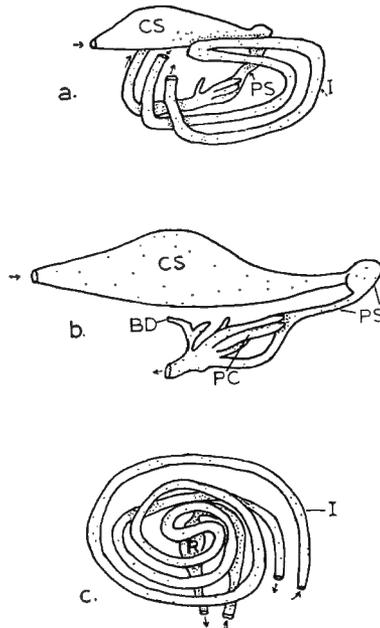
Fig. 25. Gastrointestinal Tract of *Acanthurus nigrofuscus*
a. left side, b. stomach, c. right side
BD—bile duct
CS—cardiac region of the stomach
I—intestine
PC—pyloric caeca
PS—pyloric region of the stomach
R—rectum.

This situation is identical in all the thin walled stomach group except *A. leuco-pareius* 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 greater length of the gut in *A. leucopareius*.

The coil pattern of *A. guttatus* is more like that of the thickwalled *Acanthurus* described in the next group (Fig. 26c).

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 *A. nigroris* has a stomach that tends to be of somewhat intermediate thickness but remains closer to the thin-walled group.

The much longer intestine of the surge zone dwelling *A. leucopareius* might perhaps be advantageous for increasing the area of absorption. Similarly the intestine of the subsurge reef dwelling *A. sandvicensis* is longer than any of the other species in this habitat.

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. 26 a and b) and have the short intestines. The
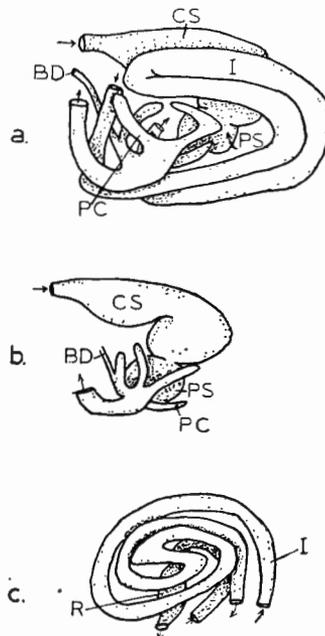
Fig. 26. Gastrointestinal Tract of *Acanthurus dussumieri*
a. left side, b. stomach, c. right side
(see Fig. 25 for abbreviations)

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. 26c). The intestine passes from the lower 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. *Mugil 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, *Mugil 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 pyloris of the acanthurid grazers show that most of the frustules are intact. Posterior to the pyloris, 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 (Table IX). 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*.
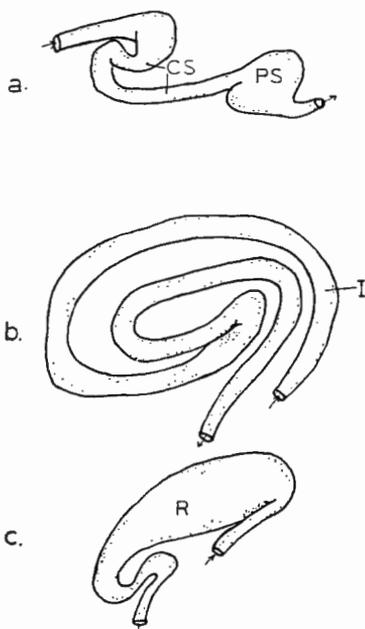
Fig. 27.   Gastrointestinal Tract of *Acanthurus thompsoni*
a. stomach, b. intestine, c. rectum
(see Fig. 25 for abbreviations).

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. 27a). The pyloric stomach is a large, thin, balloon-like sac much larger than the pyloris 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. 27b). The rectum of this species is much larger than the foregoing and has a small extra U-shaped coil (Fig. 27c).

The large balloon-like pyloris of *A. thompsoni* specimens was always distended with plankton. The species has, as expected, a shorter gut than the browsing *Acanthurus* (Table IX).

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. 28). This simplification results in a short intestine (Table IX). Figure 28 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 are 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 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. 29). This feature was also reported for *Naso unicornis* by Al=Hussaini (1947) and has been verified here.
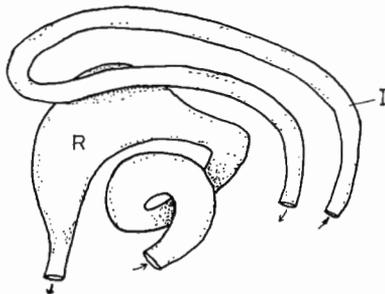
Fig. 28. Some of the Gastrointestinal Elements of *Zebrasoma flavescens*, Right Side Intestine and Rectum.
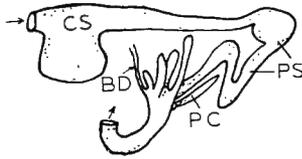
Fig. 29.   Stomach of *Naso lituratus*
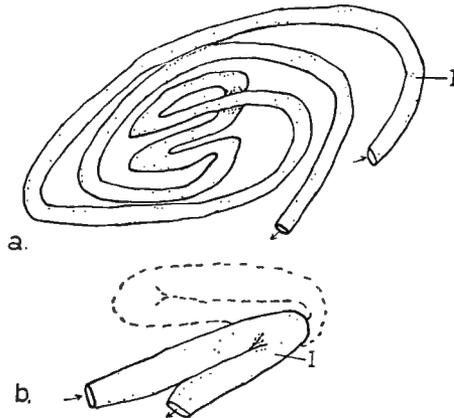
Fig. 30.   Gastrointestinal Elements of *Naso hexacanthus*
a. right side intestine, b. left side intestine (dashed line is
the normal condition in other acanthurids).

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 thick-walled stomach *Acanthurus*.   Figure 30a 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. 30b).   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 esophagus and the anterior part of the cardiac stomach have papillae, and the posterior part of the cardiac stomach has longitudinal folds.   There are no 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 large fleshy algae fed upon are more easily digested.

OTHER FACTORS OF POSSIBLE SIGNIFICANCE IN
ECOLOGICAL SEPARATION

It would be unwise to think that this study of habitat, foraging methods, food habits, and digestive morphology 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 is likely to 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 competion if their populations remain at levels such that the resource(s) for which they might compete is (are) not in short supply.

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

Reproduction

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 and b) is the only author who has observed spawning in the Acanthuridae. He observed spawning in *Acanthurus triostequs, 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 then return to the aggregation. Second, spawning occurred in the late afternoon and third, all three spawned in reef channels where strong currents were setting to the open sea.

Aside from surgeonfishes, the upward rush in spawning has also been observed 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 a 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 reefs, the majority of possible predators on the eggs are fishes that normally feed along or near the subtratum (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 all 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 mainte-nance 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 other 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 most obvious 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 part of 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 Current 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 con-sidered 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 acan-thurid eggs. Chamberlain (1968) noted 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 the positive buoyancy of the eggs versus the negative buoyancy of sand the similarity is not complete. Eggs would con-tinue 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. 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. Similar observations were made by Strasburg, et al. (1968). Thus if acanthurid eggs or larvae enter the Coastal Current System and then the North Equitorial Current there is a strong likelihood that these animals will be lost to the Hawaiian fauna.

Acanthurid larvae were found in the stomachs of pelagic fishes by Reintjes and King (1953) in the yellowfin tuna (*Thunnus albacares*) and by Rothschild (personal communication) 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 then this would be an important phenomenon for dispersal of the species to the other islands.

While discussing reproductive behavior it might be of interest to point out that *Acanthurus sandvicensis*, probably the most numerous of the Hawaiian acanthurids, transforms to 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 surgeonfishes, 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 (personal communi-

cation). If, however, these young animals had already been swept away from their "home" islands then this form of predation is irrelevant.

Randall (1961a) noted that predation on *A. sandvicensis* was probably most severe in early life stages. He found junenile *A. sandvicensis* in moray eels (Muraenidae) and has observed predation on them by lizard-fishes (Synodontidae), frogfishes (Antennariidae) and jacks (Carangidae). Randall and Brock (196) working in the Society Islands found yound surgeonfishes in the stomachs of several species of groupers (Serranidae) and snappers (Lutjanidae). Helfrich, *et al.* (1968) 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 additionally by holocentrids, scorpaenids, cirrhitids, and sphyraenids. He notes that, where there are no well-developed lutjanid and serranid populations, *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.

Throughout a four-year period of diving in the Hawaiian Islands no predation was observed by the author on adult acanthurids. Frequently adult surgeonfishes are seen swimming and feeding around holes in the reef in which large moray eels were living. These fishes seem to swim about with immunity, though practically touching the heads of the eels. Yet many times when one of these fishes is speared, an eel will snatch it from the end of the spear and retreat into a 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 torper. Since many of the Acanthuridae do "sleep" some nocturnal predation by eels and other predators might occur. Helfrich, *et al.* (1968) suggested that nocturnal predation is a major cause of adult mortality in reef fishes studied at Christmas Island.

On a dive off Molokini Island, Hawaii, two large (1.5-2 m) gray sharks (*Carcharhinus* sp.) were observed swimming repeatedly through a large school of *Naso unicornis*. The individual *N. unicornis* moved only 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 is restricted to the young it could still be great enough such that there is less likelihood of any species reaching a point where competition for food becomes limiting.

DISCUSSION AND CONCLUSIONS

In the Hawaiian and Johnston Island environment 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 which has been interpreted as saying that no two species can coexist in the same ecological niche (Odum, 1953).

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 adaptions that reduce this competition. For marine gastropods, Kohn (1959:87) 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, et al. (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 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 which has a considerable potential for niche diversification.

It was pointed out in the previous section 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 Grinnell (1904) is noteworthy for demonstrating that methods of 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 et al. (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 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 the 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, et al. (1966) pointed out a number of morphological adaptations that separated, ecologically, the fishes they studied.

Summary of 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* Günther and *A. nubilis* Fowler and Bean, 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 papilae. These sound much like the same structures found in *A. thompsoni*. The figures of *A. nubilis* show the same upturned mouth of the plankton feeders. In addition, this species 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 gizzard make these similar to *Ctenochaetus*, but the latter genus occupies a different habitat.

Commercial fishing in Hawaii has 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, are separated from the other reef dwelling genera. 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 successful *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 latter species in Hawaii might then account for the success of *C. strigosus*. Similarly, *C. 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 *C. hawaiiensis* and *C. strigosus* in feeding behavior where diet does not.

Naso lituratus, *N. unicornis*, and subadult *Naso brevirostris* 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 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 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 acanthurid 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, species of 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* cannot 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. There are also minor differences in tooth structure.

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. 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 these islands.

A. achilles is found most frequently in the surge zone at the edge of the white areas. At Johnston Island, where *A. guttatus* is 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 surge zone part of the reef that neither *A. guttatus* nor *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* tends to occupy areas with a dense coral or coralline algal growth while *A. leucopareius* occur in areas where coral growth is low and there is considerable exposed basalt surface. *A. leucopareius* seems to be more common on high, relatively recent, basalt islands with limited coral growth (Hawaiian and Easter Islands) and as Randall (1956) postulated, may be 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. 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. In Hawaii *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. achilles*. The latter species when they occur together in Hawaii or at Johnston Island is decidedly more abundant. *A. glaucopareius* is probably the rarest of the Hawaiian acanthurids (Randall, 1956), yet its dispersal mechanism seems to be quite effective since it is found all over Oceania and is one of the three Indo-Pacific acanthurids that has crossed Ekman's East Pacific Barrier to the islands off the West coast of Mexico. On Guam, where *A. achilles* is absent, *A. glaucopareius* is a common reef fish.

The remaining three *Acanthurus* to be discussed are the subsurge reef dwelling *A. nigrofuscus*, *A. nigroris*, and *A. sandvicensis*. Field observations indicate that *A. nigrofuscus* possibly defend feeding territories. 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 acanthurids and occasional scarids. The greatest number of aggressive encounters was between this species and *A. nigroris* and *A. sandvicensis*. It seems 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 large fleshy algae.

The position of *A. nigroris* in the community would seem to be quite favora-

ble, 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 also 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.

SUMMARY

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

First, it is evident that there are several possible mechanisms at work which separate the species ecologically. There are four groups of species that are separated from each other by selection of different habitats (midwater, sand patch, subsurge reef, and surge zone). There are three different ways in which acanthurid species forage (zooplankton feeders, grazers, and 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 interspecific differences in food handling.

The second point derives from the fact that there is no clear evidence to suggest that food was in limited supply in any of the several habitats 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?

Although competition for food among acanthurids is rarely severe in the environment, there must be infrequent periods when food shortages do occur. At such times, selection pressure would be high in favor of adaptations that would tend to reduce interspecific competition (i.e. changes in food habits, habitat, and feeding morphology). Return of an unlimited food supply would not necessarily be accompanied by loss or modification of adaptive features that arose during a period of food shortage. Thus even though the extant species studied have ample food supplies, they retain adaptations which would provide them with potential mechanisms for survival should food again become limited.

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