FEEDING RELATIONSHIPS OF TELEOSTEAN FISHES ON CORAL REEFS IN KONA, HAWAII

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ABSTRACT

Feeding relationships of teleostean fishes on coral reefs at Kona, Hawaii, were studied during 1969 and 1970.

Fishes that have a generalized feeding mechanism, including those carnivores whose morphologies place them close to the main line of teleostean evolution, are predominantly nocturnal or crepuscular. These include holocentrids, scorpaenids, serranids, apogonids, priacanthids, and lutjanids. The major prey of the nocturnal species are small, motile crustaceans, which are most available to the direct attacks of generalized predators when they leave their shelters after dark. The major prey of the crepuscular species are smaller fishes, whose defenses against direct attacks of generalized predators are less effective during twilight. Feeding by generalized predators during the day depends largely on being within striking distance of prey that make a defensive mistake, a position best attained by those predators that ambush their prey from a concealed position, or by those that stalk.

Ambushing and stalking tactics have produced some highly specialized forms that, during the day, prey mostly on smaller fishes. Diurnal ambushers include the highly cryptic synodontids, scorpaenids, and bothids; diurnal stalkers include aulostomids, fistulariids, belonids, and sphyraenids—all of them long, attenuated fishes.

Some predators—most notably the muraenid eels—are specialized to hunt deep in reef crevices, and here they capture some of the many small animals that shelter themselves in those crevices, day and night, when resting, injured, or distressed. Mullids use their sensory barbels to detect small animals that have sheltered themselves amid the superficial covering on the reef, or in the surrounding sand; at least some mullids further use their barbels to drive these prey into the open.

Most of the fishes on Kona reefs are among the more highly evolved teleosts, having reached, or passed, the percoid level of structural development. The adaptability of the feeding apparatus in these more advanced groups has given rise to a wide variety of specialized species, including both carnivores and herbivores, that have diverged from one another mostly on the basis of differing food habits. These fishes, most of which are diurnal, include the chaetodontids, pomacentrids, labrids, scarids, blenniids, acanthurids, and *Zanclus*, among the perciforms; and the balistids, monacanthids, ostraciontids, tetraodontids, canthigasterids, and the nocturnal diodontids, among the tetraodontiforms. With their specialized feeding structures and techniques, these fishes consume organisms like sponges, coelenterates, large mollusks, tunicates, and tiny or cryptic crustacea that are protected by behavioral or anatomical features from fishes not appropriately specialized.

Many important ecological relations among marine fishes are understood only by considering in broad overview during both day and night the different forms living together under natural conditions. With this in mind, I undertook a broad study of reef fishes at Kona, Hawaii, between June 1969 and August 1970. A segment of this study dealing with the twilight situation was published earlier (Hobson, 1972). The present report describes the situations that prevail throughout day and night. The work is centered on direct observations of activity in the fishes, as was my earlier study of predatory behavior of shore fishes in the Gulf of California (Hobson, 1968a), but here with greater emphasis on detailed analysis of food habits.

Several other workers adopted broad overviews in considering fishes of various areas. Limbaugh (1955) studied fishes in California kelp beds during the day, whereas Starck and Davis (1966) described the habits of fishes in the Florida Keys at night; both of these studies present extensive direct observations of activity, but little data on food habits. On the other hand, Hiatt and Strasburg (1960), as well as Randall (1967), and Quast (1968), treated extensively the food habits of fishes collected during daylight in the Marshall Islands, the West Indies, and southern California, respectively, but offered relatively few direct observations of activity. Suyehiro (1942) comprehensively treated the feeding morphology of fishes in Japan

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and included data on food habits; however, he included little information on activity. The 1970 United States Tektite II program provided many scientists with the opportunity to make direct observations on a Virgin Island reef, and reports concerning the fishes have been published in one volume (Collette and Earle, 1972). Many other reports of limited scope are scattered through the literature, most of them being fragmented data on food habits; nevertheless, accounts of activity based on direct observations are sparse, especially of nocturnal activity.

The great variety of feeding mechanisms for which teleostean fishes are so well known occur among coral-reef fishes far more so than among the fishes of any other habitat. I take advantage of this circumstance in the discussion that concludes the present report and consider the feeding relationships among fishes on Kona reefs in the context of teleostean evolution.

METHODS

Direct Observations

I observed activity of the fishes during 632 h underwater at all periods of day and night using scuba and by snorkeling. Except when collecting specimens, I tried not to influence the fishes or their environment, hoping that events were taking a natural course. Fishes considered in this report are those that can be seen by an underwater observer at some time during day or night. Although this includes by far most of the reef fishes, some abundant species are not included because they remain secreted in the reef at all hours.

Food Habits

The gut contents of 1,547 fish specimens of 102 species were analyzed. With a few isolated exceptions, noted below, all the specimens were collected with spears. I find spearing the most effective way to collect fishes for study of food habits. Using this method, specimens were collected in specific locations at the times of day and night that best define diurnal-nocturnal activity patterns. Because I speared all the specimens myself, I know what each individual was doing when captured, and this knowledge significantly influenced analysis of the data. Even the response of the various fishes to being stalked and speared (or missed) provided certain behavioral insights.

Food habits change over the life of at least most fishes, usually along with recognizable changes in behavior and morphology. Unless otherwise indicated, specimens selected for this study showed behavior and morphology judged typical of adults.

The collections were spread over time and space, so that possible effects of transient localized, perhaps atypical, situations were reduced. Generally, only a single individual of any one species was collected during a single period of observations; thus, for a given species, most individuals each represent a separate collecting station. For these reasons, I judge the data from the food habit analysis to accurately represent the situation existing on Kona reefs over the 15 mo of this study.

The collections were spaced throughout day and night, so that relative digestion of gut contents supplements direct observations of activity in determining specific feeding times. All specimens were sealed in individual plastic bags immediately after being speared, most while still underwater. Gut contents of specimens collected while snorkeling were preserved immediately by injecting a concentrated formaldehyde solution directly into the gut cavity, whereas gut contents of fishes taken by scuba were preserved as soon as possible after emerging from the water. I was unable to see a difference in the digestion undergone by material collected in each of these two ways, suggesting that digestion is sharply curtailed by the death of the fish. Where practical, identifications of items in the guts were carried far enough to establish such general prey characteristics as habitat and mode of life.

Quantifying Food Habits

For those species represented by enough numbers in the analysis of gut contents, I state: 1) the number of fish of that species containing each food item, and 2) the mean percent of that item in the *diet volume,* which is the total volume of gut contents in all specimens of that species. This second figure was calculated from estimates of the percent each item taken by the species contributed to the gut contents of each individual fish (0 to 100%). The food items are listed in order of a *ranking index,* which is computed by multiplying the ratio of fish containing the item to the number of fish sampled, by the mean percent that item represented of the diet volume. Thus, for example, for *Holocentrus sammara* (Table 10), the number one prey, xanthid crabs, has a ranking index of

12/17 × 52.5 = 37.05. The data are tabulated when there are more than a few items in the gut contents of a given species.

In species with a well-defined stomach, usually only stomach contents were analyzed, as materials in the intestines generally were too far digested for satisfactory analysis. On the other hand, some fishes that do not have a well-defined stomach have much material in their intestine that is suitable for study, and so was included in the analysis. Thus data sometimes are specified as being from stomach contents, but at other times the more general term gut contents is used.

Transect Counts

To characterize the fishes inhabiting each of the various inshore habitats described below, 100-m transect lines were established in locations judged typical of each habitat. Twenty-two counts of fishes within 5 m of transect lines at 17 sites representing five habitat categories (see below) were made between September 1969 and May 1970; at least 1 mo passed between counts in any one habitat.

Quantifying Relative Abundance

In the Tables below that present data from the transect counts, the relative abundance of the different species is represented by a relative abundance index. This is the percentage that species represented of all fishes (individuals) counted along all transect lines in that habitat.

Assessing Nocturnal Colorations

A number of species possess distinctive day and night differences in coloration. Earlier (Hobson, 1968b), I discussed the problem of distinguishing true nocturnal hues from those elicited as a response to the diving light—a frequent source of error in literature reports of nocturnal color patterns. No color pattern that becomes intensified under the diving light is considered here to be a nocturnal pattern; the vast majority described herein were in fact almost immediately lost when the fish was illuminated.

Study Area

The study area extends 7.7 km along the southwestern shore of the Island of Hawaii, from Keawekaheka Point just north of Kealakekua Bay, to Alahaka Bay, south of Honaunau (Figure 1). This is part of what is known as the Kona coast. Except for short stretches of sand and cobble beaches at Napoopoo and Keei, the shoreline is a rough basalt face that drops abruptly into the sea from 2 to 3 m above the water's surface (Figure 2), to a similar depth below. From the base of this face the sea floor slopes down to water depths of about 20 to 30 m, about 50 to 600 m from shore, then falls away sharply to much greater depths. Thus, along this coast water less than 20 m deep is limited to a relatively narrow shelf, the outer rim of which provided a convenient natural boundary to the study area (Figure 1).

Environmental conditions in Kona are remarkably constant, which greatly aided this study. Surface water temperatures ranged from 29°C in the fall to 22°C in the spring, but I noted no marked seasonal variations among the fishes either in their activity or species composition. Conditions

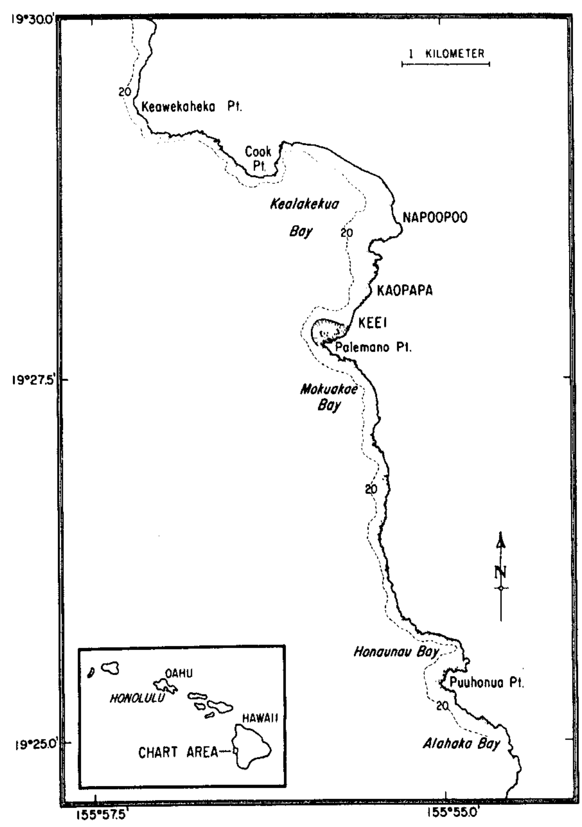

FIGURE 1.—The study area along the Kona coast, Island of Hawaii. Adapted from C. & G.S. chart 4123. Depth contour in meters.

are especially moderate on the Kona coast, in part because towering volcanoes shelter the area from the trade winds.

THE INSHORE HABITATS AND THEIR CHARACTERISTIC FISHES

The study area in Kona encompasses a variety of submarine habitats, each with a distinctive assemblage of fishes. For convenience, these habitats are here grouped subjectively into five categories: 1) coral-rich habitat, 2) boulder habitat, 3) shallow reef-flat habitat, 4) reef-face habitat, and 5) outer drop-off habitat. Along with the following habitat descriptions, there are listed the 10 fish species most often seen in each habitat, as observed in the transect counts.

Coral-Rich Habitat

In many places where there is shelter from the long Pacific swells, the sea floor in water between 2 and 12 m deep is richly overgrown with corals (Figure 3). The predominant coral is *Porites pukoensis,* which grows in a variety of massive formations. Examples occur in Honaunau Bay, in the lee of Palemano Point, and in the sheltered waters on the north side of Kealakekua Bay (Figure 1). Overall in the parts of the study area that are richly overgrown with corals, *P. pukoensis* variably shares dominance with another form, *P. compressus,* that grows as fingerlike branches 10 to 20 mm in diameter. *Porites compressus* is dominant where there is increased exposure to the prevailing swell, but where there is still some protection from a lee shore or increased water depth. Thus, in the middle of both Kealakekua Bay and Honaunau Bay, as well as in much of the study area where the water is more than about 15 m deep, broad fields of fingerlike *P. compressus* dominate the scene. In extreme situations, habitats dominated by either one of these coral forms are as distinct from one another in their characteristic faunas as any two habitat types characterized here. I group the two coral habitats together because in most of the coral-rich areas where observations were made during this study

FIGURE 2.—The shoreline at Cook Point, Kealakekua Bay (looking southeast), which is typical of the shoreline throughout most of the study area.

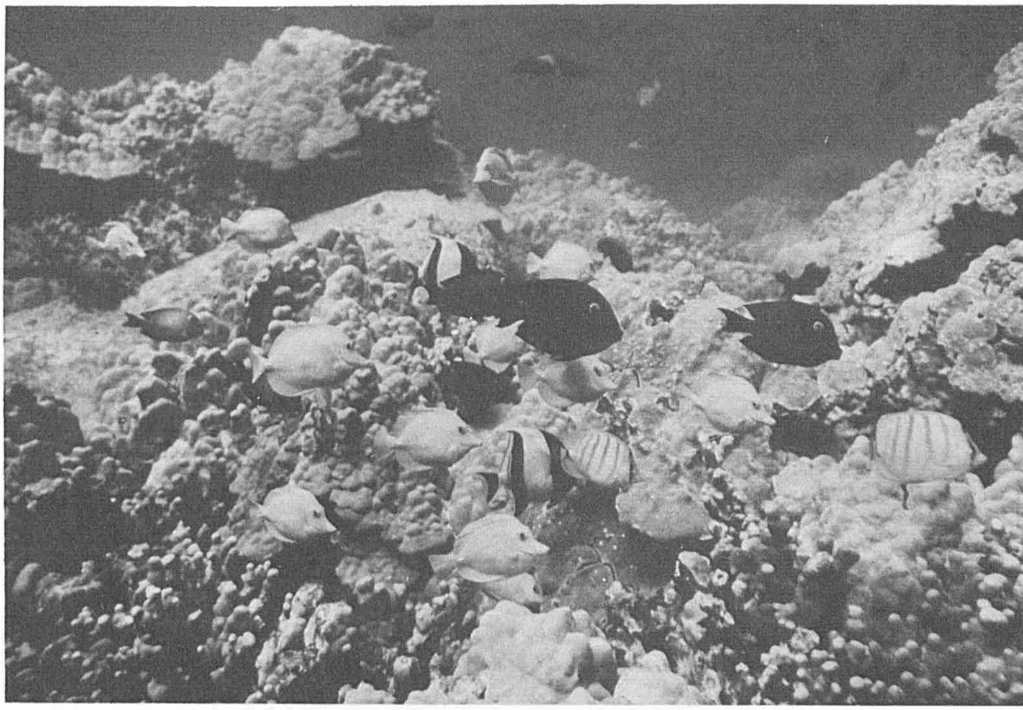

FIGURE 3.—Coral-rich habitat. Fishes shown include: *Chaetodon multicinctus, Ctenochaetus strigosus, Zebrasoma flavescens, Acanthurus nigrofuscus,* and *Zanclus canescens.*

the two forms of *Porites* share dominance. Nevertheless, the fishes listed in Table 1,[2] which are characteristic of those seen in the coral-rich habitat by day, were observed where *P. pukoensis* was the more dominant coral. Table 2[3] lists fishes characteristic of those seen in this same habitat at night. Because of difficulties inherent in making transect counts after dark, data in Table 2 are only rough approximations; they are presented primarily to illustrate the differing situation after dark, and to emphasize that the other counts reflect a situation characteristic of daytime only.

[2]Table 1 is based on data from five transects at four coral-rich sites—two at Honaunau, and two at Kaopapa in Kealakekua Bay (see Figure 1). Total number of species observed on these five transects: 82; mean number of individuals of all species for a single transect: 522.

[3]Table 2 is based on data from three nocturnal transects (one on a dark night, two on moonlit nights) at three coral-rich sites—two at Honaunau, one at Kaopapa in Kealakekua Bay (see Figure 1), all three of which were also used in daytime counts (Table 1). Counts were made by switching on a light briefly about every 10 m as we swam along the line. Listing of a species does not necessarily imply activity; as becomes clear in the species accounts, below, some of these fishes are inactive on or near the reef at night. Total number of species observed on these three transects: 36; mean number of individuals of all species for a single transect: 165.

Boulder Habitat

From shore to depths of about 15 m throughout that part of the study area lying off exposed shorelines, the sea floor is strewn with basalt boulders. Often these boulders are dotted with various algae and corals—mostly encrusting varieties—but because these forms are small, the

TABLE 1.—The 10 fish species most frequently seen along transect lines in the coral-rich habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 5$
1	*Ctenochaetus strigosus*	15.45	5
2	*Chromis leucurus*[1]	12.30	5
3	*Zebrasoma flavescens*	10.58	5
4	*Pomaentrus jenkinsi*	6.71	5
5	*Thalassoma duperrey*	5.71	5
6	*Chaetodon multicinctus*	4.41	5
7	*Acanthurus nigrofuscus*	4.37	5
8	*Acanthurus nigroris*	3.64	3
9	*Plectroglyphidodon johnstonianus*	3.07	5
10	*Centropyge potteri*	2.49	2

[1]In making transect counts I followed Gosline and Brock (1960) in recognizing *Chromis leucurus* to include two color forms. Further study may show that two (or more) species are included here (see species account for *C. leucurus* in this report).

FIGURE 4.—Boulder habitat. Fishes shown include: *Aphareus furcatus, Monotaxis grandoculis* (showing barred color pattern), *Acanthurus leucopareius,* and *Zebrasoma flavescens.*

TABLE 2.—The 10 fish species most frequently seen along transect lines in the coral-rich habitat at night.

Rank	Species	Relative abundance index	No. times in top 5 of individual transects $n = 3$
1	*Myripristis kuntee*	23.61	3
2	*Apogon menesemus*	14.52	3
3	*Myripristis murdjan*	12.33	2
4	*Apogon snyderi*	11.90	3
5	*Zebrasoma flavescens*	6.85	2
6	*Chaetodon multicinctus*	4.03	0
7	*Acanthurus sandvicensis*	2.40	1
8	*Acanthurus nigroris*	2.22	0
9	*Holocentrus lacteoguttatus*	1.21	0
10	*Chaetodon ornatissimus*	1.21	0

TABLE 3.—The 10 fish species most frequently seen along transect lines in the boulder habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 4$
1	*Acanthurus nigrofuscus*	13.74	4
2	*Ctenochaetus strigosus*	10.77	4
3	*Zebrasoma flavescens*	9.61	4
4	*Acanthurus achilles*	8.00	4
5	*Thalassoma duperrey*	6.44	4
6	*Pomacentrus jenkinsi*	5.25	4
7	*Acanthurus nigroris*	4.88	3
8	*Acanthurus leucopareius*	4.73	4
9	*Abudefduf sindonis*	3.64	4
10	*Chromis vanderbilti*	2.35	3

general appearance is one of bare rocks (Figure 4). Especially in the shallower regions, but decreasing with greater depths, this habitat is regularly swept by a strong surge. At depths varying with the relative proximity of a lee shore or protecting reef, but usually at about 12 to 17 m, the boulder habitat in many locations grades into the fields of fingerlike *Porites compressus,* one of the coral-rich habitats described above. Fishes listed in Table 3 [4] are characteristic of those seen in the boulder habitat during the day.

Shallow Reef-Flat Habitat

Shallow surge-swept reefs, the remains of ancient lava flows, extend offshore in several locations (Figure 5). Here, a solid pavement of exposed basalt, containing many cracks and crevices, supports a distinctive array of marine organisms. The predominant benthic life form is the coral

[4]Table 3 is based on data from four transects at four boulder sites—one at Cook Point, one at Mokuakae Bay, and two at Alahaka Bay (see Figure 1). Total number of species observed on these four transects: 77; mean number of individuals of all species for a single transect: 672.

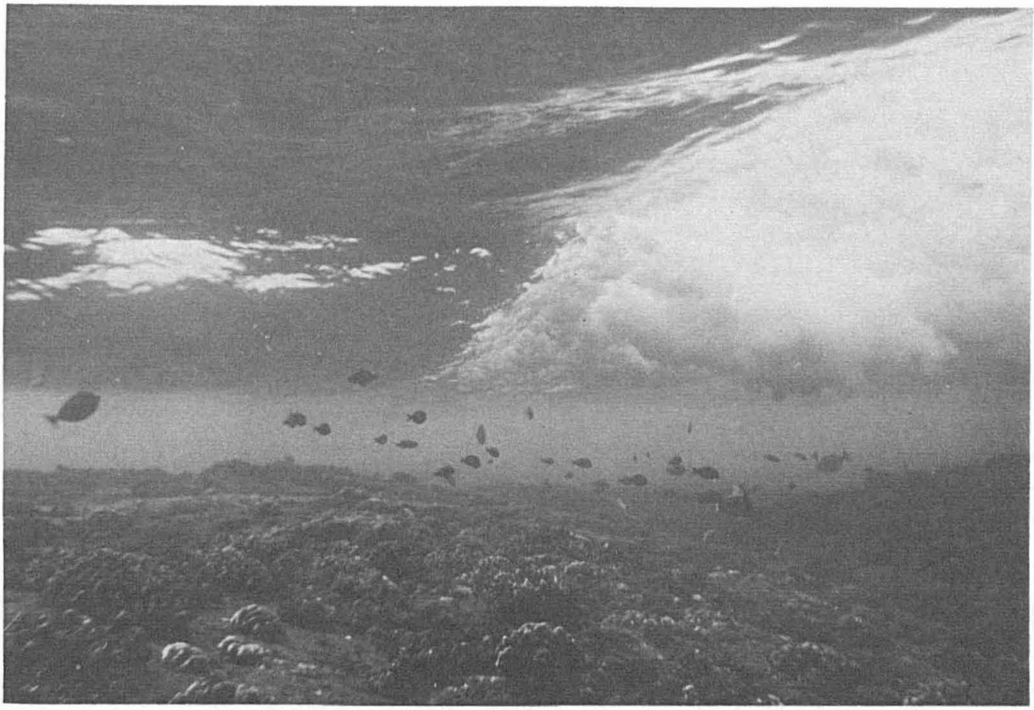

FIGURE 5.—Shallow reef-flat habitat. Most of the fishes shown are acanthurids, and include *Naso lituratus* and *N. unicornis*.

Pocillopora meandrina, growing as isolated heads 10 to 50 cm wide. The outstanding characteristics of this habitat, which generally has a maximum water depth of only about 3 to 4 m, are extreme water movement and wave shock. The fishes listed in Table 4 [5] are characteristic of those seen on shallow reef flats during the day.

[5]Table 4 is based on data from three transects at three shallow reef-flat sites at Palemano Point (see Figure 1). Note: one of the transect counts was aborted after 60 m when the surge became too strong to continue. Total number of species observed on these three transects: 54; mean number of individuals of all species for a single transect: 578.

TABLE 4.—The 10 fish species most frequently seen along transect lines in the shallow reef-flat habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 3$
1	*Acanthurus nigrofuscus*	20.23	3
2	*Thalassoma duperrey*	17.41	3
3	*Abudefduf imparipennis*	15.12	3
4	*Chromis vanderbilti*	10.33	3
5	*Thalassoma fuscus*	4.78	3
6	*Stethojulis balteata*	2.88	3
7	*Gomphosus varius*	2.78	3
8	*Naso literatus*	2.02	1
9	*Zebrasoma flavescens*	1.79	1
10	*Pomacentrus jenkinsi*	1.67	1

Reef-Face Habitat

At the offshore edge of the shallow reef flats, and at many locations along the shore, a sheer basalt face falls precipitously to water depths of 10 to 15 m (Figure 6). This situation produces a wide range of conditions within a limited area. In its upper regions the surge and wave shock are that of the reef-top habitat, but these rapidly abate with increasing depth. Conditions adjacent to the base of the reef face are essentially those of the boulder habitat, with fragmented pieces of the reef lying about as large boulders. The predominant forms of benthic life, dotting the rock surfaces, are *Pocillopora meandrina* (in the shallower regions), and smaller encrusting corals and algae. Many planktivorous fishes are concentrated in the water column adjacent to the reef face. Understandably, there is a greater variety of fishes in this habitat than in the other habitats characterized here. Fishes listed in Table 5 [6] are characteristic of those seen along the reef face during the day.

[6]Table 5 is based on data from three transects at two reef-face sites at Palemano Point (see Figure 1). Total number of species observed on these three transects: 89; mean number of individuals of all species for a single transect: 937.

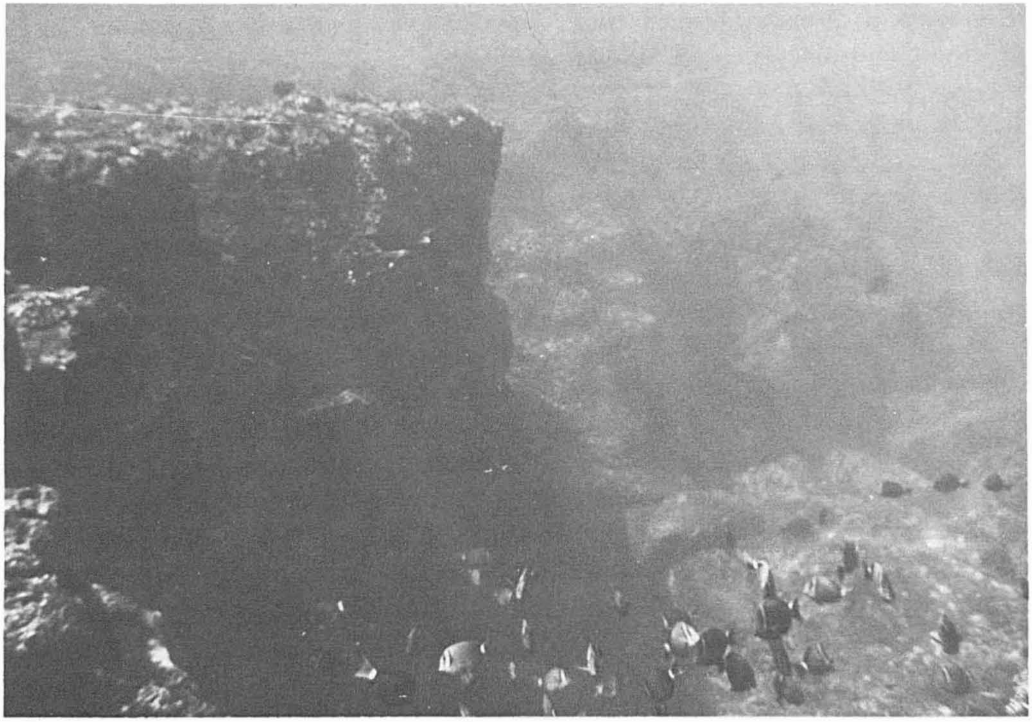

FIGURE 6.—Reef-face habitat. Most of the fishes shown swimming at the base of the reef are *Acanthurus leucopareius*. The reef face shown here drops 8 to 10 m.

TABLE 5.—The 10 fish species most frequently seen along transect lines in the reef-face habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 3$
1	*Chromis vanderbilti*	11.74	3
2	*Ctenochaetus strigosus*	9.54	3
3	*Zebrasoma flavescens*	9.11	3
4	*Acanthurus leucopareius*	7.18	3
5	*Acanthurus nigrofuscus*	6.17	3
6	*Thalassoma duperrey*	4.41	3
7	*Pomacentrus jenkinsi*	3.95	3
8	*Abudefduf abdominalis*	3.56	3
9	*Acanthurus achilles*	3.56	3
10	*Melichthys niger*	3.38	3

Outer Drop-Off Habitat

At the rim of the outer drop-off, 50 to 600 m from shore, where the sea floor falls abruptly from about 25 m to much greater depths, the sea floor generally is overgrown with the fingerlike form of *Porites compressus*, interspersed with massive heads of *P. pukoensis*, bare basalt boulders, and sand patches (Figure 7). The most striking characteristic of this habitat, aside from the spectacular way the sea floor falls away, is the large number of planktivorous fishes that abound in the water column. Obviously conditions for feeding on plankton are especially well developed here. The fishes listed in Table 6 [7] are characteristic of those seen on the rim of the outer drop-off during the day.

[7]Table 6 is based on data from four transects at four outer drop-off sites—two at Palemano Point and two at Puuhonua Point (see Figure 1). Total number of species observed on these four transects: 78; mean number of individuals of all species for a single transect: 478.

TABLE 6.—The 10 fish species most frequently seen along transect lines in the outer drop-off habitat during the day.

Rank	Species	Relative abundance index	No. times in top 10 of individual transects $n = 4$
1	*Naso hexacanthus*	11.39	4
2	*Chromis leucurus*[1]	11.19	4
3	*Xanthichthys ringens*	10.50	4
4	*Thalassoma duperrey*	6.64	4
5	*Zebrasoma flavescens*	4.76	3
6	*Ctenochaetus strigosus*	3.87	2
7	*Chaetodon multicinctus*	3.76	3
8	*Centropyge potteri*	3.45	3
9	*Chromis verater*	3.24	2
10	*Pseudocheilinus evanidus*	2.40	2

[1]In making transect counts I followed Gosline and Brock (1960) in recognizing *Chromis leucurus* to include two color forms. Further study may show that two (or more) species are included here (see species account for *C. leucurus* in this report).

FIGURE 7.—Outer drop-off habitat. Most of the fishes shown in the water column are *Acanthurus thompsoni*.

Fishes Observed on Transect Lines

All fishes observed on transect lines in the five Kona habitats are listed in Table 7, where the value given for each species in each habitat is the relative abundance index, as defined in the methods. Transect data for each habitat category (number of transects, total number of species observed, and mean number of individuals on a single transect) are given in footnotes 2 to 7.

SPECIES ACCOUNTS

This study treats only teleostean fishes, as these were almost the only kind observed on Kona reefs during this study. Elasmobranchs occurred infrequently and seemed to have little impact on the reef situation. No marine animals are more prominent than sharks in Hawaiian lore (e.g. Hobson and Chave, 1972), yet compared with most other tropical Pacific Islands, relatively few sharks are seen in Hawaiian nearshore waters today.

TABLE 7.—Relative abundance of fish species observed along transect lines in each of the Kona reef habitats.

Species	Coral-rich habitat Daytime	Coral-rich habitat Nighttime	Boulder habitat Daytime	Reef-flat habitat Daytime	Reef-face habitat Daytime	Outer Drop-off habitat Daytime
Superorder Elopomorpha:						
Order Anguilliformes:						
Family Muraenidae:						
Gymnothorax meleagris	—	—	0.04	0.06	—	—
Superorder Protacanthopterygii:						
Order Myctophiformes:						
Family Synodontidae:						
Synodus variegatus	0.04	—	—	—	—	—
Superorder Acanthopterygii:						
Order Beryciformes:						
Family Holocentridae:						
Holocentrus sammara	0.04	0.60	0.04	—	—	0.05
H. tiere	—	0.81	—	—	—	—
H. xantherythrus	—	0.60	—	—	—	—
H. diadema	—	1.01	—	—	—	0.05
H. lacteoguttatum	—	1.21	—	—	—	—
Holotrachys lima	—	0.81	—	—	—	—
Myripristis kuntee	0.23	23.61	0.19	—	0.43	0.26
M. murdjan	0.08	12.33	—	—	0.25	0.31
M. sp. (uncertain: either *M. murdjan* or *M. amaenus*)	—	5.24	—	—	—	—
Order Gasterosteiformes:						
Family Aulostomidae:						
Aulostomus chinensis	0.12	0.40	—	—	0.36	—
Family Fistulariidae:						
Fistularia petimba	—	—	—	0.12	—	—
Order Scorpaeniformes:						
Family Scorpaenidae:						
Taenianotus triacanthus	0.04	—	—	—	—	—
Scorpaena coniorta	—	0.20	—	—	—	—
Scorpaenopsis cacopsis	—	—	—	—	0.07	0.05
Order Perciformes:						
Family Serranidae:						
Cephalapholis argus	—	—	—	—	0.04	—
Family Priacanthidae:						
Priacanthus cruentatus	—	0.20	—	—	—	—
Family Apogonidae:						
Apogon menesemus	—	14.52	—	—	—	—
A. snyderi	—	11.90	—	—	—	—
Family Malacanthidae:						
Malacanthus hoedtii	—	—	—	—	—	0.16
Family Carangidae:						
Caranx melampygus	—	—	0.04	—	0.11	—
Family Lutjanidae:						
Aphareus furcatus	0.15	—	0.11	—	0.21	—
Family Sparidae:						
Monotaxis grandoculis	0.12	—	0.04	—	1.25	0.05
Family Mullidae:						
Mulloidichthys auriflamma	—	—	—	—	0.93	—
M. samoensis	0.12	—	—	—	0.14	—
Parupeneus multifasciatus	0.58	0.20	0.45	0.23	0.82	1.41
P. bifasciatus	0.12	—	0.07	—	0.71	0.05
P. chryserydros	0.27	—	0.15	—	0.25	—
P. porphyreus	0.08	—	—	—	—	—
P. pleurostigma	0.04	—	—	—	—	0.05
Family Kyphosidae:						
Kyphosus cinerascens	—	—	0.22	—	0.11	—
Family Chaetodontidae:						
Holacanthus arcuatus	—	—	—	—	0.11	0.10
Centropyge potteri	2.49	—	—	—	1.00	3.45
C. fisheri	—	—	—	—	—	0.16
Forcipiger flavissimus	0.96	—	1.01	0.35	0.78	1.41
F. longirostris	0.50	0.40	—	0.12	0.07	0.31
Hemitaurichthys thompsoni	—	0.40	—	—	—	0.73
H. zoster	—	—	0.26	—	—	2.09
Chaetodon corallicola	—	—	—	—	—	1.05
C. miliaris	—	—	—	—	—	1.05
C. quadrimaculatus	0.69	—	0.89	1.44	0.53	0.10
C. unimaculatus	—	—	0.22	1.21	—	—
C. multicinctus	4.41	4.03	1.08	0.58	0.82	3.76
C. ornatissimus	1.80	1.21	0.68	0.29	0.25	0.31
C. auriga	—	—	—	—	0.04	0.05
C. fremblii	0.08	0.20	0.30	0.12	0.32	0.05
C. lunula	0.69	1.21	0.15	0.40	2.03	0.58
C. lineolatus	—	0.20	0.11	—	0.11	—

TABLE 7.—Continued.

Species	Coral-rich habitat Daytime	Coral-rich habitat Nighttime	Boulder habitat Daytime	Reef-flat habitat Daytime	Reef-face habitat Daytime	Outer Drop-off habitat Daytime
C. reticulatus	—	—	—	0.12	—	—
C. trifasciatus	0.04	—	—	0.12	—	—
Family Pomacentridae:						
Plectroglyphidodon johnstonianus	3.07	0.20	0.07	1.04	0.25	1.25
Pomacentrus jenkinsi	6.71	—	5.25	1.67	3.95	0.68
Abudefduf sindonis	—	—	3.64	—	—	—
A. sordidus	—	—	0.22	—	0.39	—
A. imparipennis	—	—	0.22	15.12	—	—
A. abdominalis	0.35	0.20	—	—	3.56	—
Dascyllus albisella	0.19	1.21	0.07	—	—	2.30
Chromis vanderbilti	0.15	—	2.35	10.33	11.74	0.84
C. leucurus	12.30	—	—	—	0.82	11.19
C. verater	0.96	0.80	0.11	—	0.14	3.24
C. ovalis	0.11	0.40	—	—	—	—
Family Cirrhitidae:						
Paracirrhites arcatus	0.69	—	0.74	0.86	0.89	0.99
P. forsteri	0.23	—	—	0.12	0.11	—
Cirrhitops fasciatus	0.12	—	0.34	0.17	0.82	0.47
Cirrhitus pinnulatus	0.04	—	—	0.52	0.18	0.05
Family Labridae:						
Bodianus bilunulatus	—	—	—	—	—	0.05
Cheilinus rhodochrous	1.57	—	0.15	—	0.57	1.41
Pseudocheilinius octotaenia	1.30	—	0.07	—	0.82	1.93
P. tetrataenia	0.31	—	0.04	0.23	0.07	0.42
P. evanidus	0.04	—	—	—	—	2.40
Labroides phthirophagus	0.31	—	—	—	—	0.05
Thalassoma duperrey	5.71	—	6.44	17.41	4.41	6.64
T. fuscus	—	—	1.97	4.78	—	—
T. ballieui	0.04	—	0.15	0.17	0.21	0.05
T. lutescens	0.08	—	—	—	—	—
T. quinquevittata	—	—	—	0.23	—	—
Halichoeres ornatissimus	1.15	—	1.67	0.58	0.53	1.15
Stethojulis balteata	2.15	—	1.56	2.88	1.35	0.68
Anampses cuvier	0.08	—	0.34	0.06	0.07	0.05
Coris gaimard	0.81	—	0.26	0.35	0.71	1.31
C. flavovittata	—	—	—	—	0.04	—
C. venusta	—	—	—	—	0.11	—
Macropharyngodon geoffroy	0.15	—	0.07	0.52	0.21	0.73
Gomphosus varius	1.00	—	1.53	2.78	0.60	0.78
Cirrhilabrus jordani	—	—	—	—	—	0.16
Pseudojuloides cerasinus	—	—	—	—	—	0.05
Hemipteronotus taeniourus	—	—	—	—	—	0.16
Family Scaridae:						
Scarus sordidus	1.73	—	0.82	1.04	1.81	1.93
S. taeniurus	0.19	—	0.63	0.98	0.43	—
S. dubius	0.46	—	0.52	—	0.50	0.16
S. perspicillatus	0.35	0.20	1.53	—	0.28	0.10
S. rubroviolaceus	0.35	0.20	0.04	0.29	0.50	0.10
Calotomus spinidens	0.50	—	0.04	0.12	0.11	0.26
Unidentified juveniles	—	—	—	—	0.89	—
Family Blenniidae:						
Exallias brevis	0.15	—	0.11	0.06	0.11	0.05
Cirripectus obscurus	—	—	0.15	—	—	—
C. variolosus	0.31	—	0.04	—	0.07	—
Plagiotremus goslinei	—	—	0.19	0.98	0.04	—
P. ewaensis	—	—	—	—	0.04	—
Family Acanthuridae:						
Acanthurus achilles	0.69	1.41	8.00	0.35	3.56	0.10
A. dussumieri	0.35	—	0.74	—	0.28	—
A. glaucopareius	0.04	—	0.19	—	0.07	—
A. guttatus	—	—	1.64	—	—	—
A. leucopareius	0.69	1.01	4.73	0.40	7.18	—
A. nigrofuscus	4.37	0.40	13.74	20.23	6.17	1.62
A. nigroris	3.64	2.22	4.88	1.38	1.60	1.57
A. olivaceus	0.19	—	0.11	—	0.07	0.31
A. sandvicensis	0.12	2.40	1.64	0.12	0.71	—
A. thompsoni	—	—	—	—	—	1.88
A. xanthopterus	—	—	—	—	0.43	—
Ctenochaetus strigosus	15.45	—	10.77	—	9.54	3.87
C. hawaiiensis	0.58	—	0.82	—	0.75	0.05
Zebrasoma flavescens	10.58	6.85	9.61	1.79	9.11	4.76
Z. veliferum	0.15	—	0.22	—	—	—
Naso brevirostris	—	—	—	—	—	0.10
N. hexacanthus	—	—	—	—	1.28	11.39
N. lituratus	1.46	1.21	0.74	2.02	1.07	1.20
N. unicornis	0.35	—	0.60	1.50	0.25	0.05

TABLE 7.—Continued.

Species	Coral-rich habitat Daytime	Coral-rich habitat Nighttime	Boulder habitat Daytime	Reef-flat habitat Daytime	Reef-face habitat Daytime	Outer Drop-off habitat Daytime
Family Zanclidae:						
Zanclus canescens	0.38	—	1.38	1.21	0.82	1.10
Order Tetraodontiformes:						
Family Balistidae:						
Melichthys niger	1.00	—	0.82	0.12	3.38	—
M. vidua	0.04	—	—	—	—	0.15
Xanthichthys ringens	—	—	0.04	—	0.39	10.50
Rhinecanthus rectangulus	—	—	0.19	1.33	—	—
Sufflamen bursa	0.73	—	0.37	—	1.57	1.57
Balistid sp.	—	—	—	—	0.04	—
Family Monacanthidae:						
Cantherines dumerili	0.15	—	—	0.12	0.11	—
C. sandwichiensis	0.15	—	0.40	0.64	0.32	0.16
Pervagor spilosoma	0.35	—	—	—	0.04	0.10
P. melanocephalus	0.42	—	0.19	—	—	0.10
Alutera scripta	—	—	—	—	0.04	—
Family Ostraciontidae:						
Ostracion meleagris	0.19	—	0.86	0.12	0.18	—
Family Tetraodontidae:						
Arothron hispidus	—	—	—	—	0.04	—
A. meleagris	—	—	0.04	0.06	—	—
Family Canthigasteridae:						
Canthigaster amboinensis	0.12	—	0.22	0.17	0.11	—
C. jactator	0.46	—	0.04	—	0.78	0.05
C. coronatus	—	—	—	—	0.04	0.10

The observations for each species are grouped by order and family in phylogenetic sequence, as listed by Greenwood et al. (1966). Species names generally are those used by Gosline and Brock (1960), except where more recent taxonomic studies indicate change. All sizes given are standard length. For most species, the number of specimens collected is followed by, in parenthesis, their mean size and the range in their sizes. All species accounts consider individuals showing morphology and behavior of adults.

ORDER ANGUILLIFORMES

Family Muraenidae: moray eels

Most Hawaiian eels belong to this family, which comprises the moray eels, or *puhi,* as Hawaiians call them (Gosline and Brock, 1960). Morays are denizens of crevices in the reefs, and because most remain secreted under cover, their great abundance cannot be appreciated by a casual observer. Nevertheless, the morays include more species (32 reported) on Hawaiian reefs than any other family of fishes, except perhaps the wrasse family Labridae (Gosline and Brock, 1960). Most Hawaiian morays do not grow to more than about 60 cm long, although a few may attain a length of about 2 m (Gosline and Brock, 1960). Most of them remain secreted in reef crevices, but the five species considered below are examples of those that are often exposed on the reef top.

Gymnothorax meleagris (Shaw and Nodder) —spotted moray, *puhi 'oni'o*

This medium-sized eel characteristically protrudes its head from crevices during the day (Figure 8), and thus is the moray most often in view on the reef; however, I seldom saw it after dark. Of the nine specimens collected, the stomachs of five were empty, although three of these contained unidentified fragments at the posterior end of their intestines. Of the four with prey in their stomachs, one (455 mm) taken during midmorning contained a fresh damselfish, *Abudefduf imparipennis* (40 mm) that appeared to have been recently captured. Two others with full stomachs were collected during late afternoon: one (321 mm) contained a moderately digested xanthid crab, whereas the other (121 mm) contained a well-digested fish. On the other hand, the fourth specimen (361 mm) contained a moderately digested xanthid crab that appeared to have been in the eel's stomach at least several hours when it was collected during morning twilight.

CONCLUSION.—*Gymnothorax meleagris* captures small fishes and crustaceans by day and probably also at night.

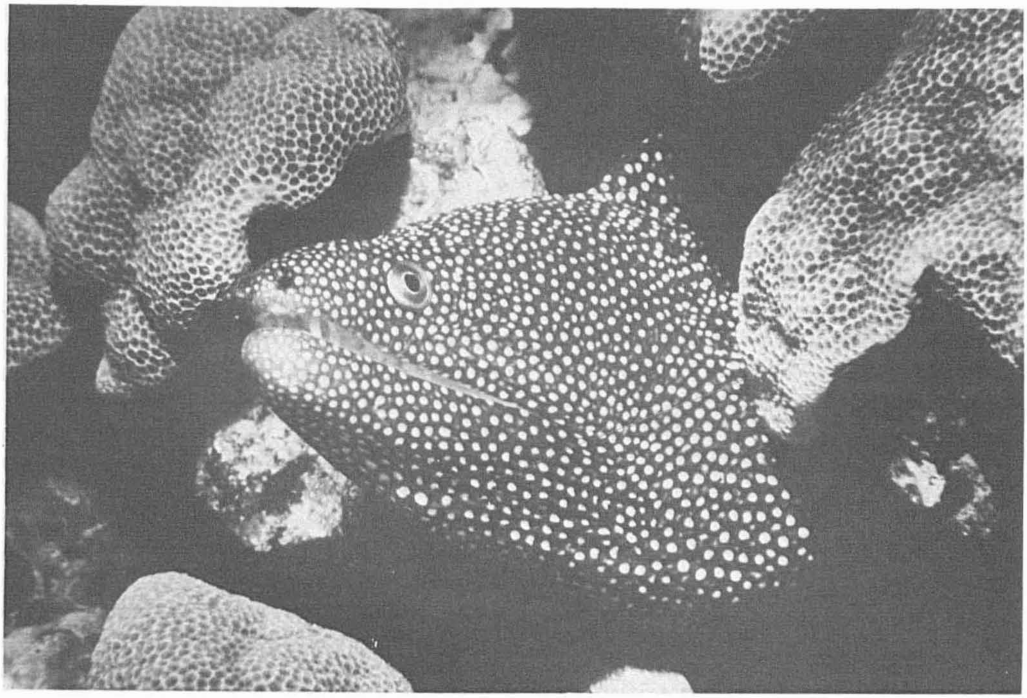

FIGURE 8.—*Gymnothorax meleagris,* a moray eel, showing daytime attitude.

Gymnothorax eurostus (Abbott)

This small species, which attains a maximum length of about 60 cm, is probably the most numerous moray in Hawaii (Gosline and Brock, 1960). However, it is a secretive species, only occasionally visible on the reef. Although the four individuals collected (360: 294-432 mm) were speared as they protruded their heads from holes in the reef during the day, this habit is not characteristic of *G. eurostus,* as it is of *G. meleagris,* above. Two of those collected had empty stomachs, but the other two, both taken during midday, contained relatively fresh prey—a caridean shrimp in one, a xanthid crab in the other.

CONCLUSION.—*Gymnothorax eurostus* captures crustaceans during the day. The nighttime situation remains uncertain.

Gymnothorax flavimarginata (Rüppell)—*puhi paka*

This eel, which attains a length of about 120 cm (Gosline and Brock, 1960), is the most numerous of the larger muraenids in Kona. Being so abundant, as well as large, this heavy-bodied eel probably represents the greatest threat among morays to humans. It is the species that most often appears when a fish has been speared during daylight. The regularity and promptness of these appearances make it clear that *G. flavimarginata* is especially sensitive to fish that are injured, or perhaps otherwise under stress. In this respect it is similar to *G. castaneus* in the Gulf of California (Hobson, 1968a). Usually when a reef fish is injured, or seriously threatened, it takes cover in a reef crevice. Usually such individuals are to some extent incapacitated, and thus vulnerable to predators equipped to seek them out. Probably *G. flavimarginata* is adapted to this task. Other large morays on the reef show the same behavior, but to a lesser degree. Most encounters with *G. flavimarginata* were by day; although its behavior would seem equally adaptive to nocturnal conditions, it was only occasionally observed after dark.

CONCLUSION.—*Gymnothorax flavimarginata* is especially sensitive to stimuli emanating from a fish in distress, and appears adapted to seeking out such individuals when they have sought shelter in reef crevices.

Gymnothorax petelli (Bleeker)—broad-banded moray

The broad-banded moray generally is out of sight within the reef during daylight, but often active in exposed locations after dark (Figure 9). A second species, *G. undulatus,* similarly forays away from cover at night, but during this study was seen less often than *G. petelli.* Although no specimens were examined, one *G. petelli* seen on the reef at night was grasping between its jaws a pufferfish, *Canthigaster jactator.* Additional evidence of nocturnal habits in *G. petelli* was given by Chave and Randall (1971), who described it pursuing crabs over underwater sand patches at night.

CONCLUSION.—*Gymnothorax petelli* is a nocturnal predator.

Echidna zebra (Shaw)—zebra moray

The zebra moray has a blunter snout than the species of *Gymnothorax* treated above, but its dentition is even more distinctive. Morays of the genus *Gymnothorax* have fanglike teeth that are suited to grasping prey, but the zebra moray, like other species of the genus *Echidna,* has blunt, pebblelike teeth that are suited to crushing prey. Gut contents are consistent with this observation: all four specimens (750: 485-835 mm) taken at various times of the day contained the crushed remains of relatively large crabs—considerably larger than crabs found in comparably sized individuals of *Gymnothorax.* The zebra moray is a sluggish animal, even for a moray, and is generally secretive. Usually all one sees of this animal, day or night, is a motionless segment of its body, visible at a narrow opening in the reef.

CONCLUSION.—*Echidna zebra* captures crustaceans within reef crevices, taking larger individuals of the more heavily armored prey than do species of *Gymnothorax.*

General Remarks on Moray Eels

Morays have been widely considered, collectively, as nocturnal animals (e.g. Winn and Bardach, 1959; Starck and Davis, 1966; Randall,

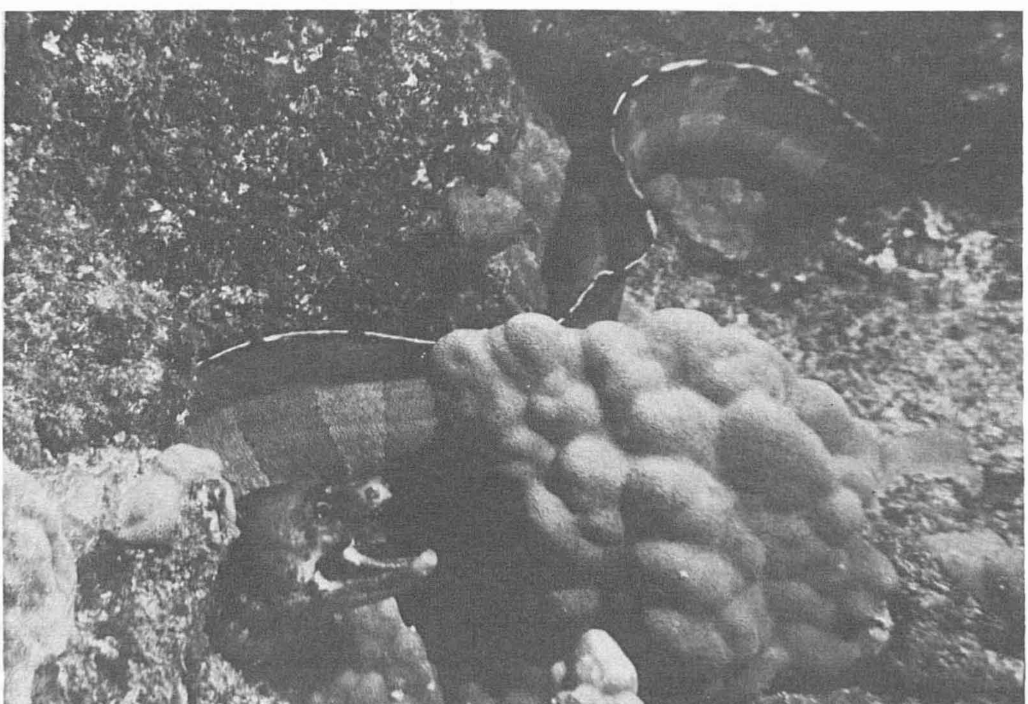

FIGURE 9.—*Gymnothorax petelli,* a moray eel, on the reef top at night.

1967; Collette and Talbot, 1972). Hiatt and Strasburg (1960) attributed the high incidence of empty stomachs in morays from the Marshall Islands during daylight to nocturnal habits; however, I concur with Gosline and Brock (1960), who attributed the empty stomachs of Hawaiian morays during the day to infrequent feeding, rather than necessarily to nocturnal feeding. Certainly some morays seem to be primarily nocturnal—*Gymnothorax petelli* and *G. undulatus*, described above, are examples. But others described here, such as *G. meleagris, G. eurostus,* and *G. flavimarginata,* feed regularly in daylight. That some morays are primarily diurnal was illustrated by Chave and Randall (1971), who described a diurnally active, nocturnally inactive pattern for *G. pictus* in the central Pacific. Conclusions on relative activity between day and night for moray eels remain tenuous if based solely on how often, and at what time, the species is seen in exposed positions. Moray eels are adapted to activity within reef crevices, and one would expect at least most of them to best capture their prey there; indeed, most species rarely expose themselves, day or night.

Family Congridae: conger eels

Conger marginatus Valenciennes—white eel, *puhi uha*

The white eel, which may exceed a length of 1 m (Gosline and Brock, 1960), is relatively numerous in Kona. It moves about in the open on the reef after dark and rests in reef crevices during daylight. In the Marshall Islands, Hiatt and Strasburg (1960) reported similar behavior in *C. noordzieki,* which preys on both fishes and invertebrates.

CONCLUSION.—*Conger marginatus* is active in exposed locations on the reef after dark.

ORDER MYCTOPHIFORMES

Family Synodontidae: lizardfishes

Saurida gracilis (Quoy and Gaimard)–*'ulae nihoa*

Attaining lengths of over 300 mm, this is the largest of those lizardfishes that are numerous on the reef. During both day and night it rests motionless and fully exposed on sand patches, rock, or coral. Despite these exposed positions, it is difficult to detect, so closely does its coloration match the surroundings. Six specimens (223: 165-315 mm) were examined. The guts were empty in five—four speared at night, between 2300 h and dawn, and one taken during midday. The sixth specimen (165 mm), taken 1 h before midnight, contained the well-digested anterior half of a trumpetfish, *Aulostomus chinensis* (about 90 mm when intact). Because digestion was far advanced, this prey may have been ingested during the previous day or evening twilight. These limited data suggest that attacks are infrequent, or perhaps that feeding habits are diurnal or crepuscular. Hiatt and Strasburg (1960) reported strictly piscivorous habits for this species in the Marshall Islands, and described daylight attacks in which it darted upward from a resting spot on the sea floor.

CONCLUSION.—*Saurida gracilis* attacks small fishes in daylight.

Synodus variegatus (Lacépède)—*'ulae 'ula*

This is the most numerous synodontid on Kona reefs. During both day and night it rests on the sea floor (Figure 10), as does *Saurida gracilis,* above. Although usually in exposed positions, it is difficult to detect because its coloration closely matches the background. Frequently it becomes even more inconspicuous by burying in the sand, leaving only its eyes and the tip of its snout exposed.

Once, during early afternoon, an individual of this species shot up from the coral and captured a small wrasse, *Thalassoma lutescens,* that I was stalking. The wrasse was watching me when the lizardfish struck, and the attacker may have sensed this distraction in its prey. I speared the predator immediately after the attack, and found it to be 166 mm long (it lost the wrasse when speared and is included below among those with an empty gut). Two other noteworthy incidents occurred at night: On both occasions I was hunting specimens among the coral, and my spear, projecting into my path, was faintly illuminated by my companion's diving light. Suddenly, an individual of this species darted up and struck the silver barb on the otherwise grey spear. Although the nearby diving light created here an unnatural nocturnal situation, these two fish obviously were alert for prey at these times.

Twelve specimens (142: 94-158 mm) were collected during day and night from exposed posi-

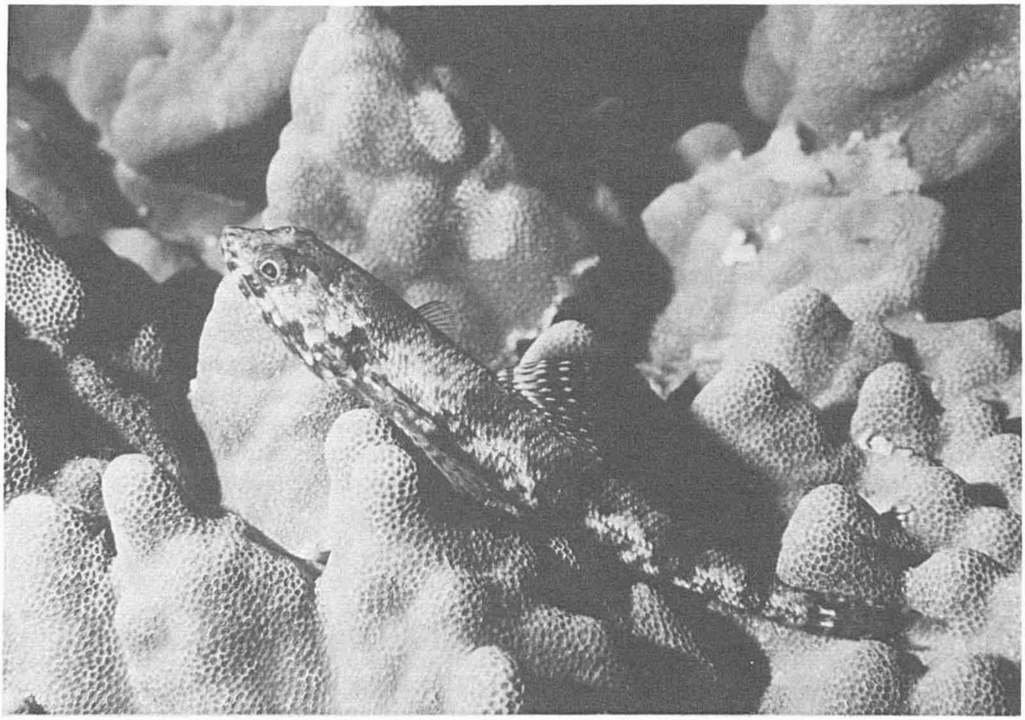

FIGURE 10.—*Synodus variegatus,* a lizardfish, poised to strike at prey in the water overhead.

tions on the sea floor. Of nine speared during afternoons, six had empty guts, but two contained fish fragments, and one contained three fish—two digested beyond recognition, and one relatively fresh *Plagiotremus goslinei* (32 mm). Of two collected during morning twilight, one was empty, while the other contained an extensively digested fish (25 mm). Finally, one collected at night, 5 h after sunset, contained fish fragments.

CONCLUSION.—*Synodus variegatus* attacks small fishes during the day and probably also at night.

General Remarks on Lizardfishes

Similar behavior is widely reported for the synodontids of tropical seas. In the Florida Keys, Starck and Davis (1966) reported that *Synodus synodus* and *Trachinocephalus myops* lie partially buried in the sand and erupt to capture prey swimming overhead during the day. Similarly, Randall (1967) noted that lizardfishes in the West Indies, including *S. synodus, S. intermedius,* and *S. foetens,* may rest on rocks, sand, or mud, where they sometimes partially bury themselves. Hartline et al. (1972) observed on several occasions during the day *Synodus* sp. in the Virgin Islands attacking the damselfish *Chromis cyaneus* from resting positions on the substratum. Similar observations were also reported by Smith and Tyler (1972). Although fishes seem to be the major prey of synodontids, Randall (1967) found some shrimps and squids in the predominantly piscivorous diet of lizardfishes in the West Indies. Suyehiro (1942) also reported shrimps and squid secondary prey to fishes in the diet of *Saurida undosquamis* in Japan. Probably any free-swimming animal of appropriate size becomes prey if it passes close above a waiting lizardfish when conditions are suitable for attack. The jaws of lizardfishes are profusely rimmed with sharp, inwardly depressible canine teeth, like those of many morays, and this type of dentition is especially well suited to grasping small fishes.

ORDER GADIFORMES

Family Brotulidae: brotulas

Brotula multibarbata Temminck and Schlegel—*puhi palahoana*

This fish is not in view during daylight, except to one who enters some of the darker caves. Although diurnally secretive, it swims into the open on the reef after dark, but even then is mostly exposed only during transit from one crevice to another.

Seven individuals (169: 73-250 mm) were speared during day and night. Two collected about 2 h before daybreak as they swam close among rocks were both full of prey, including fresh material. Of three others collected in dark caves during midmorning, one was empty and the other two contained only well-digested fragments. Finally, two individuals collected within 1 h after nightfall as they swam in exposed locations among rocks were both empty—apparently having not yet captured prey on their nocturnal foray. The four individuals containing identifiable prey had fed on the items listed in Table 8.

CONCLUSION.—*Brotula multibarbata* is a nocturnal predator that feeds mostly on crustaceans and fishes.

General Remarks on Brotulas

Hiatt and Strasburg (1960) concluded that *Dinematichthys ilucoeteoides* in the Marshall Islands is very secretive because they never saw a live one, but did not suggest that it might be nocturnal. They believed that by concealing itself in crevices this brotulid is able to dash out and capture small fishes and crustaceans that unsuspectingly venture close to its hiding place. Starck and Davis (1966) recognized nocturnal habits in an Atlantic species, *Petrotyx sanguineus,* which is unseen in daylight, but swims close among reef ledges at night.

ORDER ATHERINIFORMES

Family Atherinidae: silversides

Pranesus insularum (Jordan and Evermann)—*'iao*

This silverside is not numerous in Kona, but in daylight small schools of relatively inactive individuals occur at various places along the rocky shore, right at the water's edge. At nightfall these schools disperse, and the members move away from shore, over the reef. They swim high in the water column, just under the water surface, and some of them range out at least as far as the offshore drop-off.

Using a hard net, 13 individuals (47: 39-70 mm) were collected during both dark nights and moonlit nights—9 between 4 and 6 h after sunset and 4 during the 2 h before first morning light. Although the gut of 1 was empty, the other 12 were full, including fresh material, as listed in Table 9.

CONCLUSION.—*Pranesus insularum* is a nocturnal planktivore that takes mostly crustaceans and foraminiferans.

TABLE 8.—Food of *Brotula multibarbata.*

Rank	Items	No. fish with this item (*n* = 4)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	1	25.0	6.25
2	Fish	1	16.3	4.08
3	Decapod shrimps	1	6.3	1.58
4	Mysids	1	5.0	1.25
5	Crab megalops	1	0.3	0.08
Also,	crustacean fragments	2	37.5	18.75
	Unidentified fragments	3	9.6	7.20

TABLE 9.—Food of *Pranesus insularum.*

Rank	Items	No. fish with this item (*n* = 12)	Mean percent of diet volume	Ranking index
1	Mysids	5	14.2	5.92
2	Decapod shrimp larvae	5	6.7	2.79
3	Foraminiferans	4	6.3	2.10
4	Calanoid copepods	2	4.2	0.70
5	Larvaceans	1	2.1	0.18
6	Crab zoea	1	1.7	0.14
7	Spider	1	0.4	0.03
Also,	crustacean fragments	12	40.8	40.80
	Unidentified fragments	7	23.6	13.79

General Remarks on Silversides

It is widely recognized that silversides prey largely on zooplankton. Hiatt and Strasburg (1960) found mostly zooplankton in three species in the Marshall Islands, as did Randall (1967) in two species from the West Indies. Each report listed shrimp larvae and copepods among the major food items, but neither mentioned nocturnal habits. At Majuro Atoll, Marshall Islands, *Pranesus pinguis* is inactive in schools along lagoon beaches during the day, and then migrates offshore into the lagoon at nightfall, where it disperses and feeds on zooplankton in the surface waters (Hobson and Chess, 1973). The closely related *P. insularum* does not move so far from shore at night in Kona, presumably because its feeding grounds are over the nearshore reefs.

ORDER BERYCIFORMES

Family Holocentridae: squirrelfishes

The squirrelfishes compose one of the more prominent groups of fishes on Hawaiian reefs. The species fall into two major categories: those in one group include members of the genus *Holocentrus,* which are known by the generic Hawaiian name *ala 'ihi,* and one species of the genus *Holotrachys*; those in the second group include species of the genus *Myripristis,* which are known by the generic Hawaiian name *'u'u,* or perhaps more often today by the Japanese equivalent *menpachi.*

Holocentrus sammara (Forskål)

This solitary fish is numerous in coral-rich surroundings at depths between 4 and 20 m. It is a relatively large species—up to 300 mm long (Gosline and Brock, 1960)—and characteristically hovers in visible locations at the openings of reef caves during the day. During evening twilight it moves away from its daytime shelter-sites and throughout the night ranges over the nearby areas of the reef, staying close to the sea floor. During morning twilight it gradually moves closer to cover and by sunrise has resumed its daytime mode of behavior. After dark the coloration of this fish differs from its coloration in daylight (Figure 11a and b).

Twenty-one specimens (162: 128-202 mm) were collected during day and night for food-habit study. All 13 that were speared as they swam in exposed positions on the reef during the last hours of darkness, before daybreak, and during morning twilight contained prey in varying stages of digestion. In comparison, of seven speared as they hovered close among coral shelter during the afternoon, four were empty, two contained only well-digested fragments, and one contained an apparently recently ingested crab. Finally, one that was speared in the open 4 h after nightfall was full of prey, most of it fresh. Items in the 17 specimens containing identifiable material are listed in Table 10.

CONCLUSION.—*Holocentrus sammara* is a nocturnal predator that feeds mostly on benthic crustaceans, especially xanthid crabs and caridean shrimps, but some feed diurnally.

Holocentrus spinifera (Forskål)

This is the largest squirrelfish on Kona reefs, and of those considered in this report it is also the least numerous. A solitary species during both day and night, it is secretive within reef crevices in daylight, but ranges out and forages close to the reef after dark. In daylight, the body of this fish is a plain rosy-red, and its dorsal fin is yellow; in darkness, however, a small but prominent white spot appears on each side of its body, just behind its dorsal fin. Because this large fish is not numerous, I came to recognize certain individuals and found that after nocturnal forays on the reef each tended to return each morning to its particular shelter spot.

Six specimens (213: 68-350 mm) were speared during day and night for study of food habits. The one that was taken during midday contained a large caridean shrimp, *Saron marmoratus* (about 40 mm), that was extensively damaged by digestion and could have been taken during the previous night. A second, taken as it emerged from cover at nightfall, was the only one taken with an empty gut. Of the other four, all of which contained relatively fresh prey, three were collected as they swam in the open at night, more than 3 h after sunset, and the fourth was collected under a ledge during morning twilight.

All five specimens containing food had fed on crustaceans exclusively. Three had taken caridean shrimps (mean percent of diet volume: 34; ranking index: 20.4), three had taken xanthid crabs (mean percent of diet volume: 31; ranking index: 18.6), and one had taken a scyllarid lobster (mean percent of diet volume: 11; ranking index:

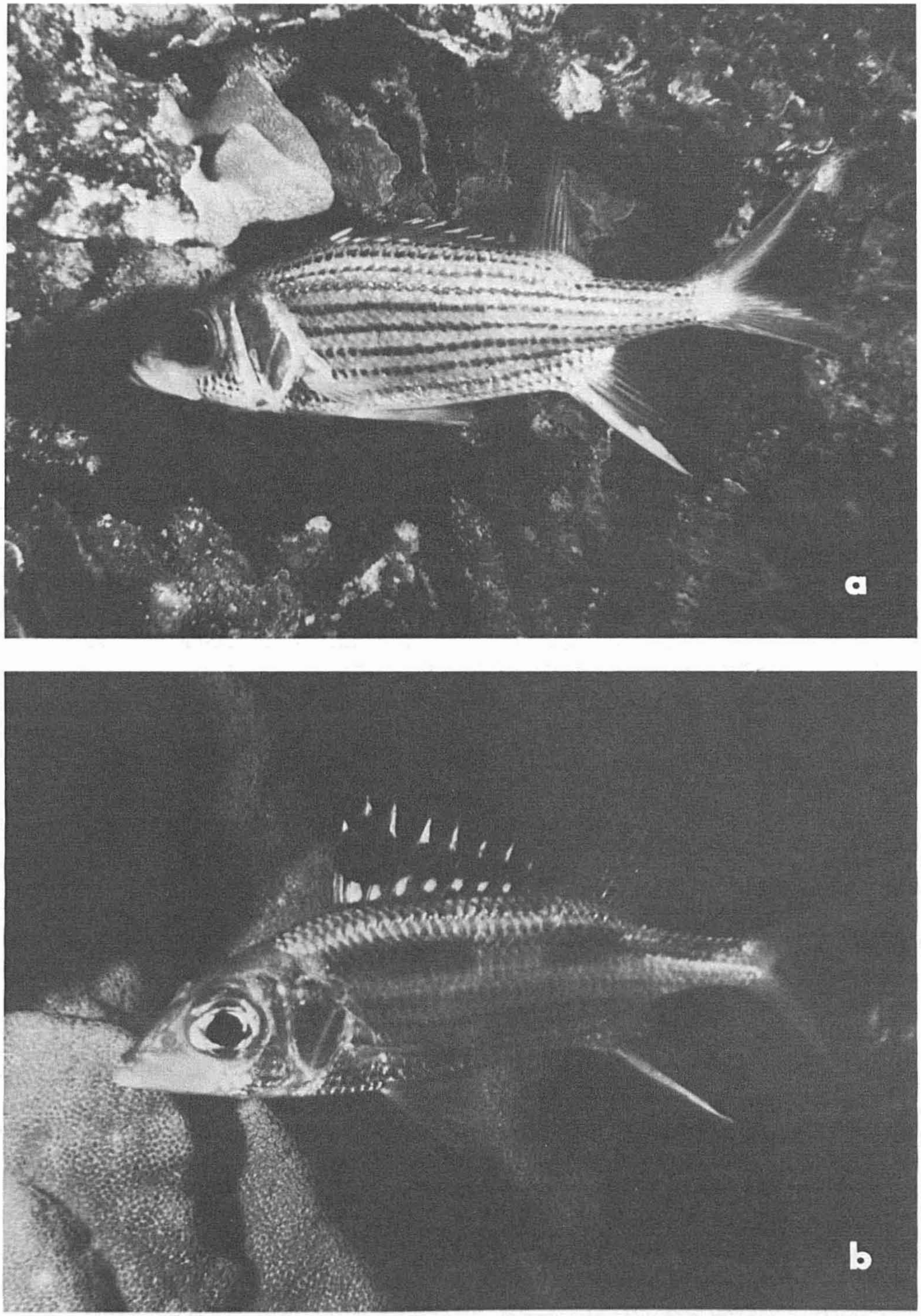

FIGURE 11.—*Holocentrus sammara*, a squirrelfish: a, showing its diurnal coloration under a ledge during the day; b, showing nocturnal coloration as it swims close to the reef at night.

TABLE 10.—Food of *Holocentrus sammara*.

Rank	Items	No. fish with this item (n = 17)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	12	52.5	37.08
2	Caridean shrimps	4	12.2	2.88
3	Portunid crabs	2	7.8	0.92
4	Fish	2	7.8	0.92
5	Penaeid shrimps	1	5.9	0.35
Also, crustacean fragments		4	13.8	3.25

2.2). Three contained unidentified crustacean fragments (mean percent of diet volume: 24; ranking index: 14.4).

CONCLUSION.—*Holocentrus spinifera* is a nocturnal predator that feeds mostly on benthic crustaceans, especially caridean shrimps and xanthid crabs.

Holocentrus tiere Cuvier

This relatively numerous holocentrid is mostly secreted in reef caves during the day, but after dark swims in exposed locations at depths below 5 m, especially along reef ledges. It emerges from cover after last evening light and regains shelter before, or at, first morning light. Like *H. sammara* and *H. spinifera*, above, *H. tiere* has distinctive diurnal and nocturnal color patterns (Figure 12a and b).

Fifteen specimens (141: 67-160 mm) were speared as they swam in the open at night, or just after they had returned to shelter at daybreak: 11 of these had food in their stomachs; 3 taken within 4 h after sunset were empty—apparently their nocturnal hunt had not yet been successful; 1 taken under a ledge during morning twilight also had an empty gut, indicating that it had passed the night without feeding. Items in the 11 specimens containing identifiable material are listed in Table 11.

CONCLUSION.—*Holocentrus tiere* is a nocturnal predator that feeds mostly on benthic crustaceans, especially xanthid crabs and caridean shrimps.

Holocentrus xantherythrus Jordan and Evermann

During the day this relatively small holocentrid aggregates in crevices and under overhangs of basalt reefs (Figure 13) in water deeper than 6 m, but especially below 20 m. After dark it ranges out from this shelter and into the surrounding areas, where solitary individuals are active close to rock, coral, or pockets of sand. By first morning light it has returned to its daytime retreats. At night this fish has prominent white vertical markings on its body like those illustrated for *H. tiere* (Figure 12b).

Of the 29 individuals (106: 88-123 mm) speared at different times of day and night, the stomachs of all 15 that were active in exposed locations on the reef during the 2 h immediately before daybreak, or were under reef shelter within an hour of sunrise, contained prey in varying stages of digestion, whereas the stomachs of all 11 taken from reef crevices during afternoons were empty. The remaining three were taken within 2 h after last light, shortly after they had begun their nightly foraging, and although one was empty, the other two contained fresh prey. Items in the 17 specimens that contained identifiable material are listed in Table 12.

CONCLUSION.—*Holocentrus xantherythrus* is a nocturnal predator that feeds mostly on benthic crustaceans, although some free-swimming crustaceans are also taken close to the bottom.

Holocentrus diadema Lacépède

After dark, many individuals of this relatively small squirrelfish swim close to the sea floor where coral growth is rich at depths below 3 to 4 m. *Holocentrus diadema* is secretive by day, generally remaining out of sight within the many narrow interstices of its coral-rich habitat, but is occasionally glimpsed in the shadows at the base of coral heads. Generally, it does not leave its daytime shelter until after last evening light, and returns to cover before or at first morning light. At night this fish, like *H. xantherythrus*, above, has prominent white vertical markings on its body that are similar to those on the nocturnally active *H. tiere* (Figure 12b).

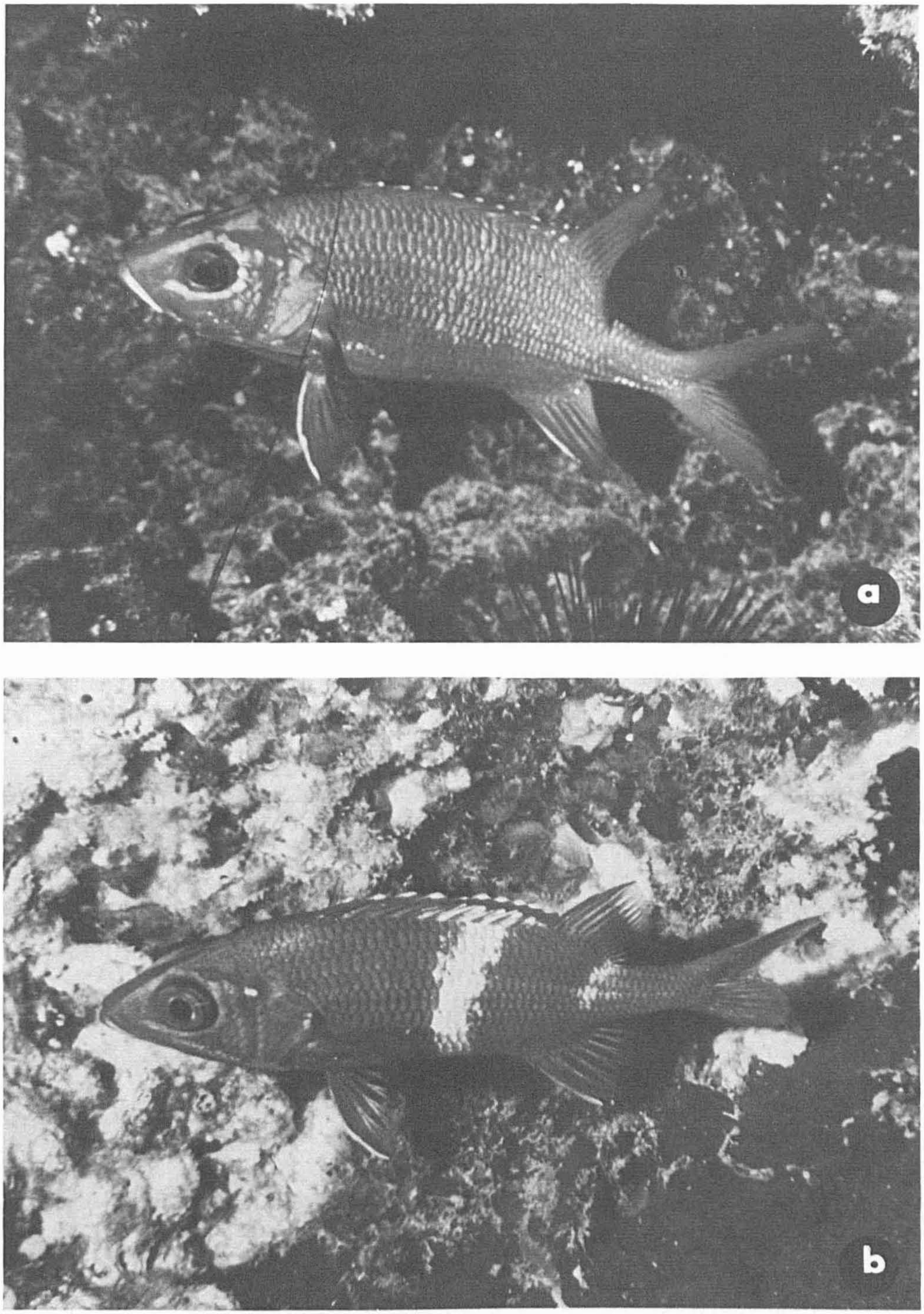

FIGURE 12.—*Holocentrus tiere,* a squirrelfish: a, showing diurnal coloration under a ledge during the day; b, showing nocturnal coloration as it swims close to the reef at night.

TABLE 11.—Food of *Holocentrus tiere*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	8	38.7	28.15
2	Caridean shrimps	5	24.7	11.23
3	Crab megalops	5	4.8	2.18
4	Fish	1	1.8	0.16
5	Polychaetes	1	0.2	0.02
6	Sipunculid introverts	1	0.1	<0.01
Also, crustacean fragments		8	29.7	21.60

TABLE 12.—Food of *Holocentrus xantherythrus*.

Rank	Items	No. fish with this item (n = 17)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	12	42.3	29.86
2	Crab megalops	11	14.8	9.58
3	Caridean shrimps	7	15.1	6.22
4	Prosobranch gastropods	4	2.3	0.54
5	Stomatopods	2	1.9	0.22
6	Opisthobranch gastropods	1	0.9	0.05
7	Sipunculid introverts	1	0.8	0.05
8	Pelecypods	1	0.6	0.04
9	Euphausiids	1	0.3	0.02
10	Oxyrhynchid crabs	1	0.3	0.02
11	Tanaids	2	0.2	0.02
12	Flabelliferan isopods	1	0.1	0.01
13	Mysids	1	0.1	0.01
Also, crustacean fragments		10	20.3	11.94

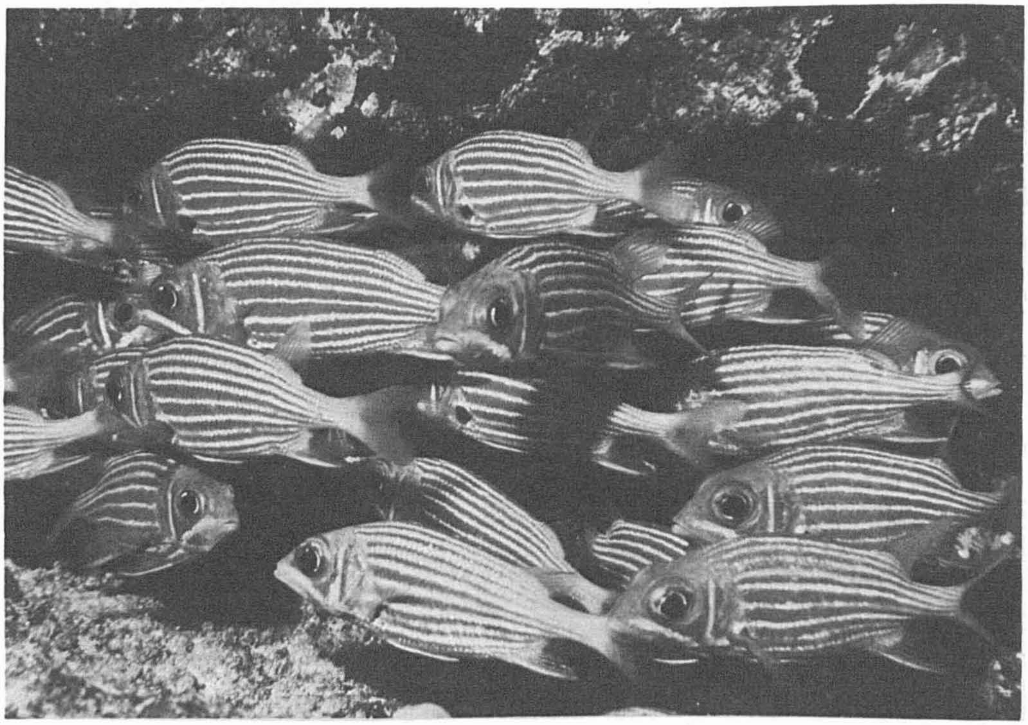

FIGURE 13.—*Holocentrus xantherythrus*, a squirrelfish, aggregated under a ledge during the day.

TABLE 13.—Food of *Holocentrus diadema*.

Rank	Items	No. fish with this item (n = 26)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	17	26.7	17.46
2	Ophiuroids	12	12.0	5.54
3	Crab megalops	11	12.4	5.25
4	Caridean shrimps	11	9.7	4.10
5	Prosobranch gastropods	13	6.2	3.10
6	Polychaetes	6	6.1	1.41
7	Gammaridean amphipods	5	1.7	0.33
8	Penaeid shrimps	2	2.3	0.18
9	Isopods	3	1.4	0.16
10	Chitons	1	1.7	0.07
11	Mysids	2	0.8	0.06
12	Portunid crabs	1	0.8	0.03
13	Holothurians	1	0.6	0.02
14	Oxyrhynchid crabs	1	0.4	0.02
15	Tanaids	1	0.4	0.02
16	Calanoid copepods	1	0.4	0.02
17	Pelecypods	1	0.4	0.02
18	Opisthobranch gastropods	1	0.2	0.01
19	Echinoids	1	0.2	0.01
20	Harpacticoid copepods	1	0.1	<0.01
21	Limpets	1	0.1	<0.01
Also, crustacean fragments		15	11.3	6.63
	Unidentified fragments	4	3.9	0.60

Twenty-eight specimens (109: 85-127 mm) were speared as they swam in exposed locations on the reef at various times during the night. Only two had empty stomachs: in one of these, taken shortly after nightfall, the entire gut was empty, which indicated it had not as yet hunted successfully that night; the other, taken with an empty stomach just before daybreak, had a full intestine, suggesting that it had fed early but not late during the night. The other 26 specimens all contained food in varying stages of digestion, most of it identifiable, as listed in Table 13.

CONCLUSION.—*Holocentrus diadema* is a nocturnal predator that feeds mostly on benthic crustaceans, although it also takes free-swimming forms close to the bottom.

Holocentrus lacteoguttatum Cuvier

This small squirrelfish is similar to *H. xantherythrus* and *H. diadema,* but frequents shallower water than the other two, being most numerous during the day in rocky crevices along surge-swept shores, often where the water is only 1 to 4 m deep. It aggregates in these crevices, and after nightfall ranges out over coral, rock, or pockets of sand on the surrounding reef. Gosline and Brock (1960) also noted the shallowwater habits of this species, but in at least some situations it occurs in depths below 30 m (Gosline, 1965). These habitat distinctions are clearest in daylight, when the three species have retired to their shelters. The differences are less clear at night, when their activity ranges overlap. *Holocentrus lacteoguttatum* does not seem to have prominent nocturnal color features, as do certain other species of *Holocentrus,* treated above; however, several individuals after having been speared at night showed faint traces of essentially the same white markings characteristic of nocturnally active individuals of *H. xantherythrus, H. diadema,* and *H. tiere* (see Figure 12b).

Twenty-one specimens (88: 52-104 mm) were collected at various times of day and night. All but 1 of 13 active individuals that were speared in the open at night (more than 4 h after sunset and before they had returned to shelter at daybreak) had food in their stomachs; the lone exception, collected 4 h after sunset, had a completely empty gut, indicating it had not yet hunted successfully that night. In comparison, only one of five collected from aggregations under shelter during midmorning had material in its stomach, and this was extensively digested (all had full intestines, however). Finally, all three that were collected from aggregations under shelter during late afternoon had completely empty guts, except for a few well-digested fragments posteriorly. Items in the 13 specimens containing identifiable material are listed in Table 14.

TABLE 14.—Food of *Holocentrus lacteoguttatum*.

Rank	Items	No. fish with this item (n = 13)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	13	36.3	36.30
2	Crab megalops	9	8.0	5.54
3	Gammaridean amphipods	8	5.1	3.14
4	Tanaids	6	3.7	1.71
5	Polychaetes	4	4.9	1.51
6	Caridean shrimps	3	1.9	0.44
7	Harpacticoid copepods	3	0.8	0.19
8	Echinoids	3	0.8	0.19
9	Sipunculid introverts	1	1.8	0.14
10	Prosobranch gastropods	1	1.0	0.08
11	Oxyrhynchid crabs	1	0.3	0.02
12	Calanoid copepods	1	0.3	0.02
13	Limpets	1	0.2	0.02
14	Ophiuroids	1	0.1	0.01
Also, crustacean fragments		13	28.1	28.10
	Unidentified fragments	4	6.7	2.06

CONCLUSION.—*Holocentrus lacteoguttatum* is a nocturnal predator that feeds primarily on benthic crustaceans, although some free-swimming forms close to the bottom are also taken.

Holotrachys lima (Valenciennes)

This fish is secreted far back in reef crevices during daylight. After dark, however, solitary individuals are widespread in exposed positions, swimming even closer to the reef than do the species of *Holocentrus*, discussed above. Unlike the others, which often swim over sand patches, this species stays over rock or coral. It did not display distinctive day or night color features, being at all times a solid rose-red.

Twenty specimens (91: 70-113 mm) were collected during day and night. Thirteen were active in exposed positions on the reef at night when speared, and the stomachs of eight contained prey, much of it fresh. Of the five taken after dark with empty stomachs, the entire gut was empty in three collected before midnight, indicating they had not yet hunted successfully that night; however, the gut was also empty in one speared just before dawn, indicating it had passed the entire night without feeding; the fifth individual with an empty stomach also was collected just before dawn, but its intestine was full, indicating that it probably had fed earlier during the night. Six of seven specimens collected from deep crevices during late morning had empty stomachs, and the extensively damaged material in the seventh individual probably had been ingested during the previous night. (Rotenone was used to collect this species during the day, a departure from the standard collecting method that was necessary because this secretive fish is only rarely seen in daylight.) Items in the 10 specimens containing identifiable material are listed in Table 15.

CONCLUSION.—*Holotrachys lima* is a nocturnal predator that feeds mostly on benthic crustaceans, although some free-swimming forms close to the bottom also are taken.

Myripristis kuntee Cuvier

This is the smallest of the three species of *Myripristis* that are numerous on the nearshore Kona reefs. It remains secreted in small crevices

TABLE 15.—Food of *Holotrachys lima*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Caridean shrimps	6	31.5	18.90
2	Xanthid crabs	5	33.0	16.50
3	Crab megalops	2	7.0	1.40
4	Fish	1	3.5	0.35
5	Gammaridean amphipods	1	0.5	0.05
Also, crustacean fragments		5	24.5	12.25

and coral interstices during the day, but emerges and aggregates in the lower levels of the water column, above the reef, about 30 min after sunset. After remaining active during the night, it returns to its daytime shelter on the reef about 30 min before sunrise (Hobson, 1972, as *M. multiradiatus*). When this fish is under cover during the day its body is solid red, but when active in the water column after dark, its lower sides are silvery, affording countershading like that described for nocturnally active *M. leiognathus* in the Gulf of California (Hobson, 1968a). This nocturnal pattern was illustrated earlier (Hobson, 1972: Figure 6).

Thirty-nine specimens (120: 74-145 mm) were speared at different times of the day and night. All 20 that were collected either over the reef at night (later than 4 h after sunset), or from shelter sites within an hour of sunrise, had their guts full of food. In contrast, 13 of 14 collected from shelter sites during the afternoon and evening twilight had empty guts (3 had a few fragments posteriorly in their intestines), and the 14th had in its stomach only well-digested fragments. Of the remaining five, collected above the reef early during the night (within 1 h after last light), four had their guts completely empty, indicating they had not as yet hunted successfully at that early hour, but the fifth was full of fresh calanoid copepods of a species that was exceptionally numerous around our diving lights for about 45 min shortly after last light on that particular evening. Items in the 22 individuals that contained identifiable material are listed in Table 16.

CONCLUSION.—*Myripristis kuntee* is a nocturnal planktivore that takes mostly crab megalops and other crustacea.

Myripristis murdjan (Forskål)

This holocentrid is numerous in Kona, where during the day it aggregates in reef crevices and under coral overhangs, especially where there is shelter from prevailing seas (Figure 14). The twilight activity of this species has been described (Hobson, 1972, as *M. berndti*). About 30 min after sunset it emerges from its daytime shelter and aggregates in the water column above the reef, generally rising to levels higher than those attained by *M. kuntee* (see above). Immediately, there is a general movement offshore. It remains uncertain how far it swims offshore —perhaps it does not go much beyond the drop-off into deep water, which is a major feeding ground for diurnal planktivores (Hobson, 1972). The offshore move is obscured by the circumstance that at any given time during the night many individuals of this species are swimming over the inshore reefs. Nevertheless, there are consistently fewer of them over inshore reefs on dark nights than on moonlit nights. Gosline (1965) also noted offshore migrations at night by species of *Myripristis* in Hawaii. About 40 min before sunrise this species begins to assemble above its diurnal shelter, and within 10 min all have taken cover for the coming day. This species shows essentially the same day-night difference in color patterns as *M. kuntee*, above.

Of 25 individuals (169: 139-270 mm) speared at different times of day and night, all 16 that were taken above the reef at night (later than 4 h after

TABLE 16.—Food of *Myripristis kuntee*.

Rank	Items	No. fish with this item (n = 22)	Mean percent of diet volume	Ranking index
1	Crab megalops	19	25.2	21.76
2	Decapod shrimps	9	11.8	4.83
3	Calanoid copepods	9	8.0	3.27
4	Mysids	7	9.3	2.96
5	Polychaetes	4	4.8	0.87
6	Fish	3	4.6	0.63
7	Stomatopods	4	2.8	0.51
8	Gammaridean amphipods	7	0.9	0.29
9	Gnathiid isopod larvae	2	1.8	0.16
10	Ostracods	2	0.1	0.01
11	Tanaids	1	0.1	0.01
12	Invertebrate eggs	1	0.1	0.01
Also, crustacean fragments		14	27.8	17.69
	Unidentified fragments	3	2.7	0.37

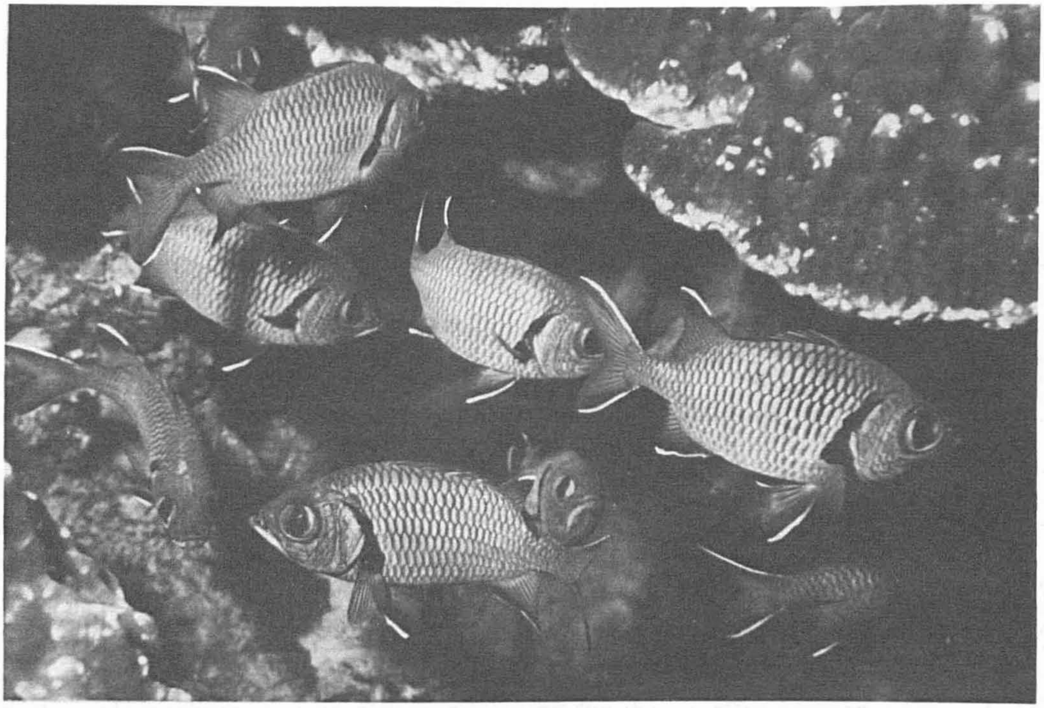

FIGURE 14.—*Myripristis murdjan*, a squirrelfish, aggregated under a coral ledge during the day.

sunset) contained food, whereas 8 of 9 that were collected from shelter sites during the afternoon were empty (the ninth specimen, collected during late afternoon, had only well-digested fragments in its stomach). Items in the 17 individuals containing identifiable material are listed in Table 17.

Hiatt and Strasburg (1960) found shrimp fragments in *M. murdjan* (reported as *M. berndti*) in the Marshall Islands, and suspected nocturnal habits, as did Randall (1955) for this species in the Gilbert Islands.

CONCLUSION.—*Myripristis murdjan* is a nocturnal planktivore that takes mostly crab megalops and other crustaceans.

Myripristis amaenus (Castelnau)

This squirrelfish, which congregates during the day in large caves cut into reefs exposed to an open-sea swell, is very similar to the preceding, *M. murdjan*, but is less numerous in most Kona habitats. Its behavior during twilight was described earlier (Hobson, 1972, as *M. argyromas*).

TABLE 17.—Food of *Myripristis murdjan*.

Rank	Items	No. fish with this item (n = 17)	Mean percent of diet volume	Ranking index
1	Crab megalops	16	53.5	50.35
2	Decapod shrimps	3	8.1	1.43
3	Mysids	3	6.5	1.15
4	Fish	2	2.0	0.24
5	Polychaetes	2	1.5	0.18
6	Stomatopods	2	0.9	0.11
7	Euphausiids	1	1.2	0.07
8	Cephalopods	1	1.2	0.07
9	Gammaridean amphipods	1	0.5	0.03
10	Prosobranch gastropods	1	0.3	0.02
11	Calanoid copepods	1	0.1	<0.01
12	Ostracods	1	0.1	<0.01
Also, crustacean fragments		8	14.5	6.82
	Unidentified fragments	4	9.6	2.26

Myripristis amaenus, like its congeners, emerges from its daytime retreats about 30 min after sunset, and at least many individuals move offshore, especially when there is no moonlight. *Myripristis amaenus* shows essentially the same day-night distinction in coloration that is described above for its congeners.

Of 19 individuals (176: 116-210 mm) speared at different times of day and night, all 14 collected above the reef at night (later than 4 h after sunset), or from shelter sites within 2 h after the species had returned to cover in the morning, contained food, whereas all 5 collected from shelter sites during late afternoon were empty. Items in the 14 individuals containing identifiable prey are listed in Table 18.

CONCLUSION.—*Myripristis amaenus* is a nocturnal planktivore that takes mostly crab megalops and other crustaceans.

General Remarks on Squirrelfishes

Squirrelfishes are known throughout tropical seas to hunt prey after dark. For example, they have been thus described in the Marshall Islands (Hiatt and Strasburg, 1960), the Gulf of California (Hobson, 1965, 1968a), and the West Indies (Randall, 1967). Similar behavior has been noted in the Florida Keys by Starck and Davis (1966), who noted there were no distinctive nocturnal color features in tropical Atlantic holocentrids, such as are reported for all but two of the Hawaiian species above.

The two major categories noted above in the introduction to the squirrelfishes each represents a generally different mode of predation. All feed primarily on crustaceans, but whereas species of *Holocentrus* and *Holotrachys lima* capture their prey close to the sea floor, species of *Myripristis* hunt prey up in the water column.

BOTTOM FEEDERS.—The seven holocentrids in this category feed mostly on benthic forms, but also take some prey that are free-swimming at the base of the water column. Xanthid crabs comprised the major prey item for all species except the largest, *Holocentrus spinifera,* which contained a slightly larger volume of caridean shrimps. Xanthid crabs are ubiquitous benthic animals in all Kona inshore habitats, and are widely active in exposed positions after dark.

Of the seven bottom-feeding squirrelfishes, only three similar species, *Holocentrus diadema, H. lacteoguttatum,* and *H. xantherythrus,* hunt significantly over sand in addition to feeding on hard reef substrata; however, even these three do not range away from cover during this activity, which is limited to sand pockets on the reef and only the fringes of more extensive sandy areas. Nevertheless, it is probably because of this habit that these three have more varied diets than do the others. Hiatt and Strasburg (1960) reported that some of the holocentrids in the Marshall Islands forage on sandy bottoms, citing sand-dwelling gastropods as being prominent prey of *H. diadema* in that area.

The other four bottom feeders, *Holocentrus sammara, H. spinifera, H. tiere,* and *Holotrachys lima,* restrict their activity largely to hard substrata on the reef, and prey more heavily on caridean shrimps—especially on snapping shrimps. Some of the larger individuals of *Holocentrus sammara* and *H. spinifera* capture the caridean *Saron marmoratus*; although individuals of this shrimp exceeding a length of 30 mm are numerous

TABLE 18.—Food of *Myripristis amaenus.*

Rank	Items	No. fish with this item (n = 14)	Mean percent of diet volume	Ranking index
1	Crab megalops	14	75.1	75.10
2	Decapod shrimps	4	9.3	2.66
3	Fish	3	2.9	0.62
4	Cephalopods	1	1.4	0.10
5	Mysids	4	0.3	0.09
6	Prosobranch gastropods	2	0.4	0.06
7	Polychaetes	1	0.4	0.03
8	Gammaridean amphipods	1	0.2	0.01
9	Calanoid copepods	1	0.1	<0.01
10	Stomatopods	1	0.1	<0.01
11	Isopods	1	0.1	<0.01
Also, crustacean fragments		8	9.7	5.54

in exposed positions on the reef after dark, most are too large to serve as prey for all but the biggest squirrelfishes.

WATER-COLUMN FEEDERS.—These are the species of *Myripristis*, all of which are primarily planktivores. This habit is reflected in their sharply upturned mouths, a feature well known as adaptive to feeding on plankton (e.g. Rosenblatt, 1967). Based on the food-habit data, crab megalops are the major prey of all three species reported here.

Earlier (Hobson, 1965, 1968a), I reported that *M. leiognathus* in the Gulf of California feeds in the water column after dark on planktonic crustaceans, including crab larvae. Similarly, Randall (1967) reported that *M. jacobus* in the tropical Atlantic feeds at night primarily on planktonic organisms, especially crustacean larvae, and Collette and Talbot (1972) noted that this species feeds at least 3 m above the reef. Probably similar habits are universal in species of *Myripristis*.

ORDER GASTEROSTEIFORMES

Family Aulostomidae: trumpetfishes

Aulostomus chinensis (Linnaeus)—*nunu*

This distinctive, solitary fish (Figure 15) is numerous on Kona reefs, where it attains the length of at least 700 mm. It exhibits three basic color forms: plain reddish brown, brown with light striping and other marks, and plain yellow. Several trumpetfish recognized as individuals were seen repeatedly in the same areas throughout the study, and none changed coloration during this time. The habitat of this species is in water deeper than about 5 m close to coral or irregular rocky substrata that offer many ledges and crevices.

I observed no difference in the behavior of this fish between day and night. At all hours it moves slowly, close to cover, propelling its long, cylindrical, rod-straight body mainly by undulating its soft dorsal and anal fins, which are set far back near the tail. The trumpetfish is a stalking predator, and on a few scattered occasions I saw it

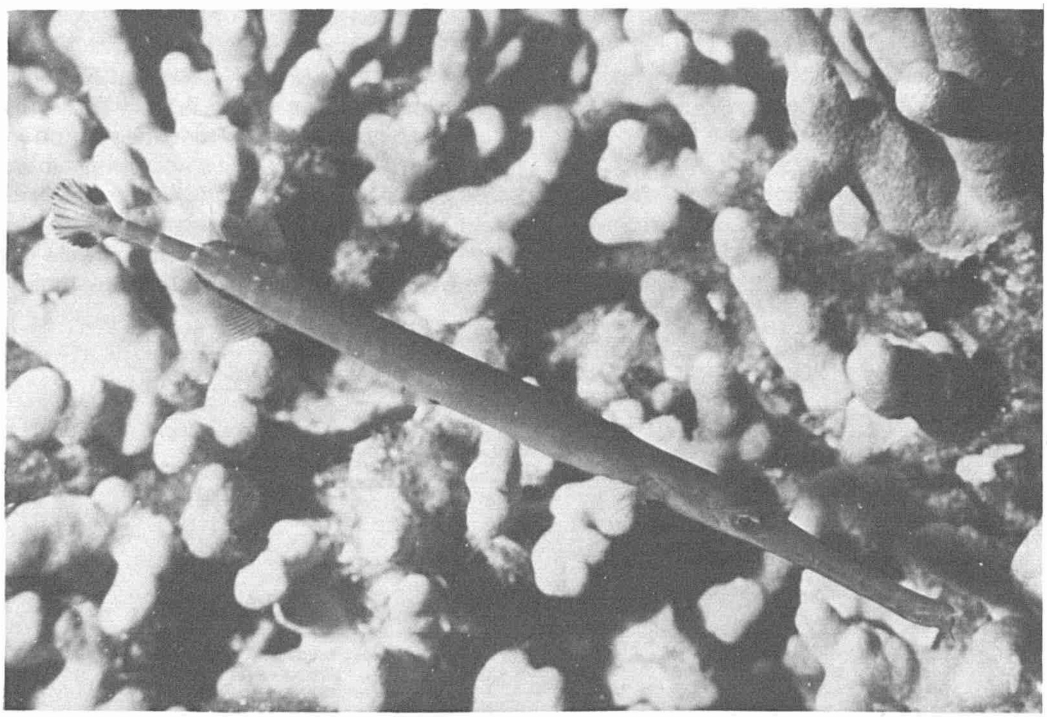

FIGURE 15.—*Aulostomus chinensis*, the trumpetfish, a stalking predator.

capture prey during daylight. After gaining a position close to its quarry, the attack is consummated with a short dart forward, the victim being literally sucked in with a sudden expansion of its tubular snout. Hiatt and Strasburg (1960) did not observe feeding, but speculated that this species in the Marshall Islands probes with its long snout in shallow holes and interstices of the reef and captures prey there by rapidly dilating its mouth. They found a small atherinid fish in the gut on one specimen. Sometimes trumpetfish accompany schools of grazing surgeonfishes—usually mixed groups of *Acanthurus sandvicensis* and *A. nigroris,* which frequently move across the reef. At these times, small organisms probably are driven out from algal cover by the grazing herbivores and become available as prey to the trumpetfish. Occasionally, the trumpetfish swims close beside large herbivores, especially parrotfishes, apparently using these large fishes as shields behind which to get close to prey not threatened by the herbivore.

Although 52 individuals (410: 220-621 mm) were speared at different times of day and night, no pattern was evident in the condition of the gut contents from specimens taken at these different times. Of 27 that contained food in their stomachs, 18 had captured fishes (mean percent of diet volume: 63; ranking index: 42), and 11 had taken caridean shrimps (mean percent of diet volume: 37; ranking index: 15.07).

It probably is significant that, with only two exceptions, those sampled had preyed on either fishes or shrimps—not both. The data cannot relate this selectivity to day or night activity or to size of predator. The 16 individuals that had preyed exclusively on fishes were within exactly the same size range (241-528 mm) as the 9 individuals that had preyed exclusively on shrimps. Furthermore, the mean sizes of the two groups differed only slightly—401 mm for the fish eaters, 396 mm for the shrimp eaters. The two individuals that had taken both fishes and shrimps were 241 and 337 mm long.

Aulostomus chinensis takes relatively large prey: the 15 fish items (representing among others *Apogon snyderi, Acanthurus nigrofuscus, Canthigaster* sp., and a labrid) that could be measured accurately had a mean standard length of 58 mm (range 25-88 mm) whereas the 11 shrimps that could be measured accurately had a mean total length of 55 mm (range 13-110 mm). Ten of the 11 shrimps were *Saron marmoratus,* the only shrimp this large that was numerous in exposed locations on the reef. Although this shrimp occupies exposed positions only at night, I have no evidence that it is taken by *Aulostomus chinensis* in greater numbers after dark.

Because the trumpetfish has an especially long, attenuated body, and because it takes relatively large prey, individuals that have recently ingested a meal often can be recognized by their distended bellies. Such individuals were occasionally seen during all periods of day and night, but most often during, or shortly after, twilight. Consistent with this, all three specimens that contained fresh prey (little or no damage by digestion) were collected during late twilight: in two of these instances (one in the morning, one in the evening) the prey were fishes; in the other instance (evening), the prey was a shrimp, *S. marmoratus.* Beyond this, the gut contents were of little help in establishing a pattern to feeding times; nor did the incidence of individuals with empty stomachs indicate a pattern, for they were collected during all periods of day and night.

CONCLUSION.—*Aulostomus chinensis* stalks prey, mostly fishes and caridean shrimps, most successfully during twilight, but also during the day and perhaps also at night.

General Remarks on Trumpetfishes

The activity of *Aulostomus chinensis* in Kona seems to be typical of the genus in other seas. Randall (1967) reported only fishes and caridean shrimps in 79 *A. maculatus* from the West Indies, and also remarked on the large size of these prey, as well as the way this trumpetfish sucks them into its mouth by expanding its tubular snout. Randall often observed *A. maculatus* hovering vertically in the water over small fishes and several times darting down on them (I did not see *A. chinensis* feed this way). Collette and Talbot (1972) judged *A. maculatus* in the Virgin Islands to be primarily crepuscular. They were uncertain about its nocturnal activity, but judged one they saw in a gorgonian at 2330 h to be quiescent. Eibl-Eibesfeldt (1955) described the way trumpetfish in the Indian Ocean use other fishes as cover behind which to approach small prey, and this was also reported by Collette and Talbot (1972) from the Virgin Islands.

Family Fistulariidae: cornetfishes

Fistularia petimba **Lacépède**

The cornetfish (see Hobson, 1968a: Figure 9) looks much like the trumpetfish, but grows considerably larger, many being over 1 m long. It is a pale-green fish with light-blue markings, and under certain circumstances instantaneously displays a series of broad bands along its body. Earlier I (Hobson, 1968a) reported that this species in the Gulf of California displays these bands when poised to strike prey. In Kona, the bands appear in similar circumstances and also in situations that suggest the fish might feel threatened, as when it is approached underwater by a human—especially a human carrying a diving light at night. *Fistularia petimba* frequently swims in loosely spaced groups of several individuals, generally in exposed shallowwater locations over the reef top.

Occasionally, *F. petimba* was seen in Kona stalking its prey during daylight, as observed in the Gulf of California (Hobson, 1968a). It does not move suddenly until within a few centimeters of its prey. When positioned for attack, it often draws its midsection into a modified "s" (as viewed from above), then darts forward for the capture. *Fistularia petimba* is more agile than *A. chinensis,* and undulating body movements not seen in the latter are regularly used to provide greater thrust in attacks and accelerated swimming. In the Gulf of California, I saw *F. petimba* use other fish as shields behind which to approach prey, as described above for *A. chinensis,* but did not see this in Kona. The behavior of *F. petima* was not seen to differ between day and night.

The 10 specimens (673: 363-1,069 mm), although collected during both day and night, were too few to provide much evidence on feeding times; however, of the 2 with empty guts, 1 was collected during late afternoon, and the other just before first morning light, indicating that these 2 had not fed during the preceding day and night, respectively. Only two specimens contained fresh prey, and both were collected shortly after twilight—one after evening twilight, the other after morning twilight. Though limited, these data suggest crepuscular feeding. Although prey in the other six specimens were in stages of digestion not inconsistent with predominantly crepuscular feeding, they clearly showed that prey are also taken at other times. All eight individuals with material in their stomachs had fed on fishes exclusively; only two prey could be identified to species, one a 70-mm cardinalfish, *Apogon snyderi,* the other a 52-mm damselfish, *Abudefduf imparipennis*. Both of these prey could have been captured close to reef crevices during the day.

Thus, *F. petimba* in Kona, as in the Gulf of California (Hobson, 1968a), was found to prey only on fishes. Hiatt and Strasburg (1960) also reported this species in the Marshall Islands to be exclusively piscivorous. My data suggest that *F. petimba* takes somewhat smaller prey than does *A. chinensis* of comparable length, as might be expected in view of the deeper body and snout of the latter. The mean length of the seven *F. petimba* containing measurable prey was 593 mm (range: 363-795 mm). The 11 measurable prey in these individuals had a mean length of 32 mm (range: 8-70). Comparable data for *A. chinensis* are given above.

CONCLUSION.—*Fistularia petimba* stalks fishes most successfully during twilight, but also during the day and perhaps at night.

General Remarks on Cornetfishes

The exclusively piscivorous habits of *Fistularia petimba* are paralleled by the similar diet of *F. tabacaria* in the tropical Atlantic (Randall, 1967). Suyehiro (1942) claimed that *F. petimba* feeds on tiny floating organisms by using its snout like a pipette, but I join Hiatt and Strasburg (1960) and Randall (1967) in contesting this opinion of the size of its prey. Starck and Davis (1966) found *F. tabacaria* to be more numerous on Florida reefs at night than during the day, but did not speculate that this reflected differences in feeding behavior.

ORDER SCORPAENIFORMES

Family Scorpaenidae: scorpionfishes

Pterois sphex **Jordan and Evermann — lionfish,** ***nohu pinao***

The lionfish is a sluggish, solitary species that usually rests motionless on the reef, yet draws attention by its spectacular appearance (Figure 16). Perhaps because its fin spines carry a potent toxin, this fish makes little effort to evade a human collector. It is not numerous in Kona, and

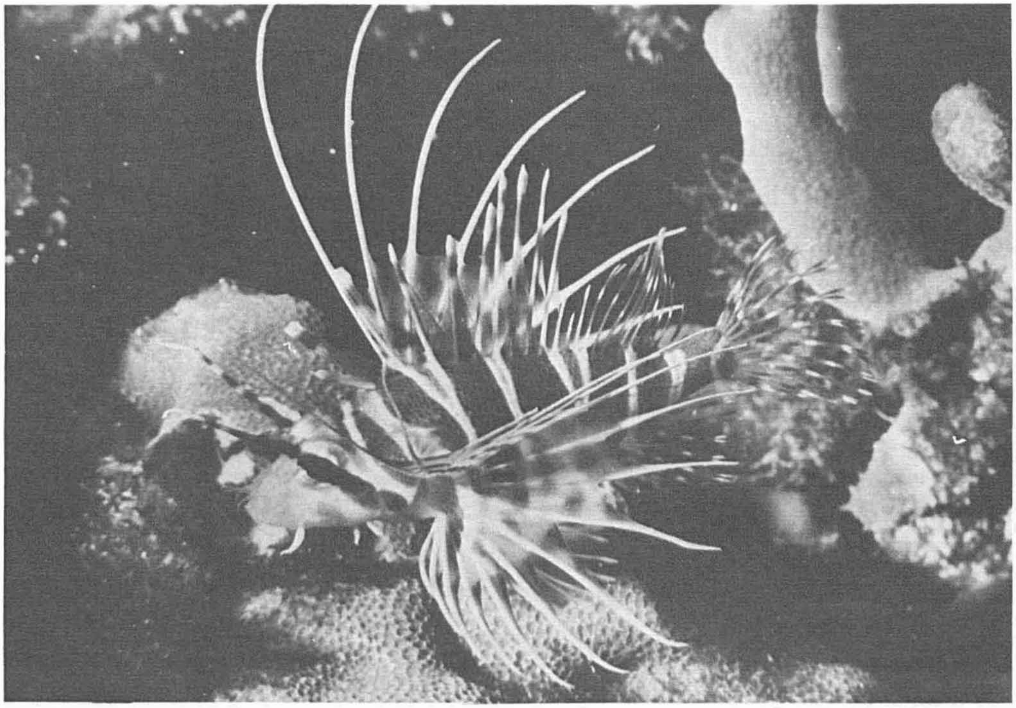

FIGURE 16.—*Pterois sphex,* a lionfish, swimming close to the reef at night.

occurs in visible locations on the reef most often after dark—though never far from shelter.

Fourteen specimens (83: 58-121 mm) were speared during day and night. Of nine that were collected during the afternoon or evening twilight, the guts in six were empty, and three had only well-digested crustacean fragments in their stomachs. On the other hand, all five specimens collected at night (more than 2 h after sunset) contained relatively fresh prey in their stomachs.

All eight specimens that contained food had fed on crustaceans exclusively. Caridean shrimps, which occurred in six, were the major food item (mean percent of diet volume: 56.3; ranking index: 42.19). Other food items were: xanthid crabs in three (mean percent of diet volume: 13.8; ranking index: 5.16) and pagurid crabs in one (mean percent of diet volume: 0.6; ranking index: 0.08). Five individuals contained unidentified crustacean fragments (mean percent of diet volume: 29.4; ranking index: 18.36).

CONCLUSION.—*Pterois sphex* is a nocturnal predator that takes benthic crustaceans, especially caridean shrimps.

Scorpaena coniorta (Jenkins)

Although this small species is the most numerous scorpaenid on Kona reefs, the casual observer will encounter it only at night. During the day individuals more than about 50 mm long are deep in reef crevices, whereas many smaller individuals are motionless among the branches of the coral *Pocillopora meandrina* (Figure 17). After nightfall, many of these fish occur in exposed positions: the larger individuals are spread widely across the reef, resting immobile on rock or coral, whereas the smaller ones are perched motionless on the sea floor close by the same coral heads that shelter them during the day. However, at any given time of night some of these fish are among the coral branches, just as in daylight.

Thirty-four specimens (46: 36-67 mm) were collected during various times of day and night. Of 12 that were taken during afternoon or early evening, most from among coral branches, only 1 had food in its gut (3 had a few fragments posteriorly in their intestine). The one containing food, taken from a coral head, had in its stomach a crab that, based on damage by digestion, probably had been

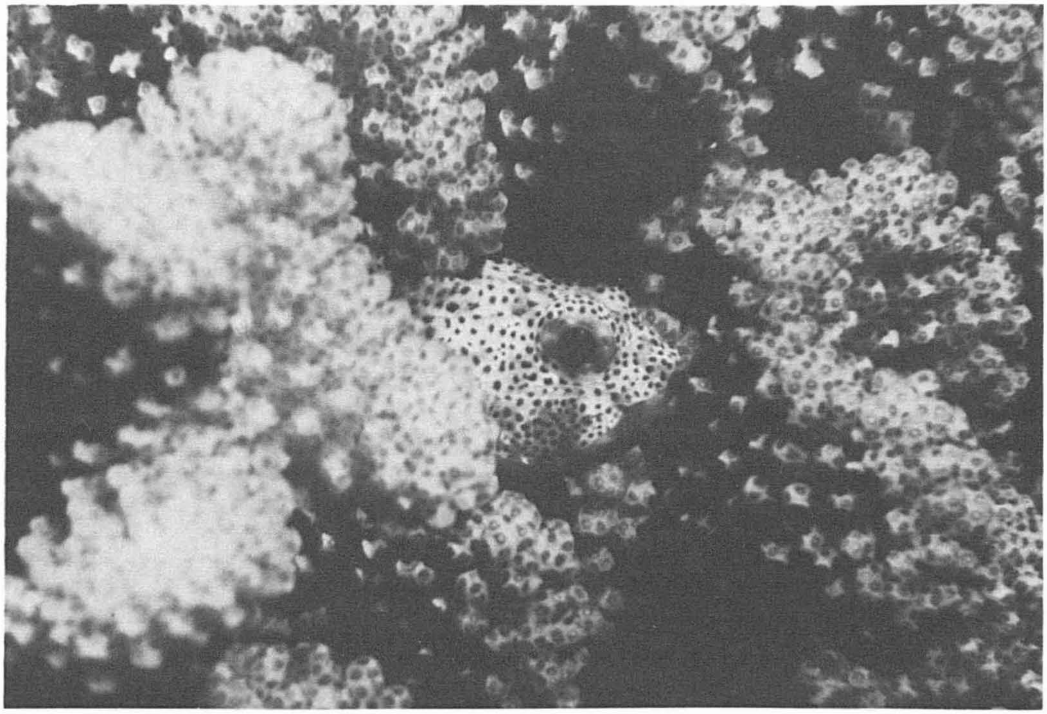

FIGURE 17.—*Scorpaena coniorta,* a scorpionfish, nestled among coral branches during the day.

captured during the day. In comparison, 14 of 22 individuals collected at night, between 3 h after sunset and first morning light, had food in their stomachs. Brachyuran crabs, almost all of them xanthids, occurred in 7 of the 15 individuals that contained identifiable items (mean percent of diet volume: 39; ranking index: 18.2). Caridean shrimps occurred in six (mean percent of diet volume: 28.3; ranking index: 11.33), and fishes in one (mean percent of diet volume: 6.7; ranking index: 0.45). Unidentified crustacean fragments occurred in six (mean percent of diet volume: 26; ranking index: 10.4). Many of the xanthids and carideans found in specimens less than 50 mm long are forms that cooccur with these fish among the coral branches.

CONCLUSION.—*Scorpaena coniorta* is a nocturnal predator that takes benthic crustaceans, mostly xanthid crabs and caridean shrimps. Some prey are also captured during the day.

Scorpaenopsis cacopsis **Jenkins—*nohu 'omakaha***

This species, the largest Hawaiian scorpaenid, grows to over 50 cm long (Gosline and Brock, 1960). I observed no overt difference in its behavior between day and night as it was seen resting immobile on the reef at all hours, often fully exposed. Despite its large size and frequent disdain for cover, this fish remains virtually unseen, owing to body hues and texture that render it much like the reef on which it rests. It was not seen feeding, but its morphology and behavior suggest that it lunges forward to attack prey that have strayed within range, and sucks them in with a sudden expansion of its cavernous mouth.

Of the five specimens (256: 73-375 mm) examined, three had prey in their stomachs: one, taken within 1 h after sunrise, contained a fresh fish, *Pomacentrus jenkinsi* (104 mm); a second taken at night, 4 h after sunset, contained a relatively fresh octopus; and the third, taken late in the afternoon, contained fish fragments. The other two, both empty, were collected during morning twilight.

CONCLUSION.—*Scorpaenopsis cacopsis* attacks fishes and motile invertebrates during the day. Its nocturnal activity remains uncertain.

General Remarks on Scorpionfishes

Scorpionfishes on tropical reefs are widely described as predators that rest on the bottom, and because they resemble their surroundings they remain unseen by small prey that swim within striking range (Longley and Hildebrand, 1941; Hiatt and Strasburg, 1960; Starck and Davis, 1966; Randall, 1967). This behavior is descriptive of some scorpaenids, but probably is overdrawn as a generalization encompassing the entire family. Such a tactic is adaptive to daylight, and is used by *Scorpaenopsis cacopsis* in Hawaii (the one fish identified as prey of this predator, a damselfish, is strictly a diurnal species that is not active over the reef at night). Significantly, the fishes that have been reported by other investigators as prey of scorpaenids on tropical reefs similarly imply diurnal predations: blennies (Longley and Hildebrand, 1941); a wrasse and a parrotfish (Hiatt and Strasburg, 1960); and an angelfish, a surgeonfish, a sardine, a sea horse, and a conger eel (Randall, 1967). With perhaps the lone exception of the conger eel, these are fishes that swim close to the reef during daylight, and at that time would be vulnerable to the ambushing tactic of scorpaenids; however, they would not be readily available after dark when most of them rest under cover on the reef or, in the case of the sardine, swim away from the reef. Conspicuously absent among the reported prey are the many species of comparable size that are numerous close above the reef at night, including apogonids and holocentrids. One can readily see how camouflage and ambush would be especially suited to daylight, but less significant after dark. Randall (1967), basing his generalization on the West Indian situation, characterized the scorpaenids as diurnal. In Hawaii, most species are predominantly nocturnal. In addition to *Pterois sphex* and *Scorpaena coniorta,* which prey largely on benthic crustaceans, as described above, other members of the family that appear on the reef in greater numbers at night include *Dendrochirus brachypterus, Scorpaenodes parvipinnis,* and *Scorpaena ballieui.* Among feeding scorpaenids, camouflage does not seem to play the important role at night that it does during the day. When these predators are abroad after dark they often contrast markedly with their surroundings. Although fishes do not seem to be significant prey at night, the behavior of these nocturnal scorpaenids indicates that their tactic remains a short lunge from a resting position to capture prey that have inadvertently come within range.

ORDER PERCIFORMES

Family Serranidae: sea basses

Sea basses are prominent on most tropical reefs, but the family has no representatives native to shallow Hawaiian reefs (Gosline and Brock, 1960). Nevertheless, the widespread Indo-Pacific serranid *Cephalopholis argus* has been introduced into Hawaii from the Society Islands, the first time in 1956, and has since become well established in Kona.

Cephalopholis argus Bloch and Schneider

This solitary fish, numerous on Kona reefs, swims close among overhanging ledges and crevices during the day, but is seen less often at night. Because it generally is wary of humans, lack of nocturnal observations could mean that it avoided our diving lights at night.

Although 6 of 10 specimens (319: 232-520 mm) speared at various times of day were empty, no temporal pattern is recognized, as the 6 were taken from early morning to late afternoon. All four that contained food, also taken at various times during the day (on four different occasions over 3 mo), had fed exclusively on fishes. One, taken during midmorning, contained, because of digestion, what was recognizable only as a fish (125 mm). The other three—one collected during midday, and two late in the afternoon—each contained a single moderately digested squirrelfish, *Holocentrus xantherythrus* (80, 110, and 130 mm, respectively). *Holocentrus xantherythrus* congregates under ledges during the day in areas where *C. argus* is active (see the species account for *H. xantherythrus* above), and thus is available as prey for the sea bass at this time. *Cephalopholis argus* has been reported to feed on shrimps as well as fishes in the Marshall Islands (Hiatt and Strasburg, 1960) and on shrimps in the Gilbert Islands (Randall, 1955). In a sample of 98 specimens from Tahiti, Randall and Brock (1960) found that 77.5% contained fishes, whereas 22.5% contained crustaceans (shrimps and crabs).

CONCLUSION.—*Cephalopholis argus* preys on fishes among reef crevices during the day. Its nocturnal habits remain uncertain.

General Remarks on Sea Basses

Diurnal piscivorous habits were reported in *Mycteroperca rosacea* in the Gulf of California, with peaks during twilight (Hobson, 1965, 1968a). On the other hand, nocturnal habits were noted in *Alphestes multiguttatus* and *Rypticus bicolor* (the latter is often placed in a separate family, the Grammistidae), both of which prey chiefly on benthic crustaceans (Hobson, 1965, 1968a). In the same reports, a fourth sea bass, *Epinephelus labriformis,* was reported to feed by both day and night, chiefly on fishes in daylight and on benthic crustaceans after dark. These data suggest that fishes may be the major prey of sea basses in daylight with crustaceans predominating after dark, a generalization consistent with the limited observations on *Cephalopholis argus* in Kona.

Starck and Davis (1966) noted that serranids of the genera *Epinephelus, Mycteroperca,* and *Petrometopon* behave similarly day and night in the Florida Keys, with probable feeding peaks around sunrise and sunset. Longley and Hildebrand (1941) reported that *Epinephelus morio* feeds during both day and night in the Dry Tortugas, Fla., and Randall (1967) noted that larger serranids in the West Indies feed both day and night, with greatest activity at dawn and dusk. Collette and Talbot (1972), on the other hand, reported *E. guttatus* in the Virgin Islands to be active by day and apparently asleep at night. They also found *E. fulvus* and *E. cruentatus* active in daylight and suspected that these sea basses rest at night. Randall (1967) considered the smaller serranids, in general, to be primarily diurnal. In Florida, Starck and Davis (1966) regarded certain small serranids of such genera as *Diplectrum, Hypoplectrus,* and *Serranus* to be active by day and inactive by night. None of these authors attempted to relate time of activity with kinds of prey.

Family Kuhliidae: aholeholes

Kuhlia sandvicensis (Steindachner)—*aholehole*

This predator occurs in only a few locations within the Kona study area, and there just sparsely, compared to its large numbers elsewhere in Hawaiian nearshore waters. Juveniles and young adults live in tide pools or in schools close to shore (Gosline and Brock, 1960), but the larger adults congregate during the day under low ledges and boulders, usually in water less than 5 m deep farther from shore. They emerge from shelter at nightfall, and the few observed after dark during this study were solitary in the water column over the reef. Gosline and Brock (1960) noted that the adults, at least, are nocturnal, a conclusion consistent with the large eyes of the species.

Of the 13 specimens (164: 132-202 mm) collected, 8 speared during midmorning from under rocky cover contained in their stomachs extensively digested crustacean fragments (including crab megalops), 1 taken under a rock at noon contained only well-digested material scattered through its intestine, and 4 speared under rocks late in the afternoon were empty.

CONCLUSION.—*Kuhlia sandvicensis* is a nocturnal predator that feeds on free-swimming crustaceans.

Family Priacanthidae: bigeyes

Priacanthus cruentatus (Lacépède)—bigeye, *aweoweo*

This priacanthid (Figure 18) is numerous in Kona, where it takes shelter under rocks or coral during the day, often in groups, and is active in the open at night. After emerging from shelter at nightfall, many individuals assemble in schools high in the water column and then migrate offshore. These do not return inshore until about 40 min before sunrise, but a lesser number of other individuals, mostly solitary or in small groups, remain over the inshore reefs throughout the night. All of these fish return to their daytime shelter by 30 min before sunrise, at least many of them to specific home caves (Hobson, 1972).

Forty specimens (173: 115-255 mm) were collected during day and night. All 17 that were speared during morning twilight (shortly after they had reappeared near their diurnal shelter, but before they had taken cover) had relatively fresh prey in their stomachs. Four others were collected from under cover during late morning, and although all had full stomachs, with many items identifiable, digestion was advanced, and most of the material was damaged beyond recognition. The other 19 were collected from caves late in the afternoon, and although only 4 of these had empty stomachs, the material in the other 15 was reduced to unidentified fragments. Items in the 21 specimens containing identifiable material are listed in Table 19.

Hiatt and Strasburg (1960) acknowledged that species of *Priacanthus* generally are thought to be nocturnal, but contested this opinion as far as *P.*

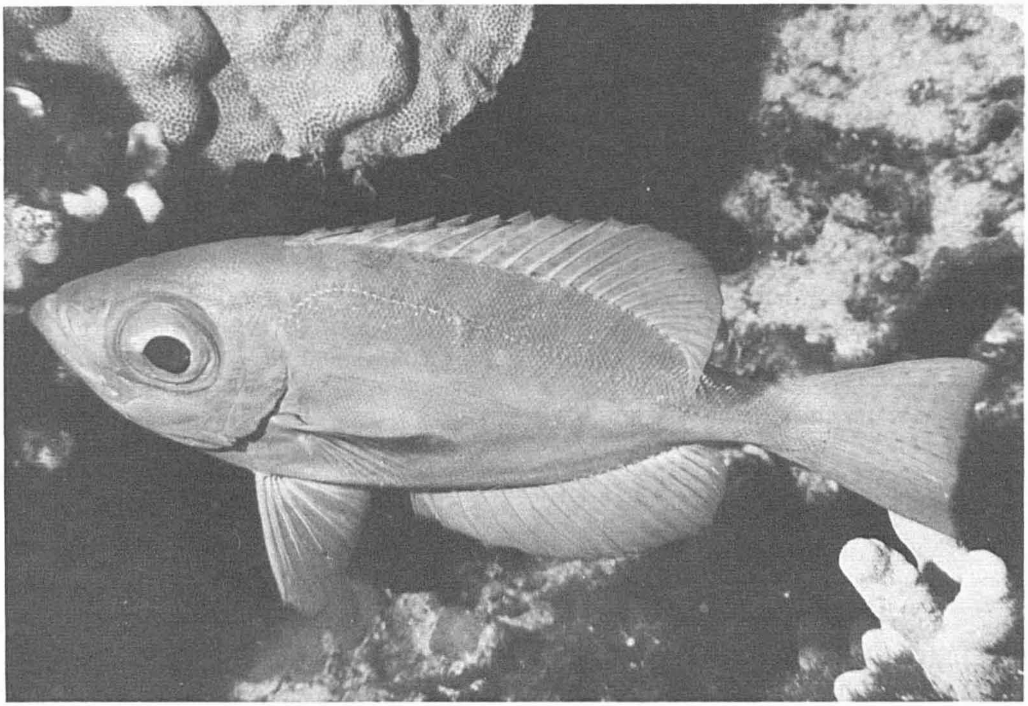

FIGURE 18.—*Priacanthus cruentatus*, a bigeye, showing the plain red coloration typical of this species when among the coral during the day.

cruentatus in the Marshall Islands is concerned. Although conceding the possibility of some nocturnal feeding, they believed that this species captures octopods, a major food there, in reef crevices and caves during the day. This conclusion was heavily influenced by finding food in the stomachs of this priacanthid during the day, but none in stomachs of the nocturnally active holocentrids. As noted above, I found a similar difference between *P. cruentatus* and holocentrids in Kona, but attribute this to the priacanthid retaining food in its stomach longer during digestion than do holocentrids.

Longley and Hildebrand (1941) noted that this circumtropical species feeds chiefly at night in Florida, a conclusion with which Starck and Davis (1966) concurred. In the West Indies, Randall (1967) was of the same opinion, but he also felt that the condition of prey in some specimens indicated diurnal feeding as well; Randall noted that *P. cruentatus* preys mostly on the larger animals in the plankton. Collette and Talbot (1972) concluded that in the Virgin Islands this is a crepuscular species that continues to feed in caves and under ledges during daytime.

Gosline (1965) reported that *P. cruentatus* in

TABLE 19.—Food of *Priacanthus cruentatus*.

Rank	Items	No. fish with this item (n = 21)	Mean percent of diet volume	Ranking index
1	Crab megalops	17	32.3	26.15
2	Cephalopods	8	20.4	7.77
3	Fish	6	11.2	3.20
4	Decapod shrimps	5	3.6	0.86
5	Adult crabs	2	7.6	0.72
6	Mysids	1	0.4	0.02
7	Stomatopods	1	0.1	0.01
Also, crustacean fragments		11	13.4	7.02
	Unidentified fragments	8	11.0	4.19

Hawaii migrates offshore at night. In Florida, however, Starck and Davis (1966) noted only that it is active at night in the same areas where it is sheltered in daylight; they illustrated this species with a mottled color pattern, which they believed to be its nocturnal coloration. The same mottled pattern occurs regularly at night in Kona when the fish is held in the beam of a diving light, and I believe it is a response to the light, rather than a nocturnal coloration—especially because the pattern is intensified upon moving the light progressively closer to the fish. In the absence of a diving light at night, this species is either plain red (as it usually is in daylight), or, more often with individuals in mid-water, overall pale-silver (occasionally this pale-silver coloration is displayed under cover during the day). The blotched pattern is the red and silver hues in combination.

CONCLUSION.—*Priacanthus cruentatus* is a nocturnal predator that feeds on free-swimming organisms, mostly crustaceans and cephalopods.

Family Apogonidae: cardinalfishes

Apogon erythrinus Snyder

After dark, this small solitary cardinalfish is numerous close to basalt reefs in water less than 6 m deep, usually in small sand and cobble pockets. The smaller ones are largely transparent, and transparency remains a characteristic of even the largest individuals, despite an increased pinkish hue (Figure 19). During the day *A. erythrinus* remains out of sight, secreted deep in reef crevices.

Of 14 individuals (36: 22-42 mm) examined, 4 that had been collected together from a deep crevice 4 h after sunrise were empty (rotenone was used to collect these 4, a departure from the standard collecting method necessary here because the species was never visible during the day). The other 10 specimens were speared from among those active in exposed locations on the reef at night (more than 4 h after sunset), and although 2 were empty, the other 8 contained prey in their stomachs.

All eight with material in their stomachs contained crustaceans exclusively. Xanthid crabs

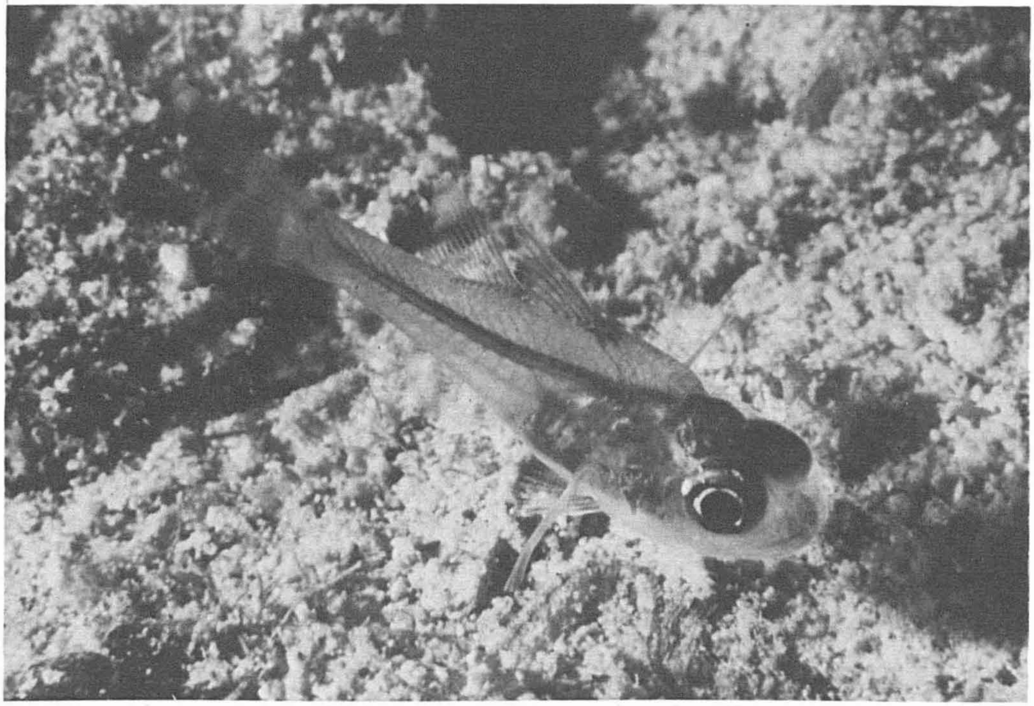

FIGURE 19.—*Apogon erythrinus*, a cardinalfish, showing the transparency typical of this species as it swims close to the reef at night.

were the major item, occurring in five individuals (mean percent of diet volume: 50; ranking index: 31.25). Most of these xanthids were in the megalops stage, except that their abdomens were reflected under their carapaces. The only other identifiable prey, occurring in three specimens, were gammaridean amphipods (mean percent of diet volume: 20; ranking index: 7.5). Four contained unidentified crustacean fragments (mean percent of diet volume: 30; ranking index: 15).

CONCLUSION.—*Apogon erythrinus* is a nocturnal predator that takes mostly benthic crustaceans.

Apogon menesemus Jenkins—*'upapalu*

This species and the very similar *A. snyderi* (below) are the largest and most abundant apogonids in Hawaii (Gosline and Brock, 1960), and they were the apogonids seen most often during the present study. During the day, *A. menesemus* hovers quietly in the deep shadows of reef crevices, but during late evening twilight emerges into the open. Throughout the night solitary individuals hover about 1 m above the coral. On several occasions after dark this cardinalfish struck at the silver barb on my otherwise dark spear: sometimes when this happened the spear was faintly illuminated by my partner's diving light, but other times moonlight provided the only illumination. At first morning light *A. menesemus* moves close to cover on the reef, and during morning twilight returns to its daytime shelter. When under cover during the day its coloration is relatively featureless, but when in the open at night distinctive fin markings appear (Figure 20a and b).

Fifty-nine specimens (114: 90-134 mm) were collected during day and night. Of the 14 that were speared from reef caves during late afternoon, only 2 had food in their stomachs—one contained an extensively digested piece of meat that probably was the remains of prey captured the previous night, whereas the other contained a relatively fresh xanthid crab that appeared to have been captured earlier that day. In comparison, 25 of 40 specimens collected at night, between 3 h after sunset and first morning light, had food in their stomachs—much of it fresh. Finally, of five specimens collected from caves during early morning, within 3 h after sunrise, four had food in their stomachs. Items in the 31 individuals containing identifiable material are listed in Table 20.

Two individuals that each contained just a single xanthid crab are the only ones that indicated exclusively benthic feeding; significantly, one of these was the lone individual, noted above, that appeared to have fed while under cover during the day. The other, collected in the open just 3 h after sunset, may also have taken its prey before leaving shelter in the evening. *A. menesemus* takes mostly free-swimming prey, presumably at its regular nocturnal station above the reef. Nevertheless, judging from the sand mixed with food in one individual collected at midnight, some prey are taken from the sea floor after dark.

CONCLUSION.—*Apogon menesemus* is a nocturnal predator that feeds mostly on free-swimming crustaceans.

Apogon snyderi Jordan and Evermann—*'upapalu*

This cardinalfish cooccurs with the very similar *A. menesemus,* above, but the two species remain at least partially segregated. During the day both species occupy the same caves, but *A. snyderi* is not so deep in the shadows and, in fact, frequently hovers at the entrances. Like *A. menesemus, A. snyderi* emerges into the open during evening twilight, but during the night stays closer to the sea floor; furthermore, whereas *A. menesemus* mostly remains over coral, *A. snyderi* tends to move over the sand patches within the reef and in the fringes of the more extensive sand areas adjacent to the reef. On several occasions at night, *A. snyderi* struck at the silver barb on my spear, just as described above for *A. menesemus. Apogon snyderi* does not have prominent nocturnal color features, as does *A. menesemus.* When over sand at night its body has a highly reflective bluish cast, also shown to a lesser extent by *A. menesemus,* but which is largely lost by both species soon after they move over coral or rocks.

Thirty specimens (96: 82-130 mm) were speared during day and night. All 3 that were taken from caves during the afternoon had empty stomachs, whereas of 24 collected in the open at night, between 2 h after sunset and first morning light, 22 had food in their stomachs. The remaining three were collected from caves during the 4 h after sunrise, and while two of these had food in their stomachs, the third was empty. Items in the 24 individuals containing identifiable material are listed in Table 21.

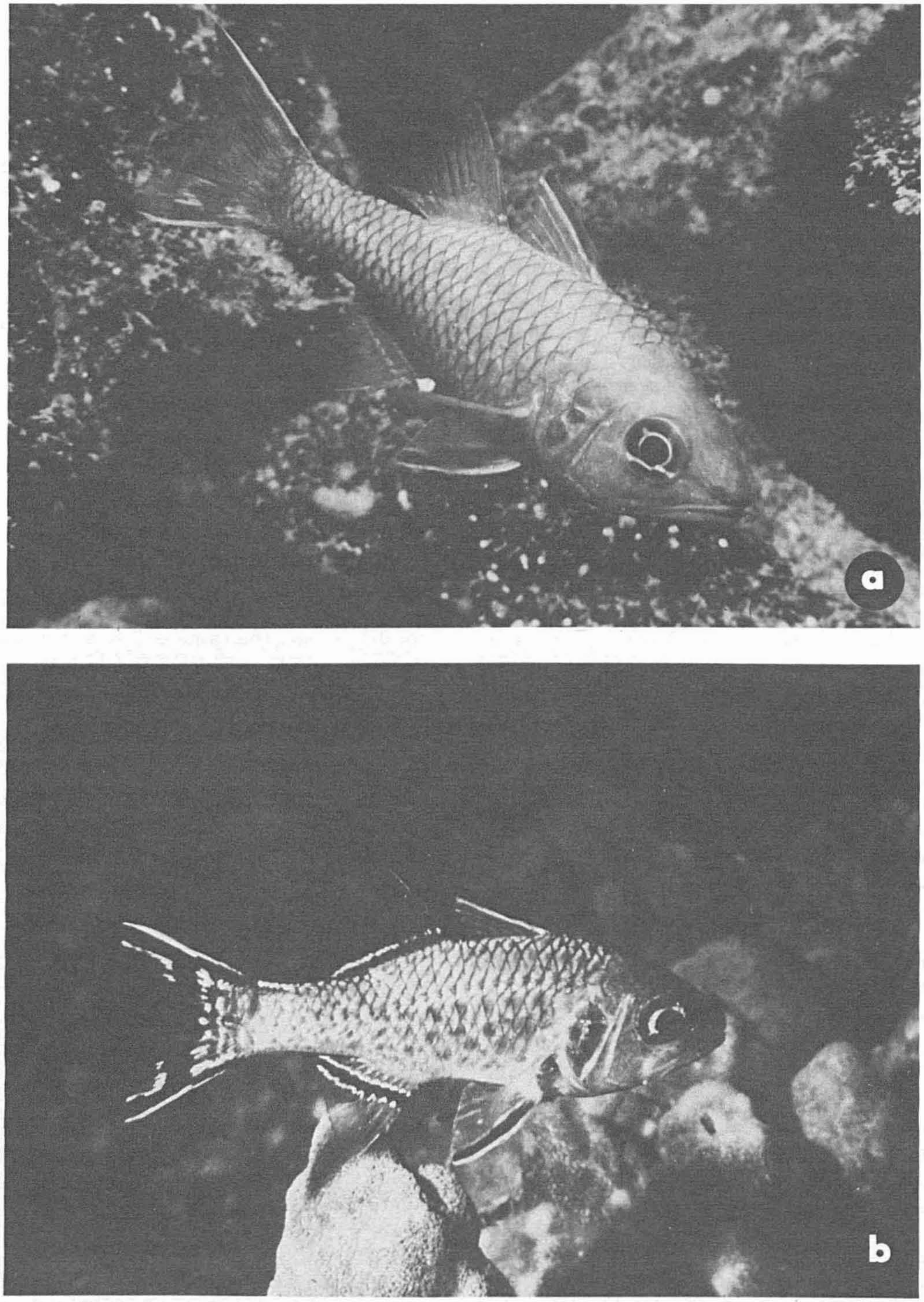

FIGURE 20.—*Apogon menesemus*, a cardinalfish: a, showing its diurnal coloration under a ledge during the day; b, showing its nocturnal coloration as it swims above the reef at night.

TABLE 20.—Food of *Apogon menesemus*.

Rank	Items	No. fish with this item (*n* = 31)	Mean percent of diet volume	Ranking index
1	Crab megalops	10	17.6	5.68
2	Decapod shrimps	11	15.7	5.57
3	Xanthid crabs	2	6.9	0.45
4	Mysids	3	2.9	0.28
5	Fish	1	2.0	0.07
6	Gammaridean amphipods	1	0.8	0.03
7	Isopods	1	0.2	<0.01
8	Copepods	2	0.1	<0.01
9	Gastropod larvae, echinospira	1	0.1	<0.01
Also,	crustacean fragments	20	40.0	25.81
	Unidentified fragments	6	13.7	2.65

TABLE 21.—Food of *Apogon snyderi*.

Rank	Items	No. fish with this item (*n* = 24)	Mean percent of diet volume	Ranking index
1	Decapod shrimps	12	34.3	17.15
2	Xanthid crabs	6	14.6	3.65
3	Crab megalops	4	7.5	1.25
4	Fish	2	5.6	0.47
5	Mysids	2	2.1	0.18
6	Hippid crabs	1	4.2	0.18
7	Polychaetes	1	2.9	0.12
8	Copepods	1	1.3	0.05
9	Gammaridean amphipods	1	1.3	0.05
10	Sipunculid introverts	1	0.2	<0.01
Also,	crustacean fragments	12	25.4	12.70
	Unidentified fragments	1	0.6	0.03

The diet of *A. snyderi*, compared with that of *A. menesemus*, includes a greater proportion of benthic organisms, especially forms from sandy bottom, like hippid crabs. Nevertheless, many of the prey of *A. snyderi* are free-swimming forms that may or may not have been in the water column when captured. The major item, decapod shrimps, were mostly in their planktonic larval stage.

CONCLUSION.—*Apogon snyderi* is a nocturnal predator that feeds on both free-swimming and benthic forms, mostly crustaceans.

General Remarks on Cardinalfishes

Cardinalfishes are widely recognized as being nocturnal. For example, Starck and Davis (1966) reported that all of the apogonids they studied in Florida Keys are nocturnal, and Randall (1967) came to the same conclusion for species in the West Indies; Randall provided food-habit data on two forms, *Apogon conklini* and *A. maculatus*, both of which prey primarily on plankton.

In the Gulf of California, *A. retrosella*, a relatively small nocturnal species (mostly <100 mm long), aggregates above the reef at night, preys on plankton, and its aggregations are more compact under moonlight than on dark nights (Hobson, 1965, 1968a). Although the relatively large *A. menesemus* is solitary when feeding on free-swimming prey above Kona reefs, it remains within about 1 m of the reef, never far from cover.

Another apogonid occasionally seen in Kona, *A. maculiferus*, has behavior more like that of *A. retrosella* in the Gulf of California. *Apogon maculiferus* is abundant on some Hawaiian reefs and attains a length of about 150 mm (Gosline and Brock, 1960). It was not abundant during this study, however, and all those seen apparently were juveniles that ranged between about 20 and 60 mm long. On nights of bright moonlight these small individuals were in aggregations 2 to 3 m above the reef; however, on dark nights they ranged even higher in the water column, their aggregations were more loosely formed, and many of them were solitary. Significantly, limited observations indicate that juveniles of both *A. menesemus* and *A. snyderi* (<50 mm long) behave more like these small individuals of *A. maculiferus* than they do like the adults of their own species, so this behavior may be characteristic only of the smaller representatives of all three species.

Finally, a fourth apogonid, *Pseudamiops gracilicauda,* is relatively numerous in Kona, but does not seem to grow longer than about 30 mm. Being such a small species, *P. gracilicauda* generally went unnoticed by me and, in fact, was seen only on dark nights when solitary individuals hovered 1 to 2 m above the reef.

Suyehiro (1942), Hiatt and Strasburg (1960), and Hobson (1965), all reported that certain apogonids cease to feed sometime during reproductive activity. Perhaps this phenomenon accounts for the relatively high incidence of empty stomachs at night in *A. menesemus* from Kona (15 of 40), especially considering that species of other nocturnal groups with similar diets, like the various holocentrids (see above), are almost always full of food at night.

E. H. Chave, University of Hawaii, is currently working on the ecology of Hawaiian apogonids.

Family Carangidae: jacks

The jacks are prominent fishes on Hawaiian reefs, but although many species were seen occasionally during this study, only one, presented below, was observed regularly.

Caranx melampygus Cuvier—blue ulua, *'omilu*

This jack (Figure 21), attains a length of about 1 m in Hawaii (Gosline and Brock, 1960), but most of those present in Kona during this study were less than half this size. During the day it usually is solitary, or in groups of several individuals. Typically, it swims actively about 1 m above the reef in a manner that suggests it is patrolling over a relatively large area. Frequently several of these jacks accompany the large piscivorous goatfish, *Parupeneus chryserydros* (see account for this species, below), probably to capture prey that are driven out of hiding as the goatfish probes the substratum. This jack swims over the reef throughout the day, but occurs there most frequently during early morning and late afternoon

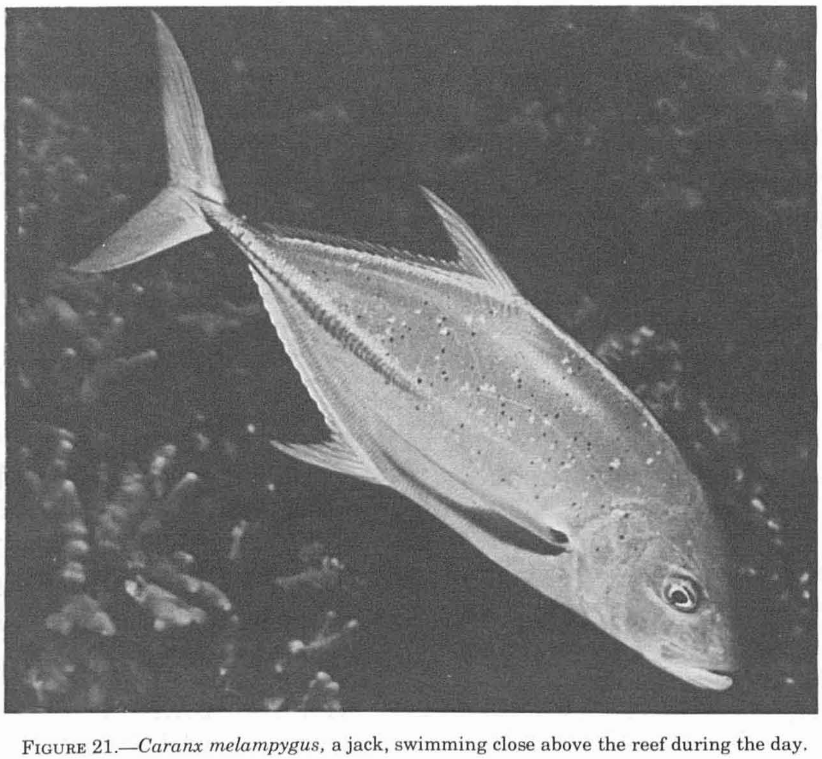

FIGURE 21.—*Caranx melampygus,* a jack, swimming close above the reef during the day.

or evening. It was only occasionally seen at night, perhaps because it avoided our diving lights after dark.

Six specimens (337: 245-570 mm) were collected at various times of the day. The only one (248 mm) that contained relatively fresh prey (three larval fishes, about 10 mm long, and a number of mysids) was collected 3 h after sunrise. A second individual (315 mm), taken shortly after noon, contained in its stomach, an unidentified fish (about 80 mm) and a shrimp, both moderately digested. Three other individuals (245-330 mm) were collected late in the afternoon, and their stomachs contained well-digested fragments—in at least one, the fragments of a fish. The last specimen (570 mm) behaved as if sick when speared early in the afternoon, and its gut was empty. Hiatt and Strasburg (1960) found only fishes in the two specimens of this species that they examined from the Marshall Islands, as did Randall (1955) in the four specimens that he examined from the Gilbert Islands.

CONCLUSION.—*Caranx melampygus* preys on free-swimming fishes and crustaceans, probably most often early and late in the day.

General Remarks on Jacks

Jacks are major predators on many widespread tropical reefs (e.g. Marshall Islands: Hiatt and Strasburg, 1960; Gulf of California: Hobson, 1965, 1968a; Florida Keys: Starck and Davis, 1966; West Indies: Randall, 1967). The larger piscivorous jacks, like *Caranx hippos caninus,* are primarily crepuscular in the Gulf of California (Hobson, 1965, 1968a) and in the Florida Keys (Starck and Davis, 1966).

Family Lutjanidae: snappers

As is true of the sea basses, Hawaiian inshore reefs lack native species of snappers, a family whose members are prominent on shallowwater reefs elsewhere in the tropical Pacific (Gosline and Brock, 1960; Randall and Brock, 1960). Only one species of this family was seen regularly on the Kona study reefs during this project.

Aphareus furcatus (Lacépède)—*gurutsu*

During the day this solitary predator swims slowly, 1 to 2 m above the reef, with never more than a few individuals in any one place. It was not seen at night during this study, perhaps because it avoided our lights. Only once did I see one attack prey: 5 min before sunrise this individual suddenly broke from its patrolling attitude 2 m above the reef and dived among a cluster of small fishes, mostly pomacentrids, that were in the process of emerging from their nocturnal shelters (see Hobson, 1972). The success of the strike was undetermined, but at the instant of attack all small fishes within a radius of about 15 m shot under cover.

Three specimens (253: 244-262 mm) were speared for study. One taken during midafternoon contained a *Plagiotremus goslinei,* a blenny that swims above the reef only in daylight (see account for this species, below); because this prey was relatively fresh, it almost certainly was captured earlier that day. Another *A. furcatus* collected during midafternoon contained moderately digested crab megalops and gammaridean amphipods; although megalops are more typically food of nocturnal predators, the relatively good condition of these small prey indicated they had been collected earlier that day. The third *A. furcatus,* speared during midmorning, was empty. Randall (1955) examined four specimens of this snapper in the Gilbert Islands, and the two with prey contained only fishes.

CONCLUSION.—*Aphareus furcatus* preys on free-swimming fishes and crustaceans during daylight. Its habits at night remain unknown.

General Remarks on Snappers

If *Aphareus furcatus* hunts prey mostly in daylight, it would seem an atypical lutjanid. Generally lutjanids are described as nocturnal fishes (e.g. Hobson, 1965, 1968a: Gulf of California; Starck and Davis, 1966: Florida Keys; Randall, 1967: West Indies).

The efforts that successfully introduced the sea bass *Cephalopholis argus* into Hawaiian waters (see account for that species, above) also included the snapper *Lutjanus vaigiensis*, which now too is well established in Kona. Although *L. vaigiensis* was not numerous in the study area during this work, one school was seen consistently during daylight on irregular visits to a location in Kealakekua Bay, and solitary individuals occasionally were encountered on the reef after dark. Thus, the habits of this fish appear to be similar to those of certain other species of *Lutjanus* elsewhere; that is, it forms relatively inactive schools during the day, then disperses at nightfall and hunts prey after dark. This pattern is known for *L. argentiventris* in the Gulf of California (Hobson, 1965, 1968a), and for *L. griseus* and others in the tropical Atlantic (Starck and Davis, 1966). Randall and Brock (1960) reported predominantly nocturnal feeding by *L. vaigiensis* in Tahiti and often found this snapper in large aggregations during the day.

Family Sparidae: porgies

Monotaxis grandoculis (Forskål)—*mu*

In Kona, this porgy is most numerous near basalt reefs that are exposed to the prevailing sea. During the day it typically hovers 2 to 3 m above the reef, either in loose aggregations of 4 to 10 fish, or as solitary individuals. When congregated, most individuals display broad bars on their sides dorsally; although this same color pattern occurs frequently in solitary fish, these often are overall pale grey. Those I observed in Kona during the day always seemed inactive; however, Hiatt and Strasburg (1960) reported individuals in the Marshall Islands excavating prey buried in the sand, presumably during daylight. In Kona, *M. grandoculis* disperses from its daytime assemblages at nightfall and forages as solitary individuals throughout the night. After dark, many move into shallower water than is frequented by the species in daylight. The nocturnally active individuals sometimes show the barred color pattern but are most often plain grey (Figure 22).

Of five specimens (312: 244-397 mm) speared during day and night, one that was taken from an aggregation late in the afternoon was empty, whereas all four that were speared at night (later than 4 h after sunset and before first morning light) were full of food, as listed in Table 22.

Although the gut contents were relatively fresh, the shelled items had been reduced to crushed fragments—presumably by the large molarform jaw teeth of this fish.

Prey taken by this porgy in Kona are much the same as taken by the same species in the Marshall Islands (Hiatt and Strasburg, 1960) and Gilbert Islands (Randall, 1955).

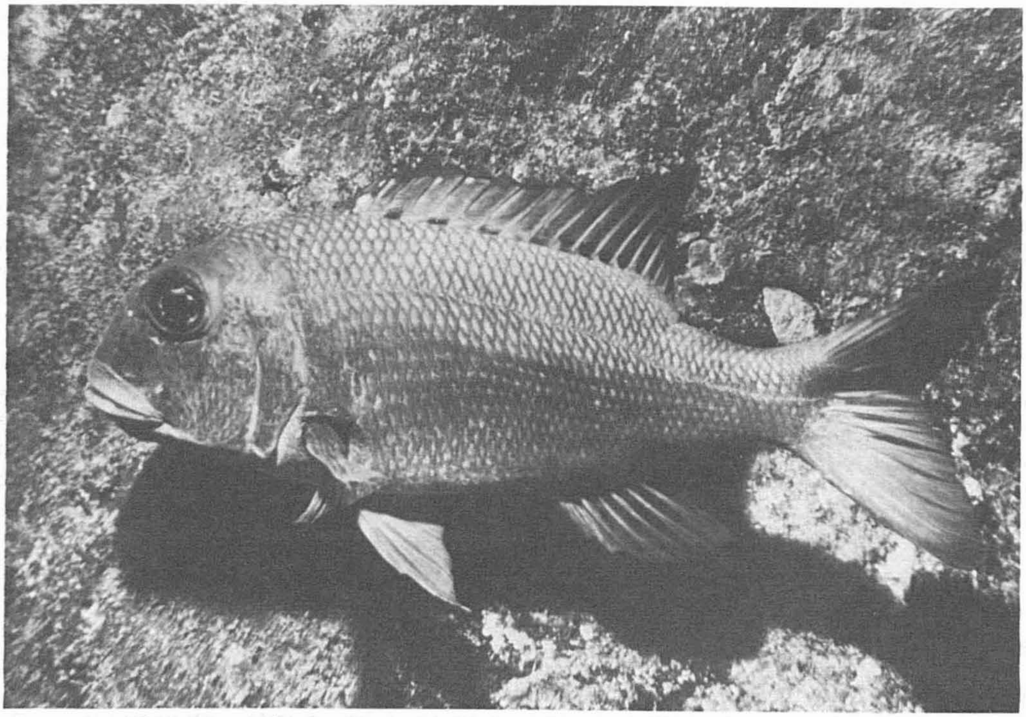

FIGURE 22.—*Monotaxis grandoculis*, a porgy, showing its plain grey coloration as it swims close to the reef at night.

TABLE 22.—Food of *Monotaxis grandoculis*.

Rank	Items	No. fish with this item (n = 4)	Mean percent of diet volume	Ranking index
1	Prosobranch gastropods	4	21.3	21.30
2	Ophiuroids	3	27.1	20.33
3	Echinoids	3	21.3	15.98
4	Opisthobranch gastropods	2	11.8	5.90
5	Pagurid crabs	2	3.8	1.90
6	Polychaetes	1	3.8	0.95
7	Brachyuran crabs	1	2.5	0.63
8	Tunicates	1	2.5	0.63
9	Egg masses (unident.)	1	1.3	0.33
10	Holothurians	1	0.8	0.20
Also, crustacean fragments		1	2.5	0.63
	Algal fragments	1	1.3	0.33

CONCLUSION.—*Monotaxis grandoculis* is a nocturnal predator that feeds on benthic invertebrates, most of them heavily shelled.

General Remarks on Porgies

Porgies are closely related to the snappers, most of which seem to be mainly nocturnal. Nevertheless, porgies have been reported as diurnal, for example species of *Archosargus, Diplodus,* and *Calamus* in the tropical Atlantic (Randall, 1967). Still, Starck and Davis (1966) recognized that species of *Calamus* in Florida may also feed at night. Diurnal habits in porgies may be attributed to their habit of excavating buried prey, which makes available to them certain nocturnal forms that have concealed themselves in the sand during daylight.

Family Mullidae: goatfishes

Mulloidichthys auriflamma **(Forskål)**—*weke'ula*

During the day this goatfish, which is relatively numerous in Kona, hovers in schools above the reef, or (occasionally) under ledges. Individuals recognized by distinguishing marks occurred in schools at the same locations each day, even though these schools disperse at nightfall. After dark, solitary or in small groups, this species probes with its barbels in the sandy areas adjacent to the reef, and in some of the larger sand patches on the reef. When illuminated by a diving light at night, it often shows a deep reddish hue that seems to be a reaction to the light, not a nocturnal coloration.

Of the 22 individuals (170: 110-235 mm) speared during day and night, all 12 collected from schools during the afternoon were either empty or contained only well-digested fragments, whereas of the 10 collected at night (later than 3 h after sunset and before sunrise), all contained food, including fresh material, as listed in Table 23.

Thus my observations concur with those of Gosline and Brock (1960), who reported that *M. auriflamma* does not feed during the day, but instead schools quietly in certain established areas and then disperses to forage at night.

Although crab megalops, a primary food, are a major element of the plankton, most of those captured by this goatfish probably were taken from the sand.

CONCLUSION.—*Mulloidichtys auriflamma* is a nocturnal predator that feeds on invertebrates that live in the sand.

Mulloidichthys samoensis **(Günther)**—*weke 'a'a*

This goatfish, widespread in Kona, often hovers in quiet schools over the reef during the day, where it looks much like *M. auriflamma,* above. Although *M. samoensis* is a more elongated fish, the two must be seen together before this distinction is obvious. Sometimes the two species school together, but more often they are segregated. Frequently instead of schooling during the day, *M. samoensis,* but not *M. auriflamma,* moves as solitary individuals or in small groups over sand patches on the reef, and there actively probes with its barbels in the sediment. These active individuals have a color pattern distinct from that of relatively inactive conspecifics in schools. When schooling, *M. samoensis* has a prominent yellow stripe running from eye to tail along its upper sides, as does *M. auriflamma* in similar schools (Figure 23a); however, this stripe is not present (or at least is indistinct) when *M. samoensis* actively

TABLE 23.—Food of *Mulloidichthys auriflamma.*

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Crab megalops	6	11.5	6.90
2	Ophiuroids	4	14.5	5.80
3	Polychaetes	4	11.7	4.68
4	Xanthid crabs	6	7.0	4.20
5	Prosobranch gastropods	7	4.7	3.29
6	Echinoids	6	4.7	2.82
7	Gammaridean amphipods	5	1.3	0.65
8	Isopods	4	1.1	0.44
9	Ostracods	2	0.6	0.12
10	Sipunculid introverts	1	0.5	0.05
11	Pelycypods	1	0.5	0.05
12	Penaeid shrimps	1	0.5	0.05
13	Portunid crabs	1	0.2	0.02
Also,	crustacean fragments	4	8.5	3.40
	Unidentified fragments	2	12.0	2.40
	Algal fragments	1	1.0	0.10
	Sand, foraminiferans, and debris	7	19.7	13.79

forages on the reef, it being replaced by a black spot on the fish's side, below the dorsal fin (Figure 23b).

At nightfall, those individuals of *M. samoensis* that had been hovering over the reef in quiet schools disperse. After dark the species not only continues the activity that some members had pursued over reef sand patches in daylight, but also extends this activity in some areas farther out over the more extensive sandy areas adjacent to the reef. When illuminated by a light at night, *M. samoensis* frequently displays a color pattern of red blotches that seems to be a response to the light, rather than being a nocturnal color feature. Its coloration at night is as described above for foraging individuals in daylight. After a night of foraging, many individuals regroup in the morning, forming schools that reappear in the same locations each day.

Twenty-three specimens (182: 136-283 mm) were speared during day and night. Of four taken during afternoons as they probed sand patches on the reef, swimming in small groups or as individuals, two had full stomachs that included relatively fresh prey; the other two contained only debris. Of three individuals taken while they hovered in schools over the reef during the afternoon, one had an empty stomach, and the other two contained only well-digested fragments. Contrasting data were provided by 16 specimens speared as they actively probed in sand patches on the reef during the 2 h immediately before first morning light, and during the first 30 min of morning twilight. Of these, 11 had full stomachs, including much fresh material, 2 contained only bits of debris, and only 3 were empty. Items in the 13 individuals containing identifiable prey are listed in Table 24.

No obvious difference was noted between prey taken during day and night although pertinent data are too few for meaningful comparison. Hiatt and Strasburg (1960) reported that fishes are an important food of this goatfish in the Marshall Islands. Otherwise, they listed foods similar to those taken by the species in Kona.

CONCLUSION.—*Mulloidichthys samoensis* preys on sand-dwelling invertebrates, mostly at night, but to some extent during the day.

Parupeneus multifasciatus (Quoy and Gaimard) —*moano*

This is the most numerous and widespread goatfish on Kona reefs. During the day solitary individuals and groups of two or three actively probe with their barbels among cracks and crevices on the reef, especially in pockets where sand and debris have accumulated. This species is active through twilight, but generally appears inactive after dark, when solitary individuals rest in exposed locations on the reef. To some extent these immobile nocturnal attitudes may be influenced by the diving light, but not to the extent indicated for *P. bifasciatus,* below; certainly the blotched red color pattern often displayed at this time is a reaction to the light. On nights of bright moonlight, at least some individuals of *P. multifasciatus* swim over the reef.

Thirty specimens (162: 125-212 mm) were speared during day and night. Of 14 collected during the hour immediately before first morning

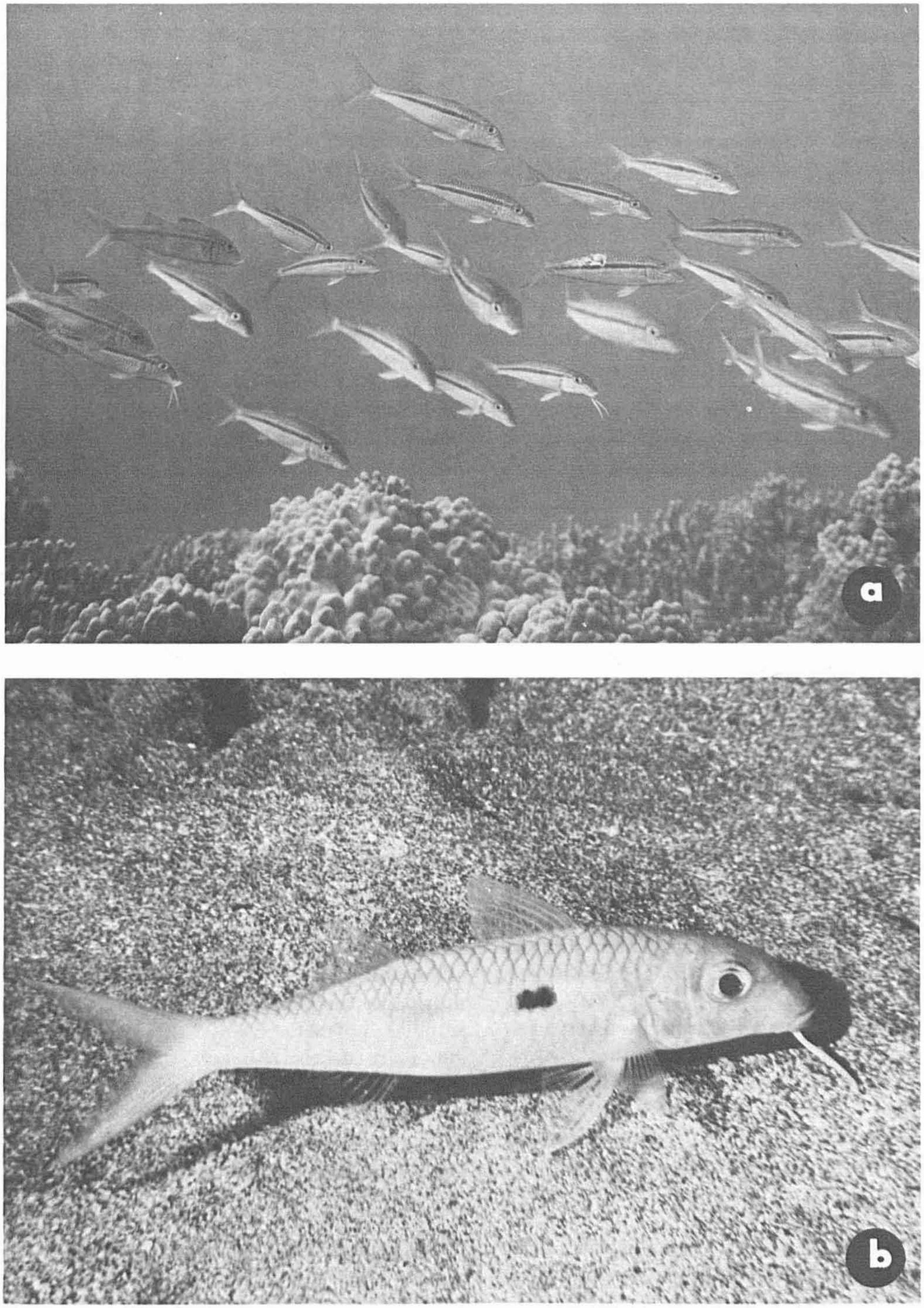

FIGURE 23.—*Mulloidichthys samoensis*, a goatfish: a, with the coloration shown when schooling during the day; b, with the coloration shown when feeding as a solitary individual or in small groups during both day and night.

TABLE 24.—Food of *Mulloidichthys samoensis*.

Rank	Items	No. fish with this item (n = 13)	Mean percent of diet volume	Ranking index
1	Pelecypods	7	10.0	5.39
2	Polychaetes	5	11.2	4.31
3	Gammaridean amphipods	7	6.7	3.61
4	Prosobranch gastropods	6	3.1	1.43
5	Sipunculid introverts	3	5.4	1.25
6	Crab megalops	3	3.1	0.72
7	Isopods	3	2.8	0.65
8	Hippid crabs	1	0.8	0.06
9	Echinoids	1	0.8	0.06
10	Xanthid crabs	1	0.4	0.03
11	Shrimps	1	0.2	0.02
Also, crustacean fragments		5	7.1	2.73
	Unidentified fragments	3	11.6	2.68
	Sand and debris, including foraminiferans	13	36.8	36.80

TABLE 25.—Food of *Parupeneus multifasciatus*.

Rank	Items	No. fish with this item (n = 18)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	14	30.6	23.80
2	Caridean shrimps	8	15.4	6.84
3	Crab megalops	5	8.6	2.39
4	Prosobranch gastropods	3	1.8	0.30
5	Tanaids	2	0.6	0.07
6	Gammaridean amphipods	2	0.4	0.04
7	Stenopid shrimps	1	0.6	0.03
8	Ostracod	1	0.1	0.01
Also, crustacean fragments		14	29.4	22.87
	Unidentified fragments	1	0.8	0.04
	Debris	7	11.7	4.55

light, and through morning twilight, the stomachs of 12 were empty, but the other 2 contained prey in varying stages of digestion that appeared to have been taken during the night (one night with, the other without, moonlight). In contrast, all 16 specimens speared on the reef during the afternoon contained prey in varying stages of digestion, including fresh material. Items in the 18 containing identifiable material are listed in Table 25.

No obvious difference in diet was noted between the 2 individuals of *P. multifasciatus* that apparently had captured their prey at night and the 14 that had been feeding in daylight; however, the data are too few for a meaningful comparison.

Juveniles of *P. multifasciatus* sometimes aggregate up in the water column where plankton abounds, apparently feeding on these organisms, but none of these individuals were collected. The relatively high incidence of crab megalops in the diet of this and other bottom-feeding goatfishes may reflect some predation on free-swimming forms in the water column, but I believe that at least most of these megalops were taken off the sea floor.

CONCLUSION.—*Parupeneus multifasciatus* is primarily a diurnal predator that takes benthic crustaceans.

Parupeneus bifasciatus (Lacépède)—*munu*

This goatfish, which exceeds 300 mm when fully grown, is especially numerous among basalt boulders—frequently solitary, but also in groups of two or three. In daylight, its actions appear much like those of *P. multifasciatus,* which it resembles, but after dark, when *P. multifasciatus* generally rests on the reefs, *P. bifasciatus* usually moves about. Nevertheless, when *P. bifasciatus* is illuminated by the diving light it often settles immobile onto the reef—an action that complicates assessing its nocturnal activity. Like *P. multifasciatus, P. bifasciatus* often displays at this time a blotched red-colored pattern that seems to be a response to the diving light.

Twenty-seven specimens (229: 164-300 mm) were speared during day and night. Of 11 taken as they swam close to the reef during early morning (between first light and 3 h after sunrise), the stomachs of 2 were empty, but the other 9 contained prey in varying stages of digestion, some of it fresh. Similarly, of 12 individuals collected as they swam close to the reef during afternoons, only 1 had an empty stomach, whereas the other 11 contained prey in varying stages of digestion, some of it fresh. Finally, of four specimens speared at night (between 4 and 5 h after sunset) the stomach of one was empty, but the other three contained prey in varying stages of digestion, some of it fresh.

These data indicate that *P. bifasciatus* feeds regularly during both day and night. Recognizing that the contrasting conditions under which it hunts may be reflected in the composition of its diet, I attempted to distinguish prey that had been taken by day from that taken at night. Although, undoubtedly there is overlap, generally specimens collected during the night and early morning should contain mostly prey captured after dark, whereas specimens taken during afternoons should contain mostly prey taken in daylight.

Thus, the 12 *P. bifasciatus* taken during the night and early morning with identifiable material in their stomachs presumably represent mostly nocturnal feeding. Items in these individuals are listed in Table 26. Using the same rationale, diurnal feeding presumably is reflected in the 11 *P. bifasciatus* collected with identifiable material in their stomachs during afternoons. Items in these individuals are listed in Table 26.

Although xanthid crabs are the major prey day and night, they assume greater relative importance in daylight, as do caridean shrimps. Xanthids and carideans are largely under cover in daylight, where they may be especially vulnerable to this predator's probing actions. Crab megalops become increasingly important to this goatfish at night, but the circumstances surrounding their capture remain uncertain; megalops are the major prey of many nocturnal planktivores, such as *Myripristis* spp. (see accounts for these species, above), but are also taken day and night by predators like certain goatfishes that probe the sea floor.

Based on the above data, fishes seem to be more available as prey to *P. bifasciatus* at night. Prey fishes that could be identified were blennies and pomacentrids, which are diurnal fishes that take cover after dark. Apparently *P. bifasciatus* is adapted to capture these resting diurnal fishes at night, but is less effective in capturing the fishes that are under cover during daylight.

CONCLUSION.—*Parupeneus bifasciatus* hunts prey on the reef during both day and night. Adult crabs and shrimps are more important as prey during the day than at night, whereas the reverse is true of fishes and crab megalops.

Parupeneus porphyreus (Jenkins)—*kumu*

This is the most numerous goatfish on some Hawaiian reefs (Gosline and Brock, 1960), but

TABLE 26.—Food of *Parupeneus bifasciatus*.

Nighttime Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	10	29.0	24.17
2	Fish	6	17.0	8.50
3	Crab megalops	5	19.4	8.08
4	Caridean shrimps	7	8.0	4.67
5	Octopods	2	3.9	0.65
6	Oxyrhynchid crabs	2	1.7	0.28
7	Prosobranch gastropods	2	0.6	0.10
8	Polychaetes	1	0.4	0.03
9	Gammaridean amphipods	1	0.3	0.03
Also, crustacean fragments		7	15.5	9.04
	Debris	2	4.2	0.70

Daytime Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	9	43.3	35.43
2	Caridean shrimps	9	15.5	12.68
3	Crab megalops	3	3.5	0.95
4	Octopods	1	7.1	0.65
5	Grapsid crabs	1	3.9	0.35
6	Oxyrhynchid crabs	1	1.1	0.10
7	Fish	1	0.7	0.06
8	Gammaridean amphipods	2	0.2	0.04
Also, crustacean fragments		8	24.7	17.96

there are relatively few in the Kona study area. During the day this species stays close to cover, where it usually occurs in small groups under ledges. At night solitary individuals are active close among rocks and coral on the reef.

Of the 11 specimens (157: 137-173 mm) collected, 6 speared close to reef crevices late in the afternoon either were empty or contained only a few well-digested fragments, whereas all 5 collected in the same places within 1 h after sunrise had stomachs full of prey, some of it fresh, as listed in Table 27.

CONCLUSION.—*Parupeneus porphyreus* is a nocturnal predator that feeds mostly on benthic crustaceans.

Parupeneus chryserydros* (Lacépède)—*moano kea

The scientific name of this goatfish remains uncertain. I follow Gosline and Brock (1960) in recognizing the nominal *P. chryserydros*, even though some authors (e.g. Lachner, 1960) refer this form to *P. cyclostomus* (Lacépède). Growing to about 600 mm long (Gosline and Brock, 1960), *P. chryserydros* is the largest of the goatfishes occurring regularly on Kona reefs.

During the day, solitary individuals or groups of two to five move over the reef, where their exceptionally long barbels work through the covering on rocky substrata. More often than not, groups of *P. chryserydros* are accompanied by a single jack, *Caranx melampygus,* which follows close behind them. For 1 mo I recorded all sightings of *P. chryserydros* that swam in groups of two or more, and of 24 such groups, 16 were accompanied by a jack. Usually solitary individuals of this goatfish are not thus accompanied, but this too was seen four times during the month. Clearly, it is the jack that maintains the association, probably as a tactic to capture prey driven from cover as the foraging goatfish disturb the substratum. Apparently the jack finds this advantage only with *P. chryserydros,* as it was not seen similarly following other species. Titcomb and Pukui (1952) listed many ancient Hawaiian fish names which they were unable to associate with species recognized today. One of these, *moano ukali ulua,* translates as "moano with ulua following," and probably refers to *P. chryserydros.* Whereas the adults of *P. chryserydros* are followed by the jack, the juveniles of this goatfish frequently swim close beneath various labrids, especially *Thalassoma duperrey,* and here it is the goatfish that maintains the associations, though to what advantage I do not know.

Of the 20 specimens (261: 123-363 mm) collected, all 3 that were speared as they rested on the reef at night (between 4 h after sunset and first morning light) had empty guts, whereas 15 of 17 taken as they swam close to the reef at various times of the day (between midmorning and late afternoon) had prey in their stomachs, and only the other 2 were empty.

Fish were the major item, occurring in 13 of the 15 individuals that contained food (mean percent of diet volume: 83.1; ranking index: 72.02). Other food items were: xanthid crabs in two individuals (mean percent of diet volume: 8.3; ranking index: 1.11), caridean shrimps in one (mean percent of diet volume: 1.3; ranking index: 0.09), and unidentified fragments in two (mean percent of diet volume: 7.3; ranking index: 0.97).

The fishes in the diet ranged between 25 and 102 mm long, and included the following species: *Abudefduf imparipennis* (1), *Cirrhitops fasciatus* (2), *Istiblennius gibbifrons* (1), *Plagiotremus goslinei* (1), *Cirripectus* sp. (4), and a labrid (1). All of these are diurnal fishes that swim close to the reef in daylight, but take cover when a predator approaches. Judging by how *P. chryserydros* feeds,

TABLE 27.—Food of *Parupeneus porphyreus.*

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	5	65.2	65.20
2	Hippid crabs	1	10.0	2.00
3	Caridean shrimps	1	2.0	0.40
4	Prosobranch gastropods	1	0.2	0.04
5	Chitons	1	0.2	0.04
6	Gammaridean amphipods	1	0.2	0.04
Also, crustacean fragments		3	21.2	12.72
	Debris	1	1.0	0.20

small fishes that have taken shelter on its approach probably are detected and even driven out from under cover by the exceptionally long barbels of this goatfish. If the probing barbels do in fact drive small fishes from their hiding places, this would account for the behavior of the jacks that follow them, described above. These same prey fishes also shelter themselves at night when they are inactive, so one might ask why this goatfish does not hunt for them at that time too. As reported above, *P. bifasciatus* preys on some of these same fishes (pomacentrids and blennies) when they are inactive under shelter at night. But capturing a relatively inert diurnal fish that is resting under cover after dark probably presents different problems for a predator than capturing an alert fish that has taken refuge from some specific threat in daylight. It appears that *P. bifasciatus* is adapted to taking these fishes when they rest under cover at night, whereas *P. chryserydros* is adapted to take them when they seek shelter in daylight. After dark, *P. chryserydros* is inactive, resting under reef cover (Figure 24).

Parupeneus cyclostomus in the Marshall Islands, which is closely related to *P. chryserydros*, if not conspecific, was reported by Hiatt and Strasburg (1960), on the basis of 16 specimens, to be an "active feeder on small benthonic fishes," but may prey more heavily on crustaceans than does the Hawaiian form.

CONCLUSION.—*Parupeneus chryserydros* is a diurnal predator that feeds mostly on small fishes.

General Remarks on Goatfishes

Despite their superficial similarity, the various goatfishes behave distinctively. Some, such as *Mulloidichthys auriflamma* and *Parupeneus porphyreus*, are primarily nocturnal; others, including *P. chryserydros* and *P. multifasciatus*, are mostly diurnal; and still others, like *P. bifasciatus* and *M. samoensis*, regularly hunt prey during both day and night. One might suppose that fishes which probe the sea floor for food would be indifferent to changes associated with day and night, but obviously this is not so. Whether a given species of goatfish is primarily diurnal or nocturnal probably relates to the differential day-night habits of its specific prey. That some goatfishes are

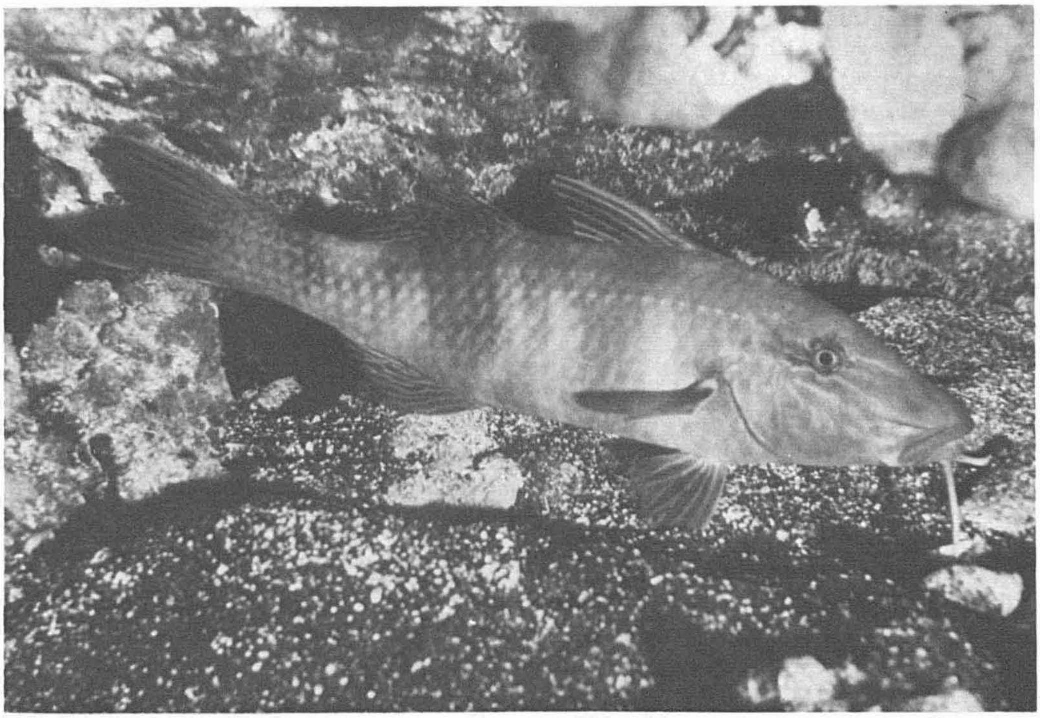

FIGURE 24.—*Parupeneus chryserydros*, a goatfish, resting under a ledge at night, with its exceptionally long chin barbels spread out before it.

nocturnal, whereas other are diurnal, is also recognized from other seas. In Florida, Starck and Davis (1966) suspected that *Mulloidichthys martinicus* feeds at night, whereas they recognized diurnal feeding habits in *Pseudupeneus maculatus*. Longley and Hildebrand (1941), as well as Collette and Talbot (1972), also regarded *M. martinicus* as nocturnal and *P. maculatus* as diurnal. Randall (1967) reported that *M. martinicus* feeds by day as well as night, and described a diet much like that of the two species of *Mulloidichthys* from Kona.

Family Kyphosidae: sea chubs

Kyphosus cinerascens* Forskål—*nenue

In Kona, *K. cinerascens* is most numerous where a basalt reef face confronts the prevailing swell in water deeper than about 8 m. Often over 500 mm long, this fish is active throughout the day—usually in groups of up to 10 or more individuals, and often swimming high in the water column. At night, solitary individuals swimming above the sea floor are often encountered in the same areas.

All three specimens (205: 166-250 mm) collected for study had guts full of a wide variety of benthic algae exclusively. Although two of these fish were taken during midday, the other was taken at night, within 1 h before first morning light. No sedimentary material was mixed in these gut contents, indicating that the algae had been bitten, not scraped, off the rocks, or else had been taken as fragments drifting in mid-water. Hiatt and Strasburg (1960) found the same gut contents in specimens from the Marshall Islands.

CONCLUSION.—*Kyphosus cinerascens* feeds during the day, cropping algae from rocks or taking them as drifting algal fragments. Its nocturnal habits remain uncertain.

General Remarks on Sea Chubs

Sea chubs generally are described as diurnal herbivores (e.g. Longley and Hildebrand, 1941; Starck and Davis, 1966; Randall, 1967). Smith (1907) reported crabs and bivalved mollusks among algae in the diet of *Kyphosus sectatrix* in the Atlantic Ocean, but these items probably were taken incidentally with the algae. Randall (1967) found only algae and a bit of sea grass in *K. sectatrix* from the West Indies. Starck and Davis (1966) reported that *K. incisor* rests in sheltered locations on Floridian reefs at night after having fed on drifting sargassum at the water's surface during the day. In the East Indies, however, William N. McFarland, Cornell University (pers. commun.) observed kyphosids active at night.

Family Chaetodontidae: angelfishes and butterflyfishes

The chaetodontids comprise two distinct groups: the angelfishes, subfamily Pomacanthinae; and the butterflyfishes, subfamily Chaetodontinae. Of the species treated below, the first two are angelfishes, the remainder are butterflyfishes.

***Holacanthus arcuatus* Gray—angelfish**

This angelfish is sparsely distributed on Kona reefs, but being relatively large and distinctive is readily noticed where it occurs. Usually solitary or paired, it swims close among rock ledges and boulders at depths below about 8 m. During the day it picks material from the surface of rocks, but was not seen active at night.

Six specimens (136: 123-150 mm) were speared during afternoons, and all had full stomachs. They had fed almost exclusively on sponges (mean percent of diet volume and ranking index: 98.3). The only other items—algae and hydroids—probably were taken incidentally with the sponges.

CONCLUSION.—*Holacanthus arcuatus* is a diurnal species that feeds on sponges.

***Centropyge potteri* (Jordan and Metz)—potter's angelfish**

An abundant species in coral-rich surroundings, this small angelfish behaves more like some of the damselfishes than it does other members of its family. A given individual limits its movements to restricted, well-defined locations close among fingerlike growths of the coral *Porites compressus*. During the day it swims about, picking at material growing over dead coral. At night it is alert, but secreted deep among the coral, apparently inactive.

All five specimens (80: 69-86 mm long) speared at various times during the day were full of food. Filamentous algae were the major identifiable item in the gut contents of all five (mean percent of diet volume and ranking index: 41.7). There also was much unidentified debris, including sand and foraminiferans (mean percent of diet volume and ranking index: 42.3) that all five apparently had scraped from the substratum, and which probably included substantial nourishment in the form of organic detritus. The other components of the diet, all minor, were: diatoms in all five (mean percent of diet volume and ranking index: 3.3), sponges in all five (mean percent of diet volume and ranking index: 2.3), and harpacticoid copepods in one (mean percent of diet volume: 0.3; ranking index: 0.06).

CONCLUSION.—*Centropyge potteri* is a diurnal species that feeds on benthic algae and probably on organic detritus.

Forcipiger flavissimus **Jordan and McGregor**—*lau wiliwili nukunuku 'oi 'oi*

This long-snouted species (Figure 25a), numerous in Kona, and widespread throughout the Indo-Pacific region, was long called *F. longirostris*. Only recently has the distinction between *F. flavissimus* and the true *F. longirostris* (Figure 25b and c; treated below) been recognized (Wheeler, 1964; Randall and Caldwell, 1970). *Forcipiger flavissimus* occurs singly, or, more often, in groups of two or three. It is active throughout the day, especially over coral-rich reefs, where it picks at objects on a variety of surfaces. At night it is alert close among rock and coral cover but apparently inactive.

Twenty-seven specimens (116: 94-137 mm) were speared during day and night. Of 11 that were taken either at night (later than 4 h after sunset) or during early morning twilight, the stomachs of 9 were empty, and those of 2 (collected between 4 and 5 h after sunset) contained only a few well-digested fragments. In contrast, all 16 specimens taken at various times of the day had full stomachs, including relatively fresh material, as listed in Table 28.

Most of the unidentified fragments among the gut contents were relatively fresh pieces that this fish apparently had recently torn from the bodies of larger animals. The similarity of its elongated snout and mouth to a pair of needle-nosed pliers (Figure 26, lower) underscores the adaptiveness of its feeding apparatus to this habit. Even the gripping surfaces on the pliers are paralleled in the snout of *F. flavissimus* by expanded contact-surfaces in both upper and lower jaws—both of which carry multiple rows of short, inwardly curving teeth (Figure 27b).

CONCLUSION.—*Forcipiger flavissimus* is a diurnal predator that tears pieces off larger benthic animals.

Forcipiger longirostris **(Broussonet)**—*lau wiliwili nukunuku 'oi 'oi*

This species is relatively numerous in Kona, although it appears to be rare elsewhere in Hawaii. Both color varieties—the yellow form (Figure 25b), which is essentially identical to *F. flavissimus*, discussed above, and the dark brown form (Figure 25c)—were observed regularly throughout the study. Like *F. flavissimus, F. longirostris* occurs typically over coral-rich reefs, and the two species overlap extensively; however, in areas where one is numerous, the other occurs less frequently. Despite this, I was unable to relate observed differences in relative numbers to specific habitat differences. *Forcipiger longirostris* is generally larger, but the most obvious morphological distinction between the two lies in the relative lengths of their snouts and in their different mouth structures (Figure 26). Less noticeable, but probably also related to feeding, *F. longirostris* has relatively larger eyes. Like its congener, *F. longirostris* is active on the reef by day, swimming singly or in groups of two or three, and probing with its long snout in cracks and crevices. At night it is close among cover of rocks or coral —alert, but apparently inactive.

Of the 26 specimens (136: 98-162 mm) collected, all 4 that were speared at night (later than 4 h after sunset and before first light in the morning) had empty stomachs, whereas the stomachs of all 22 collected at various times during the afternoon were full (including relatively fresh items). Decapod shrimps were the major prey, occurring in all 22 individuals that contained food (mean percent of diet volume and ranking index: 88.4). Other food items were: pagurid crabs, without the mollusk shell, in two individuals (mean percent of diet volume: 1.9; ranking index: 0.17), fish fragments in one (mean percent of diet volume: 0.5; ranking index: 0.02), and crustacean fragments in nine (mean percent of diet volume: 9.2; ranking index: 3.76).

In contrast to the omnivorous *F. flavissimus, F. longirostris* has a restricted diet. It does not tear

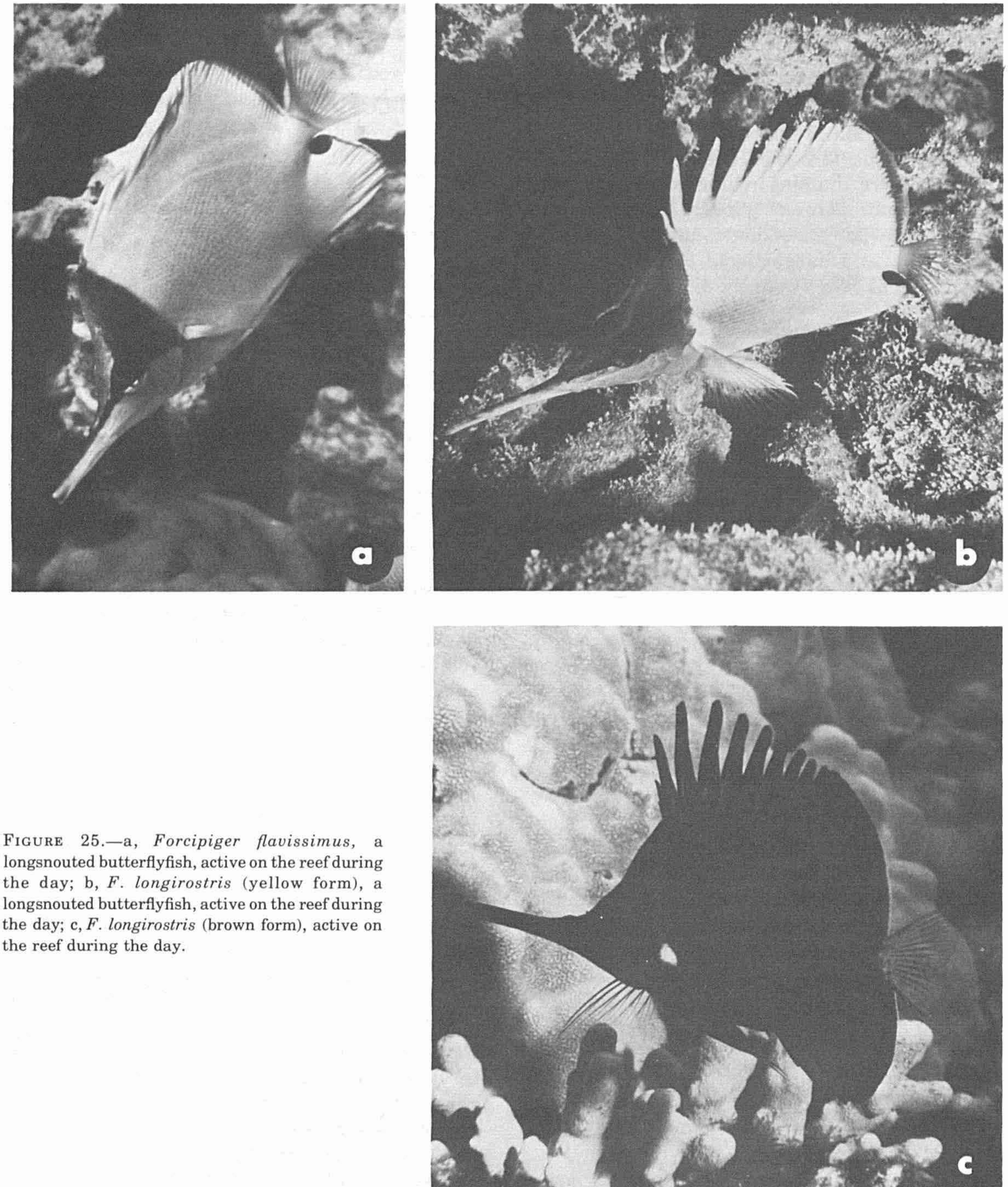

FIGURE 25.—a, *Forcipiger flavissimus,* a longsnouted butterflyfish, active on the reef during the day; b, *F. longirostris* (yellow form), a longsnouted butterflyfish, active on the reef during the day; c, *F. longirostris* (brown form), active on the reef during the day.

TABLE 28.—Food of *Forcipiger flavissimus*.

Rank	Items	No. fish with this item (n = 16)	Mean percent of diet volume	Ranking index
1	Radioles of sabellid polychaetes	10	15.4	9.63
2	Nemerteans	7	11.9	5.21
3	Podia and pedicellaria of echinoids	9	7.0	3.94
4	Calanoid copepods	8	4.1	2.05
5	Tentacles of terebellid polychaetes	7	3.6	1.58
6	Gammaridean amphipods	7	2.3	1.01
7	Hydroids	8	1.0	0.50
8	Caridean shrimps	2	1.3	0.16
9	Caprellid amphipods	4	0.5	0.13
10	Sipunculid introverts	3	0.6	0.11
11	Prosobranch gastropod egg capsules	3	0.5	0.09
12	Crab megalops	2	0.1	0.01
13	Isopods	1	0.1	<0.01
14	Demersal fish eggs	1	0.1	<0.01
Also, crustacean fragments		2	0.9	0.11
	Algal fragments	2	0.2	0.03
	Unidentified fragments	15	50.4	47.25

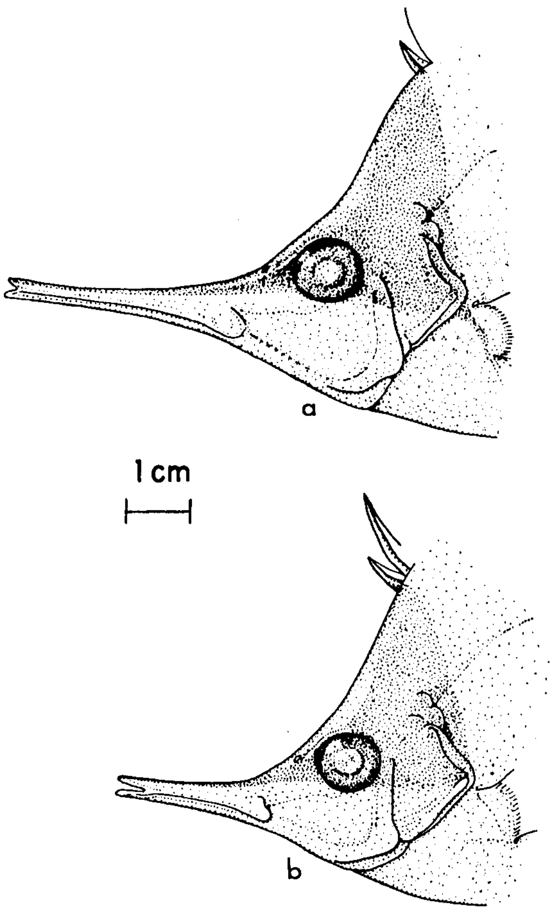

FIGURE 26.—The head and snout of: a, *Forcipiger longirostris*, 102mm long; *F. flavissimus*, 103 mm long. (Note: to discount the size difference in their snouts, lengths were measured from the posterior edge of the maxillary.)

off pieces of larger organisms, as does its congener, but instead takes only whole prey. The sharp difference between their diets is reflected in differing feeding structures. The snout and mouth of *F. longirostris* do not suggest needle-nosed pliers, as do those of *F. flavissimus;* indeed, for *F. longirostris,* the generic name *Forcipiger* (from the Latin *forcipis,* meaning pincers) is a misnomer. Compared with *F. flavissimus,* the mouth of *F. longirostris* is smaller and its jaws do not have the greatly expanded contact surfaces; the teeth are inwardly curved, as in *F. flavissimus,* but are longer and confined to only two or three rows at the front of the mouth (Figure 27a). Clearly, *F. longirostris* is adapted to grasping the tiny prey on which it feeds, but not to tearing pieces free.

CONCLUSION.—*Forcipiger longirostris* is a diurnal predator that takes small benthic animals, mostly decapod shrimps.

Hemitaurichthys thompsoni Fowler

This plain dark-brown chaetodontid seems to be generally rare in Hawaii (Gosline and Brock, 1960), but is numerous in several locations near

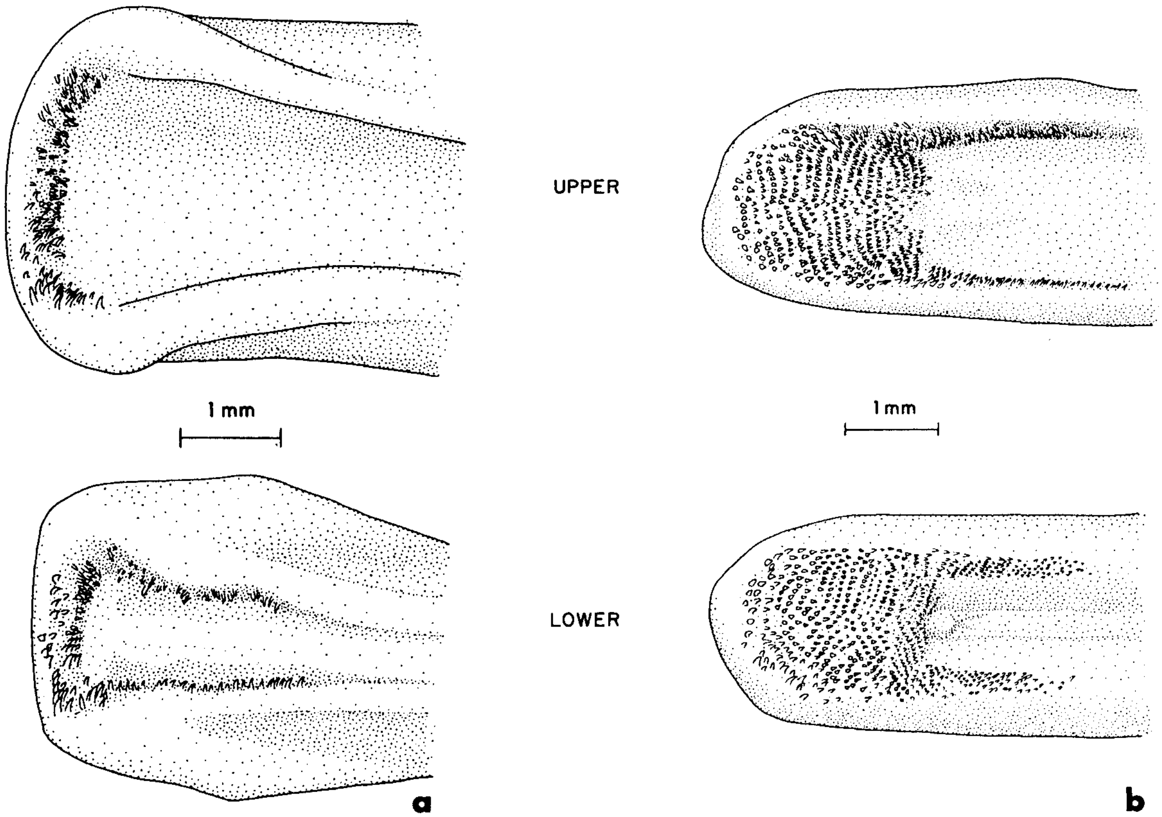

FIGURE 27.—Dentition of: a, *Forcipiger longirostris*; b, *F. flavissimus*.

the outer drop-off at Puuhonua Point, Honaunau. During the day it is active in large aggregations high in the water column, but at nightfall descends to the reef and remains close among cover until morning.

Of the 11 specimens (167: 127-185 mm) collected, all 5 that were taken from under cover on the reef at night (between 4 h after sunset and daybreak) had empty guts, whereas all 6 taken during afternoons from aggregations in midwater were full of food, as listed in Table 29.

I saw no evidence of benthic feeding by this fish. The circumstance that various planktonic copepods made up over 86% of its diet indicates that *H. thompsoni* is a more specialized feeder than its congener *H. zoster* below.

TABLE 29.—Food of *Hemitaurichthys thompsoni*.

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	6	81.9	81.90
2	Blue-green algae in gelatinous sacs	4	3.5	2.33
3	Cyclopoid copepods	4	3.5	2.33
4	Fish eggs, planktonic	4	1.0	0.67
5	Harpacticoid copepods	4	0.7	0.47
6	Hyperiid amphipods	3	0.3	0.15
7	Gastropods, planktonic	1	0.3	0.05
8	Unidentified egg masses in gelatinous matrix	1	0.2	0.03
9	Mysids	1	0.2	0.03
10	Larvaceans	1	0.2	0.03
Also, unidentified fragments		4	8.2	5.47

CONCLUSION.—*Hemitaurichthys thompsoni* is a diurnal planktivore that takes mostly copepods.

Hemitaurichthys zoster (Bennett)—blackface butterflyfish

Gosline and Brock (1960) stated that the colorful *H. zoster* (Figure 28a) and *H. thompsoni* attain a similar size (about 175 mm), but of those seen during this project, *H. zoster* was consistently smaller. Of the two, *H. zoster* also was by far the more numerous and more widespread. During the day *H. zoster* aggregates much like *H. thompsoni*, especially where the reefs drop abruptly into water deeper than about 10 m. Where *H. thompsoni* occurred, *H. zoster* was always nearby, but mixed aggregations of the two species were never seen. Unlike *H. thompsoni*, which was seen feeding only in mid-water, *H. zoster* sometimes is active in small groups close to the reef. At night *H. zoster* is generally solitary, close among cover in the same areas where it is active in daylight. Although *H. thompsoni* has the same coloration day and night, *H. zoster* displays a color pattern at night that differs strikingly from its daytime coloration (Figure 28a and b).

Twelve specimens (119: 100-128 mm) were collected during day and night. Four were speared during morning twilight from a group milling about close above the reef just prior to rising into mid-water. Two of these, taken 18 and 20 min before sunrise, respectively, both had empty stomachs; the third, taken 15 min before sunrise, contained calanoid copepods in varied stages of digestion; the fourth, taken 10 min before sunrise, contained more than 100 calanoid copepods and assorted other prey in varied stages of digestion. I cannot believe that all these prey had been taken since first light that morning, especially as no feeding was observed, and these fish had not yet risen to their customary plankton-feeding levels. And yet *H. zoster* was never seen above the reef at night. Until additional data are available, these two specimens remain anomalous. The other eight specimens, taken at various times during daylight from small aggregations above the reef, all had full stomachs. Items in the 10 individuals containing identifiable prey are listed in Table 30.

These data indicate that *H. zoster* has feeding habits that are less specialized than those of *H. thompsoni*. Planktonic copepods, constituting almost 62% of its diet, are still the major prey, but are less dominant than in *H. thompsoni*. Furthermore, *H. zoster* appears to feed significantly on benthic prey: the alcyonarian *Sarcothelia edmondsoni* constituted over 60% of the material in each of the three specimens in which it occurred.

CONCLUSION.—*Hemitaurichthys zoster* is chiefly a diurnal planktivore that takes primarily copepods, but also feeds on benthic organisms, especially alcyonarians.

Chaetodon corallicola Snyder

Observations in the western Pacific have indicated that the Hawaiian *C. corallicola* is closely related to, if not conspecific with, the widespread Indo-Pacific *C. kleini*. In Kona, this species is relatively numerous at depths below 20 m along the edge of the outer drop-off. In daylight it generally swims in loosely associated pairs that pick free-swimming organisms from the water column within a meter or so of the reef. At night it remains close among the coral—alert, but apparently inactive.

All 11 specimens (89: 75-96 mm) collected for study during afternoons had full stomachs (including fresh material), as listed in Table 31. The only evidence of bottom feeding among this material is the caprellid amphipods and hydroids, both taken from the same individual.

CONCLUSION.—*Chaetodon corallicola* is primarily a diurnal planktivore that feeds largely on copepods.

Chaetodon miliaris Quoy and Gaimard

Gosline and Brock (1960) noted that *C. miliaris* is one of the commonest inshore fishes. Although it is numerous in shallow water around Oahu, Brock and Chamberlain (1968), using a submarine off that island, found it even more abundant in deeper water. They discovered it to be a dominant form at depths below 120 m, where it hovered in aggregations 15 to 40 m above the sea floor, apparently feeding on plankton. In the Kona study area, this species rarely occurs in water shallower than 20 m, but is numerous along the outer drop-off at 30 m and deeper. During the day it aggregates 2 to 3 m above the reef, where it picks organisms from the plankton. At night it is scattered among the rocks and ledges, alert but apparently inactive.

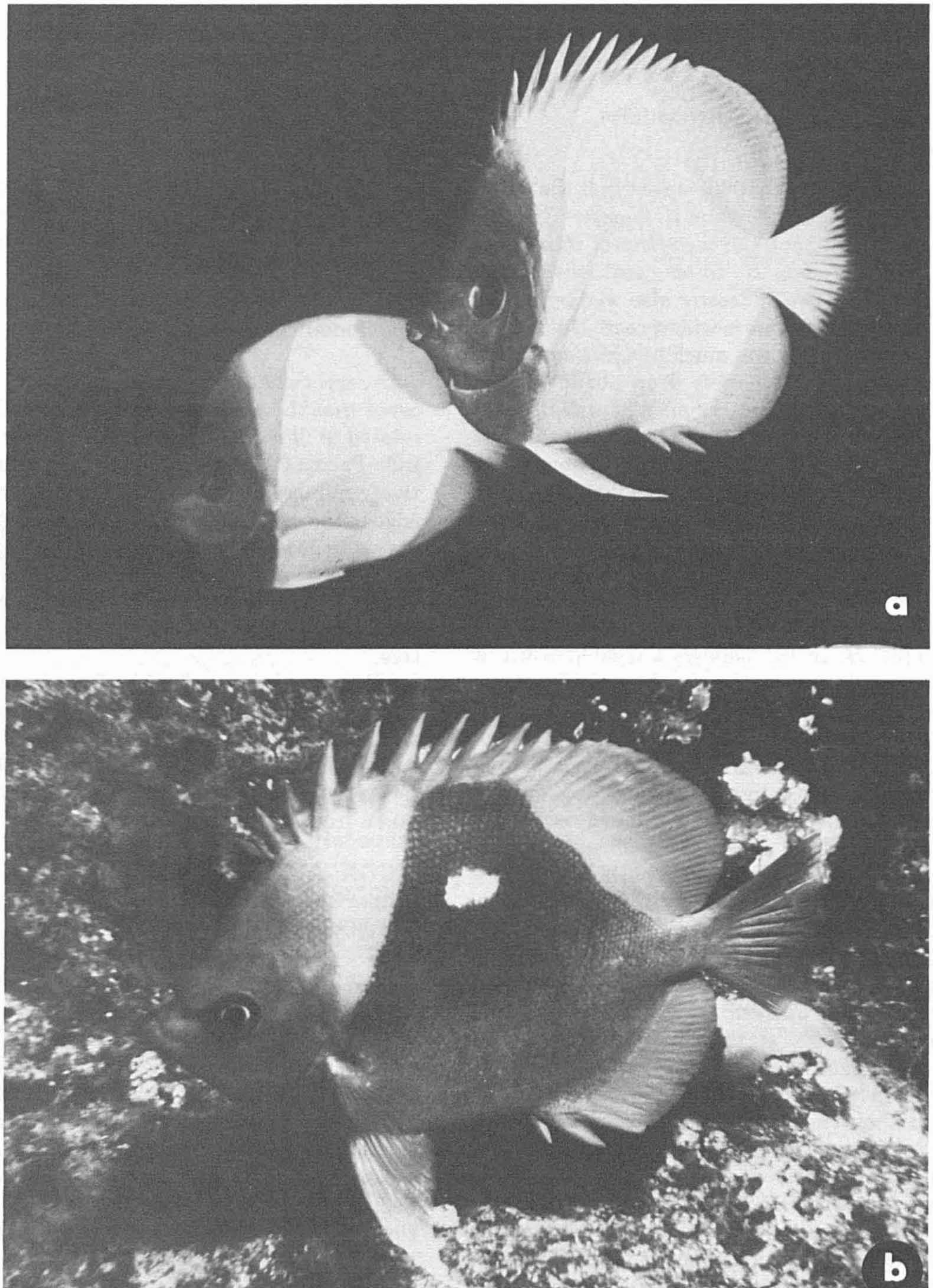

FIGURE 28.—*Hemitaurichthys zoster,* a butterflyfish: a, showing its diurnal coloration while swimming in the water column during the day; b, showing its nocturnal coloration while close to the reef at night.

TABLE 30.—Food of *Hemitaurichthys zoster*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	10	55.3	55.30
2	Alcyonarians	3	18.2	5.46
3	Cyclopoid copepods	8	6.1	4.88
4	Fish eggs, planktonic	6	1.9	1.14
5	Larvaceans	4	1.0	0.40
6	Blue-green algae in gelatinous sacs	3	1.3	0.39
7	Hydroids	2	1.9	0.38
8	Harpacticoid copepods	3	0.3	0.09
9	Gastropod veligers	2	0.3	0.06
10	Penaeid shrimps	1	0.2	0.02
11	Gastropod larvae, echinospira	1	0.1	0.01
12	Pelycypod larvae	1	0.1	0.01
13	Foraminiferans	1	<0.1	<0.01
14	Ostracods	1	<0.1	<0.01
Also, unidentified fragments		5	9.9	4.95
	Crustacean fragments	2	3.2	0.64

TABLE 31.—Food of *Chaetodon corallicola*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	11	52.6	52.60
2	Cyclopoid copepods	11	12.1	12.10
3	Fish eggs, planktonic	9	1.3	1.06
4	Larvaceans	2	5.5	1.00
5	Ostracods	3	0.5	0.14
6	Lobster phyllosomes	3	0.5	0.14
7	Mysids	2	0.3	0.06
8	Caprellid amphipods	1	0.5	0.05
9	Salps	1	0.2	0.02
10	Shrimp larvae	1	0.2	0.02
11	Hydroids	1	0.1	<0.01
12	Gammaridean amphipods	1	<0.1	<0.01
13	Blue-green algae in gelatinous sacs	1	<0.1	<0.01
Also, unidentified fragments		11	26.0	26.00

Of eight specimens (118: 110-125 mm) collected, one that was taken during early morning twilight close among cover contained only a few well-digested fragments, whereas all seven that were active above the reef when taken during the afternoon were full of food (much of it fresh), as listed in Table 32.

CONCLUSION.—*Chaetodon miliaris* is a diurnal planktivore that takes mostly copepods.

Chaetodon quadrimaculatus Gray—four-spot butterflyfish

This butterflyfish is especially numerous where the water is less than 10 m deep over reefs rich in the coral *Pocillopora*. During the day it is active, solitary or paired, close to the sea floor. Feeding strictly on the bottom, it mostly picks at the surface of living coral or in cracks within dead coral and basalt. It occurs in the same areas at night, but though alert, seems relatively inactive.

Twenty-six specimens (92: 43-110 mm) were speared during day and night. All 15 collected during midday were full of food, as were 4 of 5 taken at night during the 2 h immediately before midnight (the fifth was empty). The remaining six were collected at night during the hour immediately before daybreak, and while three of these had empty stomachs, the other three were full. Whether these findings indicate nocturnal feeding or slow digestion remains uncertain. No differences were recognized in composition or condition of gut contents between specimens taken day and night. Items in the 22 individuals containing identifiable material are listed in Table 33.

At least some of the corals taken by this fish probably are soft corals. Most material in the gut appeared as amorphous clumps rich in nematocysts and zooxanthellae. That much of this is soft coral seems likely considering how often *C. quadrimaculatus* nibbles about reef crevices where living stony corals are absent.

TABLE 32.—Food of *Chaetodon miliaris.*

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	7	68.6	68.60
2	Cyclopoid copepods	7	2.8	2.80
3	Salps	1	3.0	0.43
4	Hyperiid amphipods	3	0.4	0.17
5	Fish eggs, planktonic	3	0.4	0.17
6	Larvaceans	1	0.9	0.13
7	Egg masses in gelatinous sacs	2	0.4	0.11
8	Ostracods	1	0.1	0.01
9	Harpacticoid copepods	1	0.1	0.01
10	Mysids	1	0.1	0.01
Also, unidentified fragments		6	23.2	19.89

TABLE 33.—Food of *Chaetodon quadrimaculatus.*

Rank	Items	No. fish with this item (n = 22)	Mean percent of diet volume	Ranking index
1	Anthozoans (no skeletal material)	22	81.4	81.40
2	Polychaetes (mostly tentacles and fragments)	13	6.2	3.66
3	Hydroids	13	1.6	0.95
4	Sipunculid introverts	7	1.9	0.60
5	Opisthobranch gastropods	3	1.3	0.18
6	Caprellid amphipods	6	0.4	0.11
7	Gammaridean amphipods	4	0.2	0.04
8	Cyclopoid copepods	2	0.1	<0.01
9	Calanoid copepods	1	<0.1	<0.01
10	Mites	1	<0.1	<0.01
11	Demersal eggs	1	<0.1	<0.01
Also, unidentified fragments		5	4.5	1.02
	Algal fragments, including diatoms	12	2.1	1.15

Opisthobranch gastropods had been taken by three of the individuals collected at night. Perhaps significantly, these same opisthobranchs are a major prey of *C. lunula* after dark (see below).

CONCLUSION.—*Chaetodon quadrimaculatus* feeds during the day mostly on corals, but also on polychaetes and other benthic organisms. Some nocturnal feeding is likely.

Chaetodon unimaculatus Bloch—one-spot butterflyfish

This chaetodontid is numerous on shallow reefs exposed to a strong surge where the coral *Pocillopora* is also abundant. Generally occurring in pairs, it is active during the day, picking at the surface of living *Pocillopora,* and to a lesser extent other reef surfaces. At night it is alert, but appears inactive as it hovers close among cover on the reef.

Twenty-six specimens (85: 66-102 mm) were speared during night and day. Of three that were collected during the 2 h immediately before midnight, two had empty stomachs, and the third contained a few well-digested fragments. Of four collected during the hour immediately before daybreak, two had empty stomachs, and two contained only well-digested fragments. Thus, there was no evidence of recent feeding by individuals taken after dark. In contrast, all 19 specimens collected during the day had full stomachs, including fresh material, as listed in Table 34.

The major food item, scleractinian corals (mostly *Pocillopora*), included many skeletal fragments.

CONCLUSION.—*Chaetodon unimaculatus* feeds during the day, mostly on the coral *Pocillopora.*

Chaetodon multicinctus Garrett—pebbled butterflyfish

Chaetodon multicinctus is probably the most numerous chaetodontid on Kona reefs in water

TABLE 34.—Food of *Chaetodon unimaculatus.*

Rank	Items	No. fish with this item (n = 19)	Mean percent of diet volume	Ranking index
1	Scleractinian corals	15	45.3	35.76
2	Sponges	5	12.4	3.26
3	Gammaridean amphipods	4	1.3	0.27
4	Pelycypods	1	3.2	0.17
5	Sipunculid introverts	1	1.6	0.08
6	Calanoid copepods	2	0.3	0.03
Also, unidentified fragments		18	29.1	27.57
	Algal fragments and diatoms	9	6.8	3.22

TABLE 35.—Food of *Chaetodon multicinctus.*

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Scleractinian coral polyps	11	91.6	91.60
2	Gammaridean amphipods	7	1.8	1.15
3	Sipunculid introverts	5	1.3	0.59
4	Polychaetes (fragments and tentacles)	3	0.4	0.11
5	Hydroids	2	0.2	0.04
6	Calanoid copepods	1	0.1	0.01
Also, unidentified fragments		2	3.4	0.62
	Algal fragments and diatoms	6	1.2	0.66

shallower than 20 m, especially where stony corals abound. During the day it generally occurs in pairs, and is active close to the reef, often picking at living corals—both *Porites* and *Pocillopora.* At night it rests close among cover on the reef, alert but apparently inactive.

Of the 26 specimens (84: 78-94 mm) examined, all 15 that were collected at night (between 4 h after sunset and first morning light) were empty, whereas all 11 that were collected during midday were full of food (including fresh material), as listed in Table 35.

More so than the other butterflyfishes that feed on stony corals, *C. multicinctus* does so without also taking fragments of the surrounding skeleton.

CONCLUSION.—*Chaetodon multicinctus* is a diurnal predator that feeds primarily on scleractinian corals (mostly *Porites* and *Pocillopora).*

Chaetodon ornatissimus Solander—ornated butterflyfish

This butterflyfish is numerous over coral-rich reefs, generally swimming in pairs during the day. It moves from one growth of coral to another, locating and working its mouth over abrasions on the surface of the coral. In this way it feeds on a variety of scleractinian corals, including *Porites, Pavona,* and *Cyphastrea.* At night it rests quiet, but alert, close among cover on the reef. Its daytime and nighttime colorations differ strikingly (Figure 29a and b).

Nineteen specimens (119: 95-140 mm) were examined. All eight that were collected at night, later than 4 h after sunset and before first morning light, had the stomachs and anterior half of the intestines empty. All four that were taken during morning twilight—the earliest 25 min before sunrise—had material in their stomachs, but their intestines were empty (apparently they had just begun to feed). Finally, all seven that were collected during midday were full of food.

All 11 specimens with material in their stomachs contained only a thick mucus rich in nematocysts, zooxanthellae, and organic debris (mean percent of diet volume and ranking index: 99.8). The balance of the gut contents was made up of diatoms and a few algal fragments.

It is well known that stony corals increase their production of mucus when injured, so this chaetodontid's habit of seeking out abrasions on coral may explain why its gut contents include so much mucus. This species probably obtains significant nourishment from coral mucus, but judging from the numbers of zooxanthellae and

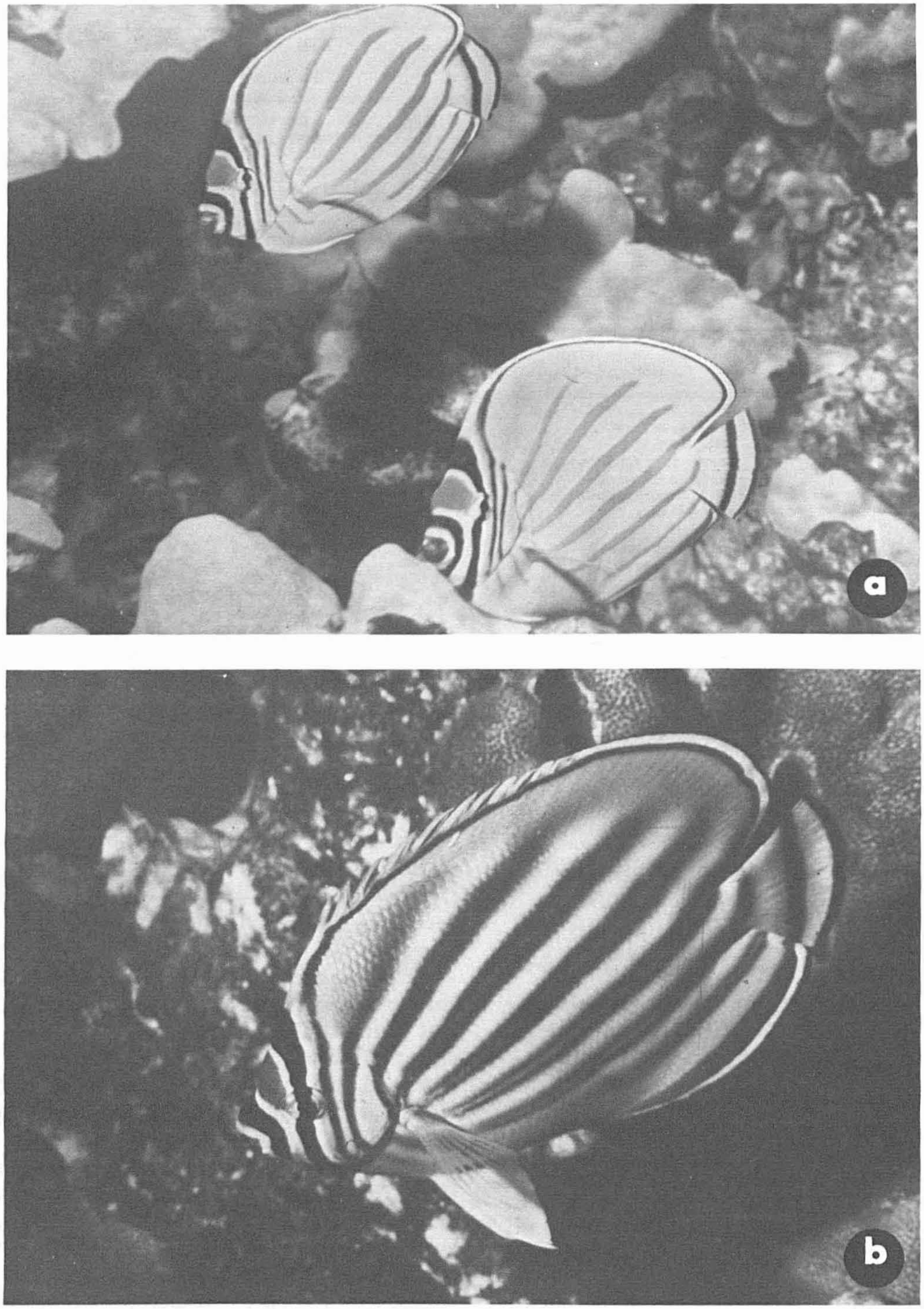

FIGURE 29.—*Chaetodon ornatissimus,* a butterflyfish: a, showing its diurnal coloration while swimming above the reef during the day; b, showing its nocturnal coloration while close to the reef at night.

nematocysts present, at least some coral tissue is also taken (although nothing was found recognizable as such). Presumably at least much of this material had been freshly ingested, because it came from individuals that were actively feeding when collected. Johannes (1967) and Coles and Strathman (in press) have shown there are significant quantities of organic material in coral mucus that could nourish a wide range of animals, including fishes. A similar butterflyfish, *Chaetodon trifasciatus,* not numerous in Kona, has feeding behavior similar to *C. ornatissimus.*

CONCLUSION.—*Chaetodon ornatissimus* is a diurnal fish that feeds on coral during the day, obtaining significant nourishment from coral mucus.

Chaetodon auriga Forskål

In Kona this chaetodontid is less abundant than many of its congeners. Generally paired, it swims close to the reef in daylight, occasionally picking at objects on the sea floor. At night it is alert close among ledges and other reef irregularities.

All six specimens (151: 132-160 mm) collected had full stomachs including four taken during the afternoon and two taken on a dark night, 3 h after sunset. All these specimens contained similar prey in what seemed similar condition. The data are too few to draw conclusions regarding nocturnal activity, but suggest that this species may feed after dark. Items in the stomachs of these six specimens are listed in Table 36.

Most of the food items were fragmented, including the unidentified material, and many of them were relatively fresh. Clearly, this chaetodontid obtains most of its food by tearing pieces from larger sessile organisms. Hiatt and Strasburg (1960) found similar prey in *C. auriga* from the Marshall Islands.

CONCLUSION.—*Chaetodon auriga* preys on a wide variety of benthic organisms during the day, obtaining most of its food by tearing off pieces of larger sessile animals. It also seems to feed to some extent after dark.

Chaetodon fremblii Bennett—blue-striped butterflyfish

This butterflyfish is most numerous where large basalt boulders are interspersed with small pockets of sand. Sometimes paired, but more often solitary, this chaetodonid picks at objects on the rocks and in the sand during the day. At night it occurs close among cover, alert but seemingly inactive.

Fourteen specimens (103: 86-120 mm) were speared during day and night. All eight collected during the afternoon had full stomachs, whereas the two taken from among rocks at night, between 4 and 5 h after sunset, were empty. On the other hand, three others collected together among the rocks during morning twilight, about 25 min before sunrise after a moonless night, had material in their stomachs. Two of them contained only a few well-digested fragments that could have been

TABLE 36.—Food of *Chaetodon auriga.*

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Alcyonarians	5	31.0	25.83
2	Terebellid polychaete tentacles	6	18.4	18.40
3	Gastropod egg masses	6	8.8	8.80
4	Errant polychaete fragments	5	5.4	4.50
5	Sabellid polychaete radioles	4	2.2	1.47
6	Echinoid podia	4	2.0	1.33
7	Caridean shrimps	4	1.4	0.93
8	Anemones	1	4.0	0.67
9	Sponges	1	3.1	0.52
10	Sipunculid introverts	3	0.4	0.20
11	Gammaridean amphipods	3	0.4	0.20
12	Hydroids	1	0.2	0.03
13	Serpulid polychaete fragments	1	0.2	0.03
Also,	Unidentified fragments	6	20.7	20.70
	Algal fragments	3	1.8	0.90

taken the previous day, but in the third individual a wide variety of differentially digested items indicated either nocturnal feeding or unusually slow digestion. A fourth individual taken during morning twilight was empty. Items in the eight specimens containing identifiable material, much of it fragments torn from larger sessile animals, are listed in Table 37.

CONCLUSION.—*Chaetodon fremblii* preys on a wide variety of benthic organisms during the day, obtaining much of its food by tearing off pieces of larger sessile animals. With some uncertainty, it seems largely inactive after dark.

Chaetodon lunula (Lacépède)—masked butterflyfish

This butterflyfish, one of the more numerous in Kona, is most abundant where a coral-crested reef face falls among basalt boulders, yet occurs in a variety of habitats. Setting it apart from all other chaetodontids reported here, I never saw this species feed during the day. It generally hovers close to the reef in daylight, sometimes solitary, or in twos or threes, and often in large aggregations (Figure 30). These aggregations form day after day in the same locations, and several occurred in the same places over the entire 15-mo period of the study. The aggregations disperse at nightfall, and after dark the species scatters over the reef, either solitarily, or in twos or threes.

Of the 26 specimens (134: 112-150 mm) examined, all 14 speared at night (more than 4 h after sunset), or during morning twilight, had stomachs full of food in varying stages of digestion, much of it fresh; the other 12 were collected during afternoons (some from the daytime aggregations), and although they too had full stomachs, the contents generally were further digested. There was no recognizable difference in the composition of the diet between specimens collected during each of these three periods. Items in the stomachs are listed in Table 38.

Clearly, *C. lunula*, like *C. auriga* and *C. fremblii*, habitually tears pieces off the bodies of larger sessile animals, but, more so than the others, also takes whole organisms. In fact, its major prey, based on these data, are opisthobranch gastropods, which it takes whole. The opisthobranchs are mostly one form of Anaspidea and one form of Cephalaspidea. Significantly, all individuals of *C. lunula* that contained what seemed to be freshly ingested opisthobranchs were speared at night. Opisthobranchs in *C. lunula* speared during the afternoon were consistently far digested. These opisthobranchs are mostly about 4 to 10 mm long, and are relatively solid pieces of meat that may take longer to digest than many other kinds of food. Similarly, the polychaete heads and prosobranch gastropod heads taken by this fish are relatively dense pieces of meat that probably resist digestion (the shells of the prosobranch gastropods were never present—only the heads, which this butterflyfish apparently is adept at snipping off). Smaller organisms that would be rapidly digested like the amphipods and isopods, generally, but with two exceptions, were absent in specimens speared during the afternoon. Generally then, the stomach contents appeared to have been taken mostly at night. Finally, it may be significant that the eyes of *C. lunula* are relatively larger than the eyes of all other species of this genus studied at Kona.

TABLE 37.—Food of *Chaetodon fremblii*.

Rank	Items	No. fish with this item (n = 8)	Mean percent of diet volume	Ranking index
1	Terebellid polychaete tentacles	6	25.0	18.75
2	Sipunculid introverts	6	15.0	11.25
3	Gammaridean amphipods	8	10.1	10.10
4	Errant polychaete fragments	4	3.1	1.55
5	Hydroids	2	2.9	0.73
6	Isopods	3	1.6	0.60
7	Gastropod egg capsules	1	3.6	0.45
8	Caprellid amphipods	1	2.3	0.29
9	Acorn worms	1	2.3	0.29
10	Opisthobranch gastropods	1	1.4	0.18
11	Caridean shrimps	1	0.1	0.01
12	Gastropod opercula	1	0.1	0.01
Also, unidentified fragments		6	21.3	15.98
	Algal fragments	7	11.2	9.80

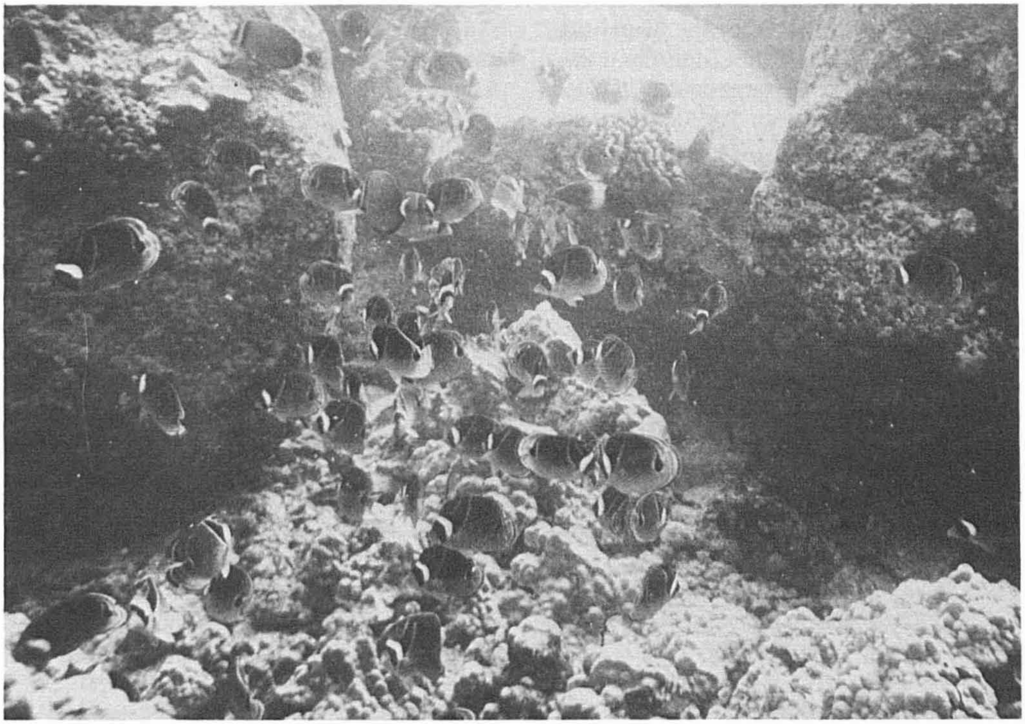

FIGURE 30.—Diurnal aggregation of *Chaetodon lunula*, a butterflyfish.

TABLE 38.—Food of *Chaetodon lunula*.

Rank	Items	No. fish with this item (n = 26)	Mean percent of diet volume	Ranking index
1	Opisthobranch gastropods	21	29.2	23.58
2	Terebellid polychaete tentacles	11	8.7	3.68
3	Errant polychaete fragments	17	2.2	1.44
4	Sipunculid introverts	9	1.7	0.59
5	Polychaete heads	8	1.9	0.58
6	Prosobranch gastropod heads	7	0.7	0.19
7	Gammaridean amphipods	9	0.3	0.10
8	Holothurians	2	1.3	0.10
9	Fish eggs	2	1.1	0.08
10	Caridean shrimps	4	0.3	0.05
11	Echinoid podia	4	0.2	0.03
12	Alcyonarians	2	0.3	0.02
13	Sabellid polychaete radioles	3	0.2	0.02
14	Caprellid amphipods	3	0.1	0.01
15	Crustacean eggs	1	0.2	<0.01
16	Tanaids	2	0.1	<0.01
17	Hydroids	2	0.1	<0.01
18	Anemones	1	0.1	<0.01
19	Calanoid copepods	1	0.1	<0.01
20	Crabs	1	0.1	<0.01
21	Tunicates	1	0.1	<0.01
Also, unidentified fragments		24	50.3	46.43
	Algal fragments	5	0.5	0.10
	Crustacean fragments	4	0.2	0.03

Hiatt and Strasburg (1960) noted only tips of coral polyps in one *C. lunula* from the Marshall Islands. Although the diet of this individual diverges sharply from that of representatives in Kona, one cannot speculate on its significance from one specimen.

CONCLUSION.—*Chaetodon lunula* preys on benthic invertebrates, especially opisthobranchs, at night.

General Remarks on Angelfishes and Butterflyfishes

The two Hawaiian angelfishes, *Holacanthus arcuatus* and *Centropyge potteri,* have feeding habits that set them apart from the butterflyfishes. *Holacanthus arcuatus* is the only chaetodontid that feeds strictly on sponges, and *C. potteri* is the only one that takes just algae and detritus. Thus the Hawaiian situation parallels that in the tropical Atlantic, where species of *Holacanthus* and of *Pomacanthus* (another genus of angelfish) feed mostly on sponges and where species of *Centropyge* feed almost exclusively on algae and detritus (Randall, 1967). Similarly, Hiatt and Strasburg (1960) reported a strictly herbivorous diet for *C. flavissimus* in the Marshall Islands.

Although butterflyfishes in Kona are more strictly predators in the conventional sense than are the angelfishes, Hiatt and Strasburg (1960) reported *Chaetodon reticulatus* in the Marshall Islands to be strictly herbivorous. That species is seen only occasionally in Kona, and so was not included in the present study. Otherwise, Hiatt and Strasburg found scleractinian corals and polychaetes to be the major food of butterflyfishes in the Marshall Islands, and this is in broad accord with the habits of certain species in Kona. Randall (1967) reported that West Indian butterflyfishes feed primarily on anthozoans and the tentacles of polychaetes, again paralleling the habits of certain Kona species. On the other hand, the number of planktivorous butterflyfishes in Kona seems on a scale without parallel in published accounts of other reef areas.

Chaetodontids have been widely described as diurnal fishes, e.g. in the tropical Atlantic (Starck and Davis, 1966; Collette and Talbot, 1972), and in the Gulf of California (Hobson, 1965, 1968a). Although diurnal habits are generally characteristic of chaetodontids in Kona, the fact that at least one, *Chaetodon lunula,* is nocturnal and that several others feed at least somewhat after dark may reflect increased interspecific pressures associated with the large number of *Chaetodon* species on Kona reefs. I treat the nine most numerous species of *Chaetodon* here, but also saw five others during this study.

Family Pomacentridae: damselfishes

Plectroglyphidodon johnstonianus Fowler and Ball

This solitary species is most numerous where stony corals abound. During the day it swims close to the reef, each individual seemingly associated with a particular location, and here it picks frequently at the substratum, especially around coral. At night it is secreted deep among the coral, relatively inactive, but alert.

Of the eight specimens (60: 39-70 mm) examined, the stomachs of two that were speared among the coral shortly before dawn contained only a few well-digested fragments (probably material that had been ingested during the previous day), whereas the stomachs of all six taken during midday were full of food, much of it fresh.

The major food item in all six was anthozoans: nematocysts and zooxanthellae, with tissue fragments and mucus, but no skeletal material (mean percent of diet volume and ranking index: 94.3). All other items made up only a minor part of the diet: algal fragments in three (mean percent of diet volume: 2; ranking index: 1), sipunculid introverts in one (mean percent of diet volume: 0.2; ranking index: 0.03), and unidentified fragments in four (mean percent of diet volume: 3.5; ranking index: 2.33). Because *P. johnstonianus* is closely associated with scleractinian corals, these probably are the anthozoans so prominent in its diet. However, specific identifications of the fragmented gut contents remain uncertain, and because direct observations of feeding are limited, other anthozoans may also be involved. In any event, the observations indicate that this fish is adept at snipping off pieces of anthozoan tissue and mucus without taking any of the surrounding skeletal material.

CONCLUSION.—*Plectroglyphidodon johnstonianus* is a diurnal predator that feeds chiefly on anthozoans.

Pomacentrus jenkinsi Jordan and Evermann

This species is one of the more widespread and numerous in Kona, especially in relatively quiet water over coral and rocks. During the day, individuals are scattered among reef irregularities, each seemingly associated with specific locations, and here they pick at coral and rock surfaces. At night they hover under cover, remaining alert but relatively inactive until shortly after first light, when diurnal activity is resumed.

Twenty-two specimens (89: 80-100 mm) were collected during day and night. All 12 that were speared as they swam close to the reef during midday were full of food, much of it fresh, whereas of 5 that were speared in reef crevices at night (between 4 and 5 h after last evening light), the stomachs of 3 were empty and those of the other 2 contained only a few well-digested, unidentified fragments. Finally, of five active individuals that were collected during morning twilight and during the first 30 min after sunrise, two were empty, and three contained in their stomachs a few fresh fragments that appeared to have been recently ingested. The 15 specimens that contained at least some fresh material had consumed the items listed in Table 39.

The amorphous organic fragments that constituted the bulk of the gut contents in this fish were in part items that had been digested beyond recognition; however, most of this material appeared to be detritus—organic deposits—that had been scraped from the reef. Gosline and Brock (1960) noted that *P. jenkinsi* inhabits quiet water, where it feeds on algae, and perhaps detritus. Hiatt and Strasburg (1960) also found this fish in quiet water in the Marshall Islands and reported it to be primarily a herbivore that feeds occasionally on small fishes.

CONCLUSION.—*Pomacentrus jenkinsi* is a diurnal omnivore that takes mostly organic detritus, algae, and small animals from reef surfaces.

Abudefduf sindonis (Jordan and Evermann)

This damselfish occurs where basalt boulders are swept by a strong surge. Activity is limited to daylight; at night it remains under cover among the rocks.

All five specimens (91: 81-102 mm) were speared during the day, and their guts were full of the material listed in Table 40, much of it fresh. The amorphous organic fragments, the major food item, probably are largely detritus from the reef, such as is also taken by *Pomacentrus jenkinsi*, discussed above. Where a strong surge sweeps the boulder habitat, *A. sindonis* replaces *P. jenkinsi* in depths shallower than about 3 m.

Gosline and Brock (1960) noted that *A. sindonis* seems restricted to surge areas among lava rocks and appears to be omnivorous.

CONCLUSION.—*Abudefduf sindonis* is a diurnal omnivore that takes mostly organic detritus, algae, and small animals from the substratum.

Abudefduf sordidus (Forskål)—*kupipi*

Although juveniles of *A. sordidus* are prominent in tide pools, the adults, which are the largest of the Hawaiian pomacentrids, seem to occur only where a precipitous basalt reef face confronts a prevailing swell. In this situation large individuals of this species are fairly numerous among rocky crevices and close to boulders at the base of the reef. Generally a solitary fish, *A. sordidus* is

TABLE 39.—Food of *Pomacentrus jenkinsi*.

Rank	Items	No. fish with this item (n = 15)	Mean percent of diet volume	Ranking index
1	Algae, including diatoms	15	24.1	24.10
2	Sponges	6	5.7	2.28
3	Calanoid copepods	1	4.6	0.31
4	Errant polychaetes	2	2.0	0.27
5	Fish eggs, demersal	2	1.0	0.13
6	Cyclopoid copepods	4	0.4	0.11
7	Gammaridean amphipods	2	0.2	0.03
8	Barnacle cirri	1	0.1	<0.01
9	Pelecypod mollusks	1	0.1	<0.01
Also, amorphous organic fragments		15	60.1	60.10
	Sand	4	1.7	0.45

TABLE 40.—Food of *Abudefduf sindonis*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Algae, including diatoms	5	39.4	39.40
2	Polychaetes	4	2.2	1.76
3	Gammaridean amphipods	4	2.2	1.76
4	Caridean shrimps	1	7.0	1.40
5	Cyclopoid copepods	4	1.0	0.80
6	Hydroids	1	1.0	0.20
7	Sipunculid introverts	1	0.2	0.04
8	Insects	1	0.2	0.04
Also, amorphous organic fragments		5	46.8	46.80

TABLE 41.—Food of *Abudefduf sordidus*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Algae, including diatoms	5	35.0	35.00
2	Crabs	4	20.0	16.00
3	Sponges	4	12.2	9.76
4	Prosobranch gastropods	4	9.2	7.36
5	Gammaridean amphipods	5	4.4	4.40
6	Prosobranch gastropod eggs	2	1.2	0.48
7	Tanaids	3	0.6	0.36
8	Hydroids	2	0.4	0.16
9	Bryozoans	2	0.4	0.16
10	Polychaetes	2	0.4	0.16
11	Pycnogonids	2	0.4	0.16
12	Insects	1	0.4	0.08
Also, unidentified fragments		5	15.4	15.40

active only during daylight, close to the substratum. After dark it is secreted under rocky cover, alert but relatively inactive.

All five specimens (147: 129-160 mm) were speared during midday, and their guts were full of the material listed in Table 41, much of it fresh. Gosline and Brock (1960) reported that the young of *A. sordidus* are very prominent tide-pool inhabitants and that the omnivorous adults apparently live just outside of the reef edge.

CONCLUSION.—*Abudefduf sordidus* is a diurnal omnivore that takes chiefly algae and small animals from the substratum.

Abudefduf imparipennis (Sauvage)

This pomacentrid is numerous on shallow, surge-swept reefs where exposed basalt is dotted by the coral *Pocillopora meandrina*. It is a solitary, bright-eyed little fish that is active in daylight, and does not swim away from the substratum. Appearing tense and alert, even when hovering motionless at the base of a coral head, its movements are short but rapid darts from one spot to another. At night it takes shelter deep within reef crevices.

All 15 specimens (42: 29-50 mm) were active on the reef during the day when collected, and all contained food, including fresh material, as listed in Table 42. Gosline and Brock (1960) noted that this fish seems to occur over all rocky areas in the surge zone, and that it appears to be entirely carnivorous, with the predominant food organism being a polychaete annelid.

CONCLUSION.—*Abudefduf imparipennis* is a diurnal predator that feeds mainly on small benthic crustaceans and polychaetes.

Abudefduf abdominalis (Quoy and Gaimard)—*maomao*

This damselfish is most numerous where basalt boulders lie at the base of a vertical reef face in water 5 to 10 m deep. During daylight it hovers in aggregations high in the water column close to the

TABLE 42.—Food of *Abudefduf imparipennis*.

Rank	Items	No. fish with this item (n = 15)	Mean percent of diet volume	Ranking index
1	Gammaridean amphipods	12	12.6	10.08
2	Polychaetes	7	17.6	8.21
3	Cyclopoid copepods	9	7.1	4.26
4	Sipunculid introverts	8	1.9	1.01
5	Fish eggs, demersal	3	3.1	0.62
6	Unidentified eggs, demersal	4	1.8	0.48
7	Opisthobranch gastropods	2	1.7	0.23
8	Diatoms	6	0.5	0.20
9	Algae fragments	2	0.8	0.11
10	Prosobranch gastropod eggs	1	0.8	0.05
11	Isopods	2	0.4	0.05
12	Sponge spicules	1	0.3	0.02
13	Caprellid amphipods	1	<0.1	<0.01
14	Harpacticoid copepods	1	<0.1	<0.01
15	Caridean shrimps	1	<0.1	<0.01
16	Mites	1	<0.1	<0.01
17	Insects	1	<0.1	<0.01
Also, unidentified fragments		15	50.9	50.90

TABLE 43.—Food of *Abudefduf abdominalis*.

Rank	Items	No. fish with this item (n = 10)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	10	54.0	54.00
2	Cyclopoid copepods	8	6.5	5.20
3	Fragments of algae	4	2.6	1.04
4	Fish eggs, planktonic	4	2.0	0.80
5	Polychaetes	4	1.9	0.76
6	Decapod shrimps	4	1.7	0.68
7	Larvaceans	1	4.0	0.40
8	Harpacticoid copepods	4	0.8	0.32
9	Gelatinous clumps of blue-green algae	2	1.3	0.26
10	Pelecypod larvae	2	0.2	0.04
11	Penaeid shrimp larvae	1	0.2	0.02
12	Gastropod veligers	1	0.1	0.01
13	Naupilius larvae	1	0.1	0.01
Also, unidentified fragments		9	24.6	22.14

reef, where it picks organisms from the plankton. Although members of an aggregation are close to one another, each feeds independently. The plankters are taken with what seems to be a visually directed action in which the fish suddenly thrusts both jaws forward, then immediately retracts them. Presumably the sudden expansion of the oral cavity sucks the prey in.

A given aggregation maintains station over a particular location although its position in the water column is influenced by several factors. Fish size is important, because the larger individuals tend to be farther above the reef than the smaller ones. Prevailing light is another factor; thus, when clouds pass in front of the sun, and light diminishes, individuals of all sizes descend closer to the reef. In addition, the appearance of a large predator, or some other disturbance, intermittently sends this fish diving to cover on the reef. However, after such an event it quickly returns to its feeding stations in the water column.

As light progressively fades late in the day, this species gradually descends to the reef so that by evening twilight it is sheltered among the coral (Hobson, 1972). On dark nights it remains under cover, relatively inactive but alert; however, under bright moonlight it swims in exposed positions close to the reef. Then, during morning twilight, it begins to ascend to its daytime feeding stations in the water column (Hobson, 1972).

Of 14 specimens (142: 105-162 mm) examined, the 4 that were speared as they hovered among the rocks on dark nights (between 4 and 6 h after sunset) contained only well-digested fragments, whereas all 10 that were speared from mid-water aggregations during afternoons had their stomach full of food (including much fresh material), as listed in Table 43.

CONCLUSION.—*Abudefduf abdominalis* is a diurnal planktivore that preys primarily on copepods.

Dascyllus albisella **Gill**

Where corals are abundant, this damselfish is numerous to depths of at least 35 m. During daylight, it aggregates in the water column and picks small organisms from the plankton, much as does *Abudefduf abdominalis,* described above, and its aggregations rise and fall in the water column in response to the same variables that influence that species. Also like *A. abdominalis, D. albisella* descends to the reef during evening twilight and spends the night close among the rocks—under cover on dark nights, and in exposed positions when there is moonlight.

Twelve specimens (79: 42-95 mm) were collected during day and night. The six that were speared shortly before first morning light as they hovered among the coral contained only a few well-digested fragments (five were taken after nights of bright moonlight, one after a dark night). On the other hand, the six that were collected from aggregations in the water column during afternoons had stomachs full of food, including much fresh material as listed in Table 44.

Gosline and Brock (1960) reported that *D. albisella* occurs in small schools around certain large coral heads and listed stomach contents as follows: shrimp and crab larvae, mysids, and calanoid copepods.

CONCLUSION.—*Dascyllus albisella* is a diurnal planktivore that takes primarily larvaceans and copepods.

Chromis vanderbilti **(Fowler)**

This, the smallest pomacentrid in Kona, is numerous where exposed basalt ledges are interspersed with coral. During the day it aggregates in the water column, but even under bright sunlight rarely moves more than 50 cm above the reef. On overcast days it generally remains sheltered, and shortly before sunset is the first planktivorous damselfish to descend to cover on the reef (Hobson, 1972). At night, it usually remains out of sight deep within reef crevices, and in the morning is the last pomacentrid to appear.

All 12 specimens (38: 17-46 mm) taken from feeding aggregations during midday had stomachs full of food, including fresh material, as listed in Table 45.

CONCLUSION.—*Chromis vanderbilti* is a diurnal planktivore that takes primarily copepods and larvaceans.

Chromis leucurus **Gilbert**

Gosline and Brock (1960) considered *C. leucurus* to include two distinct color phases: in one the body is very dark anteriorly and abruptly white posteriorly; in the other, the whole body, except black pectoral base and white caudal fin, is mostly plain orange-brown. Although I followed this judgment when making the fish counts, the probability that at least two species are represented, and that neither one may in fact be *C. leucurus,* is currently under study by John E. Randall, B. P. Bishop Museum, and Stanley Swerdloff, Government of American Samoa. In any event, the specimens collected for study of food

TABLE 44.—Food of *Dascyllus albisella.*

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Larvaceans	6	43.1	43.10
2	Calanoid copepods	6	11.2	11.20
3	Cyclopoid copepods	6	9.2	9.20
4	Gelatinous clumps of blue-green algae	4	7.2	4.80
5	Fragments of algae	4	1.5	1.00
6	Decapod shrimp larvae	2	2.2	0.73
7	Fish eggs, planktonic	2	1.1	0.37
8	Hydroid fragments	1	0.2	0.03
9	Pelecypod larvae	1	0.2	0.03
10	Gammaridean amphipods	1	0.2	0.03
11	Harpacticoid copepods	1	0.2	0.03
Also, unidentified fragments		5	23.7	19.75

TABLE 45.—Food of *Chromis vanderbilti*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	11	30.5	27.96
2	Larvaceans	8	21.7	14.47
3	Cyclopoid copepods	12	8.8	8.80
4	Polychaetes	5	0.9	0.38
5	Fish eggs, planktonic	4	0.9	0.30
6	Decapod shrimps	2	1.7	0.28
7	Harpacticoid copepods	3	1.1	0.28
8	Siphonophores	1	1.7	0.14
9	Gelatinous clumps of blue-green algae	2	0.5	0.08
10	Ostracods	1	0.5	0.04
11	Hyperiid amphipods	1	0.1	0.01
Also, unidentified fragments		12	31.1	31.10

habits, below, all represent the orange-brown form.

Of the two, the orange-brown form is the more numerous in Kona, but both abound over coral-rich reefs, often together in plankton-feeding aggregations that hover within 1 m of the substratum during the day. As is true of *Abudefduf abdominalis* and *Dascyllus albisella,* described above, *C. leucurus* remains closer to the reef when light is diminished, and dives to cover when threatened (Figure 31). At night it generally is out of sight within crevices.

All five specimens (57: 37-70 mm) speared during midday had their stomachs full of food, including fresh material, as listed in Table 46.

Swerdloff (1970a) described the behavior of two spatially related species of *Chromis* in the Marshall Islands, *C. leucurus,* and *C. dimidiatus,* and reported their food to be calanoid copepods, fish eggs, and larval tunicates.

CONCLUSION.—*Chromis leucurus* is a diurnal planktivore that takes primarily copepods and larvaceans.

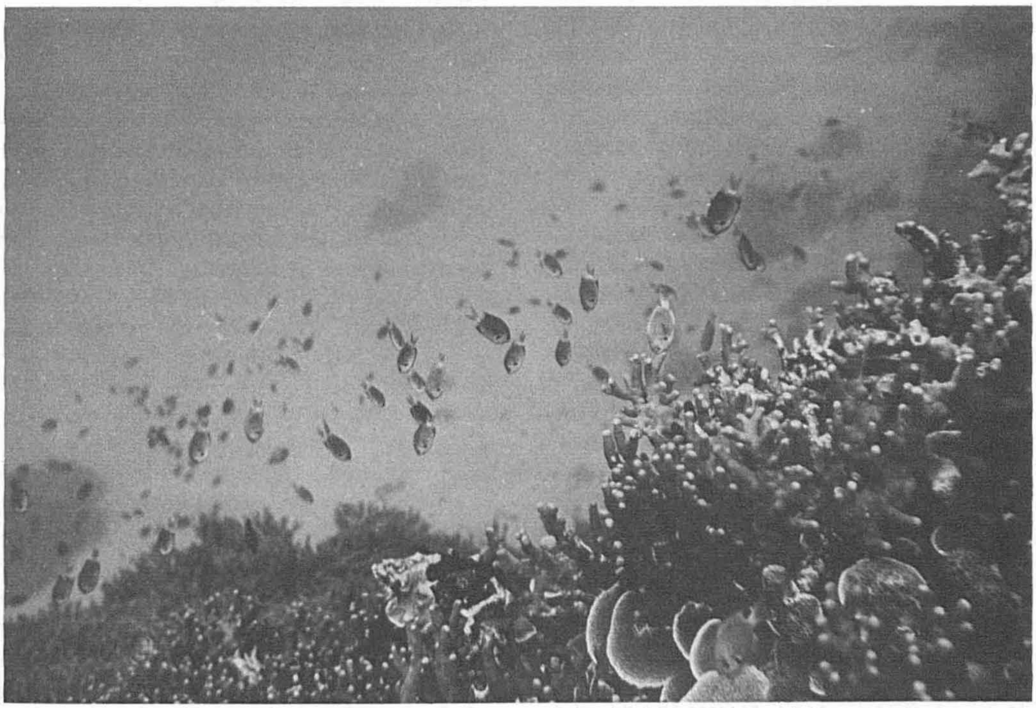

FIGURE 31.—Members of an aggregation of *Chromis leucurus,* a damselfish, having been threatened, dive from their plankton-feeding location in the water column toward shelter among the coral below.

TABLE 46.—Food of *Chromis leucurus*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Cyclopoid copepods	5	19.0	19.00
2	Larvaceans	3	22.0	13.20
3	Calanoid copepods	3	4.0	2.40
4	Fish eggs, planktonic	4	2.8	2.24
5	Gelatinous clumps of blue-green algae	3	3.6	2.16
6	Fragments of algae	2	2.0	0.80
7	Harpacticoid copepods	1	0.4	0.08
Also, unidentified fragments		5	46.2	46.20

TABLE 47.—Food of *Chromis verater*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	5	29.6	29.60
2	Larvaceans	4	36.0	28.80
3	Cyclopoid copepods	5	2.2	2.20
4	Fish eggs, planktonic	3	2.4	1.44
5	Decapod shrimps	1	7.0	1.40
6	Siphonophores	1	0.8	0.16
7	Mysids	1	0.4	0.08
8	Chaetognaths	1	0.4	0.08
9	Polychaetes	1	0.2	0.04
10	Harpacticoid copepods	1	0.2	0.04
Also, unidentified fragments		5	20.8	20.80

Chromis verater Jordan and Metz

This damselfish is one of the more prominent fishes over both coral and basalt reefs in Kona at depths below about 15 m. During the day it swims in plankton-feeding aggregations that hover 2 to 5 m above the reef, where changing light levels and the appearance of certain predators produce effects much as described above for *Abudefduf abdominalis* and other planktivorous pomacentrids. Also as in these other species, *C. verater* passes the night among cover on the reef, relatively quiet but alert. It moves about under moonlight, but rests in crevices on dark nights.

Of the seven specimens (120: 100-141 mm) examined, two that were collected from among cover on the reef shortly before first morning light (one after a night of bright moonlight, the other after a dark night) contained only a few well-digested fragments, whereas, all five speared from aggregations above the reef during afternoons were full of food (including fresh material), as listed in Table 47.

Swerdloff (1970b), who recognized that *C. verater* inhabits relatively deep water, reported the following categories of prey in 13 specimens from one collection on the island of Oahu (ranked as percent of the diet): copepods, 71.5%; tunicates, 17.6%; malacostracans, 4.7%; mollusks, 2.5%; fish eggs, 1.7%; and siphonophores, 1.7%. He also presented additional data of food habits, as he compared the ecology of *C. verater* with that of its congener *C. ovalis* see below).

Gosline and Brock (1960) noted that *C. verater* occurs in deeper water than other Hawaiian pomacentrids. This conclusion was later supported by Brock and Chamberlain (1968) who, making observations from a submarine, found *C. verater* to be the most abundant reef fish around rocky outcrops at a depth of 70 m.

CONCLUSION.—*Chromis verater* is a diurnal planktivore that takes primarily copepods and larvaceans.

Chromis ovalis (Steindachner)

This species is less numerous in Kona than any of the other planktivorous damselfishes described above. It occurs over irregular substrata of exposed basalt interspersed with coral at depths between 5 and 20 m. During the day it aggregates 2 to 5 m above the reef—at about the same level as *C. verater*, with which it often forms mixed groups (Swerdloff, 1970b). Its reactions to changing light and threatening situations are as described above

TABLE 48.—Food of *Chromis ovalis*.

Rank	Items	No. fish with this item (n = 2)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	2	47.5	47.50
2	Larvaceans	2	7.5	7.50
3	Cyclopoid copepods	2	3.0	3.00
4	Mysids	1	2.5	1.25
5	Decapod shrimps	1	2.5	1.25
Also, unidentified fragments		2	37.0	37.00

for *Abudefduf abdominalis* and for other planktivorous pomacentrids; its nocturnal behavior also is like that described for these other species.

Of six specimens (124: 121-138 mm) examined, all four that were speared among corals shortly before first morning light (two after dark nights, two after moonlit nights) contained only a few well-digested fragments, whereas two that were speared from aggregations above the reef during midafternoon were full of food (including fresh items), as listed in Table 48.

Swerdloff (1970b) reported the following categories of prey in eight *C. ovalis* from one collection on the island of Oahu (ranked as percent of the diet): copepods, 60.1%; tunicates, 16.9%; malacostracans, 9.5%; mollusks, 9.5%; polychaetes, 2.3%; fish eggs, 0.8%; and siphonophores, 0.8%. Gosline and Brock (1960) reported "a mass of copepods" in the stomach of one individual of this species.

CONCLUSION.—*Chromis ovalis* is a diurnal planktivore that takes primarily copepods.

General Remarks on Damselfishes

Pomacentrids are widely recognized as being active by day and relatively inactive at night. For example, they were so described in the Gulf of California (Hobson, 1965, 1968a), and also in the tropical Atlantic (Starck and Davis, 1966; Collette and Talbot, 1972). Food-habit data from the various members of this family in areas as widely separated as the West Indies (Randall, 1967) and the Marshall Islands (Hiatt and Strasburg, 1960) show widely divergent habits: some are strictly herbivorous, others are omnivorous, and still others are strictly carnivorous.

The habitat of each pomacentrid in Kona is especially well defined. Two major categories exist: those that forage on the bottom and those that feed in the water column.

BOTTOM FEEDERS.—Pomacentrids that forage on the sea floor have especially diverse diets. Algae and organic detritus are the major foods of many, especially among species of *Pomacentrus* (Hiatt and Strasburg, 1960; Randall, 1967). In Kona, *P. jenkinsi* is in this category, but *P. pavo* in the Marshall Islands is primarily a predator on small fishes and crustaceans (Hiatt and Strasburg, 1960). The diets of species of *Abudefduf* appear even more diverse. *Abudefduf sindonis* in Kona has food habits similar to those of *P. jenkinsi,* but the highly omnivorous *A. sordidus* forages on a wide variety of benthic animals and plants, whereas the predaceous *A. imparipennis* takes mostly benthic crustaceans and polychaetes. *Abudefduf saxatilus* in the West Indies is, according to Randall (1967), "one of the most diversified of all fishes in its food habits," feeding as it does on a wide assortment of plants and animals from both sea floor and water column. Similarly, *A. troschelii* in the Gulf of California feeds on zooplankton and bits of algae from the water column, as well as organisms from the substratum (Hobson, 1968a).

WATER-COLUMN FEEDERS.—Planktivorous pomacentrids are prominent on coral reefs throughout tropical seas. Their characteristic mid-water aggregations have been described in the Indian Ocean (Eibl-Eibesfeldt, 1962), central Pacific (Hiatt and Strasburg, 1960), Gulf of California (Hobson, 1965, 1968a), and the tropical Atlantic (Starck and Davis, 1966). In the Bahamas, Stevenson (1972) showed that the height in the water column at which *Eupomacentrus partitus* feeds on plankton is determined largely by light and current. The progressive ascent of planktivorous pomacentrids into the water column during morning twilight, as they rise to their mid-water feeding grounds, and their subsequent descent to the reef during evening twilight, has been described in Kona (Hobson,

1972) and the West Indies (Collette and Talbot, 1972).

Some of these planktivorous pomacentrids, for example *Abudefduf saxatilus* and *A. troschelii,* noted above, also forage part time on the sea floor. However, most of them, including the species of *Chromis* and *Dascyllus,* are specialized as predators on zooplankton, especially copepods. Examples include the representatives of these genera on Kona reefs, described in the present report, as well as others from the central Pacific (Hiatt and Strasburg, 1960) and tropical Atlantic (Randall, 1967).

Family Cirrhitidae: hawkfishes

Paracirrhites arcatus (Cuvier)—*pili ko'a*

This hawkfish is numerous in areas richly overgrown by the coral *Pocillopora meandrina.* Typically, it rests immobile on the coral heads during day, and takes shelter among the coral branches at night. Individuals shorter than about 50 mm are among the coral branches day and night, whereas those longer than about 90 mm frequently occur on the other hard substrata—perhaps because they are too large to fit between the branches of most *Pocillopora* heads. *Paracirrhites arcatus* moves only infrequently—a short dash to capture prey, or when threatened.

Forty-five specimens (82: 49-101 mm) were collected during day and night. The nighttime situation is reflected in the 17 that were speared during the 2 h before first morning light (13 on moonlit nights, 4 on dark nights). Of these, 16 (52 to 95 mm) were resting among branches of *Pocillopora,* whereas the other (99 mm) was amid a fingerlike growth of *Porites compressus.* The stomachs were empty in 13 and contained only well-digested fragments in 3. The last individual, taken during new moon, contained a caridean shrimp that probably had been captured that night.

The daytime situation is reflected in the 12 individuals speared during afternoons, all perched in exposed positions on the reef when collected. Ten of these (71 to 101 mm) rested on *Pocillopora,* and two (95 and 97 mm) rested on rocks. Ten had stomachs full of food, much of it fresh, and although the remaining two had empty stomachs, their intestines were full.

Specimens collected at other times of day and night offer less conclusive data. Of nine speared at night (between 3 and 5 h after sunset), seven were deep among coral branches, but two rested in exposed positions (the latter situation was only rarely seen). Six of these had food in their stomachs, but although the material was well-digested in five, the sixth was full of a species of cyclopoid copepod that often swarmed around our diving lights for about 30 min, an hour or so after last evening light. Finally, of the seven speared within 2 h after sunrise as they rested on top of *Pocillopora* heads, four had the stomachs empty and three contained fresh prey. Identifiable material occurred in 20 of the 46 specimens examined, as listed in Table 49.

Hiatt and Strasburg (1960), reporting on this species from the Marshall Islands, remarked that it habitually lies motionless on the upper surface of living coral heads and listed a diet of crustaceans and fishes.

CONCLUSION.—*Paracirrhites arcatus* is a diurnal predator that feeds primarily on xanthid crabs and other benthic crustaceans.

Paracirrhites forsteri (Bloch and Schneider)—*hilu pili ko'a*

This hawkfish is numerous in coral-rich areas, where it rests immobile in exposed positions on the reef during the day (Figure 32). Its attitude is

TABLE 49.—Food of *Paracirrhites arcatus*.

Rank	Items	No. fish with this item (n = 20)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	12	43.3	25.98
2	Decapod shrimps	6	15.5	4.65
3	Fish	3	10.5	1.58
4	Ophiuroids	1	5.0	0.25
5	Calapid crabs	1	4.3	0.22
6	Cyclopoid copepods	1	4.0	0.20
7	Crab megalops	2	1.8	0.18
8	Gammaridean amphipods	2	0.5	0.05
9	Calanoid copepods	1	0.3	0.02
Also, crustacean fragments		6	13.5	4.05
	Unidentified fragments	1	1.3	0.07

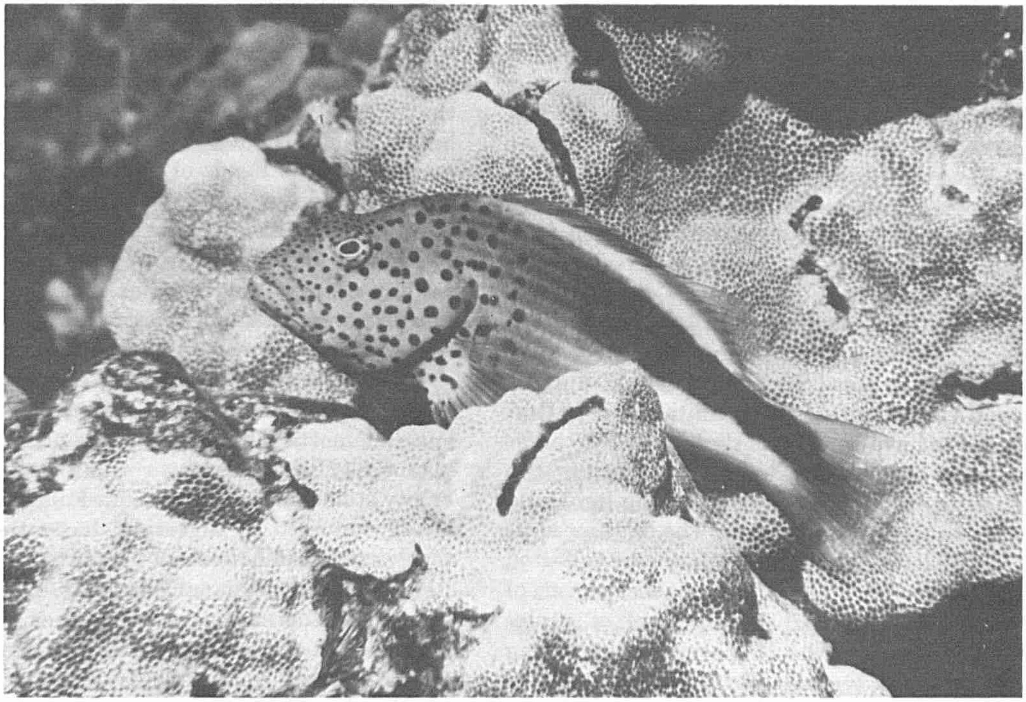

FIGURE 32.—*Paracirrhites forsteri,* a hawkfish, seated on the reef during the day.

much like that of *P. arcatus,* above, but it occurs widely on different hard surfaces, rather than being mostly associated, as is *P. arcatus,* with one type of coral. In the manner typical of hawkfishes, *P. forsteri* moves only infrequently, attacking prey that have come within range of a short, explosive dash. Such attacks were seen only during the day; at night *P. forsteri* generally is out of sight in reef crevices.

Thirty-six specimens (139: 93-181 mm) were collected during day and night. Of the 28 that were speared as they rested during midday on a variety of reef substrata, 18 contained food in the stomach, much of it relatively fresh (although in 1 the material was reduced to unidentifiable fragments). In contrast, among eight others that were speared from deep within reef crevices during the 2 h immediately before first morning light, four had empty stomachs and three contained only well-digested fragments; only the eighth specimen contained relatively fresh prey—a shrimp, *Saron marmoratus*—that appeared to have been taken that night.

Fish were the major prey, occurring in 14 of the 21 individuals that contained identifiable material (mean percent of diet volume: 66.6; ranking index: 44.4). Other food items were: caridean shrimps in four (mean percent of diet volume: 16.2; ranking index: 3.09), xanthid crabs in one (mean percent of diet volume: 4.8; ranking index: 0.23), and unidentified crustacean fragments in three (mean percent of diet volume: 12.4; ranking index: 1.77). The only identifiable fish among the gut contents was a wrasse, *Thalassoma duperrey*. Three of the four individuals containing caridean shrimps had preyed on *Saron marmoratus*. Of the larger shrimps (to about 50 mm), this was the one most frequently seen after dark, but only one of these, noted above, appeared to have been captured at night. Perhaps significantly, the specimens of *P. forsteri* that were examined had preyed on either fishes or crustaceans, but never on both.

Hiatt and Strasburg (1960), citing the similarity in habits between *P. forsteri* and *P. arcatus,* noted that the diet of *P. forsteri* runs more to fishes than crustaceans. I agree with them that this difference probably relates to the size difference between these two congeners.

CONCLUSION.—*Paracirrhites forsteri* is a diurnal predator that preys mostly on small fishes.

Cirrhitops fasciatus (Bennett) — *'o'opu kaha 'iha 'i*

This hawkfish is numerous on both coral and basalt reefs, and unlike the two species of *Paracirrhites,* above, occurs in exposed positions at night as well as during the day. In typical hawkfish fashion, it generally rests immobile on the substratum, except when attacking prey; thus, it is difficult to differentiate periods of activity from periods of inactivity.

Twenty-three specimens (76: 39-91 mm) were collected during night and day. Seven of nine speared from exposed positions under moonlight between 4 and 5 h after sunset contained prey that appeared to have been recently ingested. In addition, three of six individuals taken during the hour immediately before first morning light also contained relatively fresh prey. The daytime situation is reflected by specimens that were collected during afternoons, where the stomachs from six of eight individuals contained prey, much of it relatively fresh. Items in the 16 specimens containing identifiable prey are listed in Table 50.

CONCLUSION.—*Cirrhitops fasciatus* regularly feeds during both day and night, mostly on xanthid crabs and other benthic crustaceans.

Cirrhitus pinnulatus (Bloch and Schneider)— *po'o pa'a*

This hawkfish is numerous at depths of less than 5 m in and around crevices on surge-swept basalt reefs (Figure 5). Corals in this habitat are mostly isolated heads of *Pocillopora meandrina* and encrusting patches of *Porites compressus*. As do other hawkfishes, *C. pinnulatus* generally rests motionless on the substratum. During the day it usually remains under at least partial cover; at night it more frequently occurs in exposed positions on the reef.

All 32 specimens (152: 103-221 mm) that were examined were resting immobile on the reef when speared, most of them partially concealed in crevices. Of 17 taken during the afternoon, 14 had empty stomachs, and 3 contained material extensively damaged by digestion. In contrast, of 15 that were taken between 1 h before first morning light and 2 h after sunrise, only 4 had empty stomachs, whereas each of the other 11 had the stomach full of food, much of it fresh. Items in the 14 individuals containing identifiable material are listed in Table 51.

Most of the xanthid crabs among these gut contents were *Trapezia,* a genus common among branches of the coral *Pocillopora.* Hiatt and Strasburg (1960) also reported a crab of this genus in one *C. pinnulatus* that they examined from the

TABLE 50.—Food of *Cirrhitops fasciatus.*

Rank	Items	No. fish with this item (n = 16)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	7	30.9	13.52
2	Decapod shrimps	5	20.9	6.53
3	Crab megalops	2	7.8	0.98
4	Ophiuroids	1	6.3	0.39
5	Octopods	1	6.3	0.39
6	Gammaridean amphipods	1	0.6	0.04
Also, crustacean fragments		5	22.2	6.94
	Unidentified fragments	1	5.0	0.31

TABLE 51.—Food of *Cirrhitus pinnulatus.*

Rank	Items	No. fish with this item (n = 14)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	11	60.0	47.14
2	Oxyrhynchan crabs	3	7.5	1.61
3	Decapod shrimps	3	2.9	0.62
4	Ophiuroids	1	7.1	0.51
5	Octopods	1	7.1	0.51
6	Echinoids	1	3.2	0.23
7	Pagurid crabs	1	1.1	0.08
Also, crustacean fragments		3	11.1	2.38

Marshall Islands. Randall (1955) reported only brachyuran crabs in the diet of two specimens that he examined from the Gilbert Islands.

CONCLUSION.—*Cirrhitus pinnulatus* is a nocturnal predator that hunts mostly xanthid crabs.

Family Labridae: wrasses

Bodianus bilunulatus (Lacépède) — *'a'awa*

This relatively large, solitary wrasse occurs only infrequently on the shallow reefs in Kona as it lives mostly at depths below 15 m. Two individuals (172 and 283 mm) were speared during midafternoon as they moved actively among coral at 25 m along the outer drop-off, and the guts of both were full of crushed mollusks.

CONCLUSION.—*Bodianus bilunulatus* feeds on mollusks during the day.

Cheilinus rhodochrous Günther—*po'ou*

This labrid is numerous over both coral and rocky substrata deeper than about 10 m. It is a solitary species that hovers close to the reef during the day and takes shelter in the reef at night. Several times larger individuals attempted to take fish that were impaled on my spear, and twice they succeeded despite my attempts to drive them away.

Among 16 specimens (175: 129-242 mm) collected during afternoons, 6 contained only a few well-digested fragments posteriorly in the gut, and most of the material in the other 10 was far digested. Fish were the major prey, occurring in 4 of the 10 individuals that contained identifiable material (mean percent of diet volume: 40; ranking index: 16). Other food items were: decapod shrimps in three (mean percent of diet volume: 30; ranking index: 9), brachyuran crabs in one (mean percent of diet volume: 8; ranking index: 0.8), unidentified crustacean fragments in two (mean percent of diet volume: 12; ranking index: 2.4), and other unidentified fragments in two (mean percent of diet volume: 10; ranking index: 2). The only fish that could be identified was a pomacentrid, *Pomacentrus jenkinsi,* and the only identifiable shrimp was *Saron marmoratus*. Generally *C. rhodochrous* preys on large organisms, but because it crushes them upon ingestion, identifications are difficult. Presumably crushing the food items accelerates digestion, thus contributing to the poor condition of this material. However, because all these specimens were collected during afternoons, the advanced digestion could also reflect early morning feeding.

Cheilinus rhodochrous is a stalking predator, equipped by a relatively large mouth and pair of large canine teeth at the front of each jaw to hunt prey that are relatively larger and more active than those taken by most other labrids. Most of the specimens that were examined contained a single large prey organism, indicating that feeding is infrequent and that each successful attack provides enough nourishment to sustain the predator for some time.

CONCLUSION.—*Cheilinus rhodochrous* is a diurnal predator that stalks relatively large fishes and crustaceans. It may have peaks in feeding early and late in the day, but is inactive at night.

Pseudocheilinus octotaenia Jenkins

This small species is one of the more numerous labrids on coral-rich reefs at depths to at least 30 m, but its large numbers are difficult to appreciate because it occurs close among the many narrow interstices of the reef. It is strictly a diurnal species that takes shelter in the reef at night.

All 12 specimens (77: 50-95 mm) taken during afternoons had material in their stomachs, but the food items were difficult to identify because they were small and had been crushed when ingested. Thus, most of the gut contents of all 10 individuals that contained recognizable material can be listed only as unidentified crustacean fragments (mean percent of diet volume and ranking index: 71.9). Items that could be identified are: brachyuran crabs in three (mean percent of diet volume: 22; ranking index: 6.6), echinoids in one (mean percent of diet volume: 5; ranking index: 0.5), demersal fish eggs in one (mean percent of diet volume: 1; ranking index: 0.1), and copepods in one (mean percent of diet volume: 0.1; ranking index: 0.01).

CONCLUSION.—*Pseudocheilinus octotaenia* is a diurnal predator that feeds mostly on brachyuran crabs and other benthic crustaceans.

Labroides phthirophagus Randall

This small wrasse (most are less than 100 mm long) is specialized to pick ectoparasites from the bodies of other fishes at well-defined cleaning stations (Figure 33). Usually two or several of these cleaners are active at each station. It is a diurnal species that shelters in reef crevices at night (Hobson, 1972).

This is the major cleaner fish on Hawaiian reefs, and its habits are well known (e.g. Randall, 1958; Youngbluth, 1968; Losey, 1971; Hobson, 1971). Because the activity of this species has been extensively documented, it was only incidentally observed during the present study.

CONCLUSION.—*Labroides phthirophagus* cleans ectoparasites from the bodies of other fishes during the day.

Thalassoma duperrey* (Quoy and Gaimard) — *hinalea lauwili

This is probably the most ubiquitous fish on Kona reefs (Figure 33): it is numerous everywhere, from the surge-swept reef tops to the outer drop-off on both coral-rich and exposed basalt substrata. In the daytime fish counts along transect lines, *T. duperrey* ranked among the five most numerous species in all the sampled habitats. An opportunist, it is consistently the first fish to appear when a sea urchin has been crushed, or when a rock has been overturned and vulnerable organisms exposed. Sometimes it follows close to the feeding jaws of scarids to snap up prey uncovered when these herbivores disturb the substratum. This wrasse is adapted to a wide range of habits: it forages in the water column when plankton are abundant, but mostly picks organisms off a variety of substrata. It is strictly a diurnal species that shelters in reef crevices at night (Hobson, 1972).

Many of the juveniles are cleaners and maintain stations at certain prominent coral heads. On one survey 5 m deep along approximately 1 km of the north shore of Honaunau Bay, I found a cleaning station maintained by these fish at every large head of *Porites pukoensis* that was of a distinctive mustardlike hue and characterized by golf-ball-sized nodules separated by narrow, shallow depressions. The general extent of this cleaner's relationship to this type of coral was not determined, but I saw cleaning stations nowhere else during the survey. Because the juveniles of *T. duperrey* always discontinued cleaning when a human was near, incidental observations of this activity were rare. And, as noted above in discussing *Labroides*

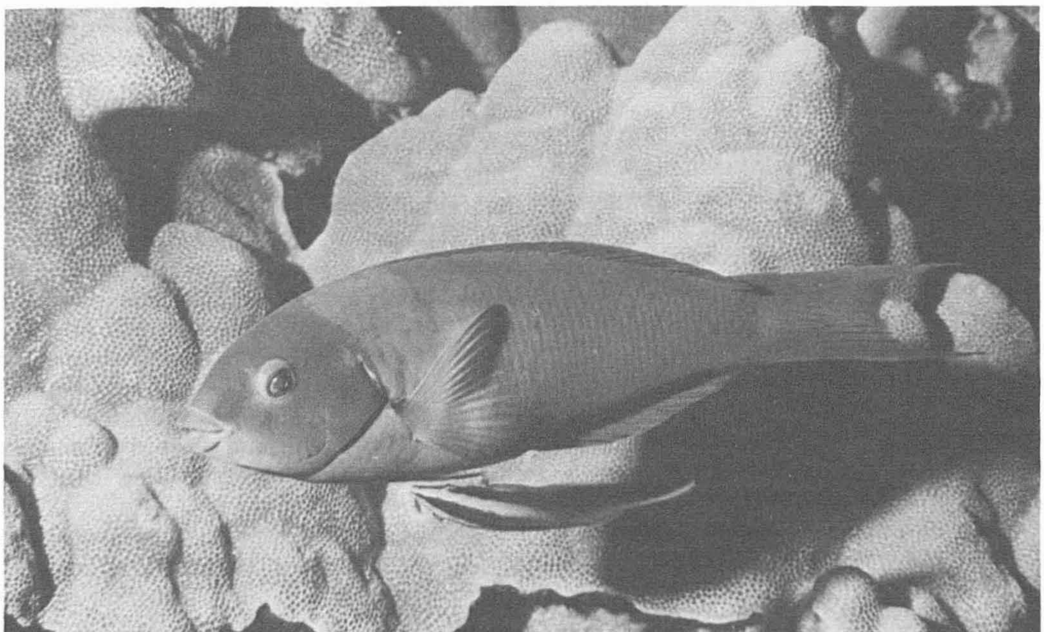

FIGURE 33.—A wrasse, *Thalassoma duperrey*, being cleaned by another wrasse, *Labroides phthirophagus*.

phthirophagus, my observations of cleaning were mostly incidental. Nevertheless, it was evident that cleaning by *T. duperrey* is mostly an activity of juveniles. Adults clean only infrequently, and not at well-defined cleaning stations.

To indicate the food of the post juveniles of this species, 24 specimens, 125 (103-146) mm long, were speared during the day as they swam actively over the reef. All contained identifiable items, as listed in Table 52. In contrast with the diet of most fishes examined during this study, no single item or certain few items predominate in the diet of *T. duperrey,* a circumstance that undoubtedly relates to its populating a wide range of habitats.

CONCLUSION.—*Thalassoma duperrey* is a diurnal predator that feeds on a very wide range of shelled organisms, most of them benthic.

Thalassoma fuscus **(Lacépède)—*hou***

This species was shown by numerous observations of spawning aggregations to include the nominal *T. umbrostigma* (which represents the juveniles and females). It is a fish of shallow water along rocky, surge-swept shores and is one of the most numerous species on the shallow reef flats. Generally it does not occur in water deeper than about 5 m and is strictly a diurnal fish that shelters in reef crevices after dark.

All 14 specimens (132: 60-200 mm) speared as they swam on the reef during daylight contained identifiable food material, as listed in Table 53. Hiatt and Strasburg (1960) reported on two specimens of this species (as *T. umbrostigma)* in the Marshall Islands: one had consumed a stomatopod, the other a fish. Randall (1955) reported (also as *T. umbrostigma*) that one specimen taken in the Gilbert Islands contained a crab.

CONCLUSION.—*Thalassoma fuscus* is a diurnal predator that feeds mostly on crabs and mollusks.

Halichoeres ornatissimus **(Garrett)—*la'o***

In Kona this labrid is nowhere particularly numerous, yet it occurs regularly in all inshore habitats. It is generally solitary and swims close to cover during the day. At night it is out of sight, presumably resting in crevices or under the sand.

All 13 specimens (96: 76-115 mm), speared during daylight, had a full gut that included fresh material, as listed in Table 54. Food items more than about 4 mm in greatest dimension were crushed, and this included most of the mollusks. Probably at least much of the unidentified material constituted fragmented molluscan soft parts. This fish plucks small benthic organisms off the substratum, including some forms, like the didemnid tunicates, that are attached to the reef.

TABLE 52.—Food of *Thalassoma duperrey.*

Rank	Items	No. fish with this item (n = 24)	Mean percent of diet volume	Ranking index
1	Gastropod mollusks	9	7.5	2.81
2	Echinoids	3	7.9	0.99
3	Brachyuran crabs	3	6.1	0.76
4	Pelecypod mollusks	3	5.0	0.63
5	Gammaridean amphipods	9	1.5	0.56
6	Calanoid copepods	2	6.3	0.53
7	Tanaids	6	1.3	0.33
8	Cyclopoid copepods	4	1.4	0.23
9	Scleractinian corals	2	2.5	0.21
10	Polychaetes	2	2.1	0.18
11	Ophiuroids	2	1.5	0.13
12	Tunicates	2	1.5	0.13
13	Isopods	2	0.9	0.08
14	Fish eggs	2	0.6	0.05
15	Caprellid amphipods	2	0.4	0.03
16	Pagurid crabs	2	0.4	0.03
17	Foraminiferans	1	0.2	<0.01
18	Sipunculid introverts	1	0.2	<0.01
19	Fish	1	0.2	<0.01
20	Unidentified eggs	1	<0.1	<0.01
Also, crustacean fragments		11	9.4	4.31
	Algae fragments	8	11.5	3.83
	Unidentified material	15	31.5	19.69

TABLE 53.—Food of *Thalassoma fuscus*.

Rank	Items	No. fish with this item (n = 14)	Mean percent of diet volume	Ranking index
1	Brachyuran crabs	7	35.5	17.75
2	Mollusks	5	17.2	6.14
3	Octopods	1	7.1	0.51
4	Ophiuroids	1	5.0	0.36
5	Polychaetes	2	1.8	0.26
6	Sipunculid introverts	2	1.4	0.20
7	Crab megalops	1	2.8	0.20
8	Fish	1	2.5	0.18
9	Gammaridean amphipods	3	0.7	0.15
10	Cyclopoid copepods	3	0.6	0.13
11	Calanoid copepods	1	1.4	0.10
12	Isopods	1	0.1	<0.01
Also, crustacean fragments		2	3.7	0.53
	Unidentified fragments	8	20.2	11.54

TABLE 54.—Food of *Halichoeres ornatissimus*.

Rank	Items	No. fish with this item (n = 13)	Mean percent of diet volume	Ranking index
1	Mollusks	6	13.5	6.23
2	Gammaridean amphipods	7	7.7	4.15
3	Colonial diatoms	4	6.9	2.12
4	Didemnid tunicates	3	8.8	2.03
5	Tanaids	5	1.5	0.58
6	Harpacticoid copepods	4	1.7	0.52
7	Sipunculid introverts	3	1.2	0.28
8	Ophiuroids	1	3.1	0.24
9	Cyclopoid copepods	2	0.8	0.12
10	Polychaetes	1	1.5	0.12
11	Isopods	2	0.5	0.08
12	Demersal eggs	1	0.8	0.06
13	Echinoids	1	0.4	0.03
14	Ostracods	1	0.1	<0.01
Also, crustacean fragments		7	10.8	5.82
	Sand and foraminiferans	3	4.5	1.04
	Algal fragments	2	1.2	0.18
	Unidentified fragments	10	35.0	26.92

The widespread occurrence of this fish probably relates to the fact that no single item, or certain few items, especially predominate in its diet. This is true to an even greater degree in the ubiquitous *Thalassoma duperrey,* above, but is unlike most fishes on Kona reefs.

CONCLUSION.—*Halichoeres ornatissimus* is a diurnal predator that picks a wide variety of small benthic animals from the sea floor.

Stethojulis balteata (Quoy and Gaimard) — *'omaka*

This wrasse is most numerous on the shallow reef flats and on some of the reefs richly overgrown with corals. During the day it swims close to rocks or coral, at which it periodically picks. At night it rests in reef crevices, or buried in the sand.

All five specimens (90: 76-102 mm) collected during daylight had a gut full of material, some of it fresh, as listed in Table 55. The major food items—small crustaceans shorter than about 4 mm—were mostly intact. Larger items, such as some of the gastropods, were crushed.

CONCLUSION.—*Stethojulis balteata* is a diurnal predator that mostly picks small crustaceans and gastropods off the sea floor.

Anampses cuvier Quoy and Gaimard—*'opule*

Although this wrasse occupies all inshore reef habitats in Kona, it is most numerous where the sea floor consists of basalt boulders. During the day, solitary individuals swim close to the substratum, where they inspect the surface, and frequently pluck at the low growth of algae on the

TABLE 55.—Food of *Stethojulis balteata.*

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Harpacticoid copepods	5	19.4	19.40
2	Prosobranch gastropods	4	15.6	12.48
3	Gammaridean amphipods	3	8.6	5.16
4	Tanaids	3	5.0	3.00
5	Foraminiferans	2	2.4	0.96
6	Isopods	2	2.4	0.96
7	Polychaetes	1	4.0	0.80
8	Echinoids	1	1.0	0.20
9	Sipunculid introverts	1	0.6	0.12
10	Cyclopoid copepods	1	0.4	0.08
Also, crustacean fragments		5	15.0	15.00
	Sand and debris	4	10.2	8.16
	Unidentified fragments	4	15.4	12.32

TABLE 56.—Food of *Anampses cuvier.*

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Gammaridean amphipods	10	28.9	24.08
2	Mollusks	10	18.1	15.08
3	Polychaetes	3	4.3	1.08
4	Xanthid crabs	3	1.8	0.45
5	Fish eggs, demersal	1	5.0	0.42
6	Echinoids	2	1.9	0.32
7	Tanaids	3	0.3	0.08
8	Isopods	3	0.3	0.08
9	Didemnid tunicates	2	0.3	0.05
Also, crustacean fragments		9	14.1	10.58
	Sand and foraminiferans	4	4.3	1.43
	Algal fragments	3	1.9	0.48
	Unidentified fragments	8	18.8	12.53

rocks. Much sand has accumulated here, and periodically they pause during their foraging to blow a small cloud of sand and debris from their mouths. At night this wrasse is out of sight, presumably resting in reef crevices.

All 12 specimens (169: 110-225 mm) speared during daylight had a gut full of material, much of it fresh, as listed in Table 56. The gammaridean amphipods, all shorter than 3 mm, were the major prey of even the largest individuals. Furthermore, the mollusks, which were the only other significant prey, were mostly prosobranch gastropods also shorter than 3 mm.

Undoubtedly, the small size and other characteristics of these prey are reflected in the feeding morphology of *A. cuvier* and its congeners, certain features of which set them apart from most other labrids in Kona. In dentition, the species of *Anampses,* with two flattened teeth projecting forward from the front of each jaw, are unlike those of any other genus of Hawaiian fishes (Gosline and Brock, 1960). Obviously this specialized dentition effectively captures gammarideans that inhabit the low stubble of algae overgrowing most basalt boulders. Compared with most other labrids, species of *Anampses* have the pharyngeal teeth reduced, which is expected considering the relatively small proportion of crushed items in the diet. The food items are mostly so small they need not be crushed upon ingestion. Gammarideans and certain other prey of similar size regularly pass intact through the pharynx of even those labrids with well-developed pharyngeal teeth (see accounts of other labrids in this report).

CONCLUSION.—*Anampses cuvier* is a diurnal predator that mostly plucks small benthic organisms, especially gammarideans, from rocky substrata.

Coris gaimard (Quoy and Gaimard)—*hinalea lolo*

This wrasse is most numerous where the reef is interspersed with small patches of sand. It forages in this sand during daylight, usually close to the base of rock or coral. Of all the wrasses treated in this report, this one is the most adept at excavating buried organisms. Moving its head sidewise, it effectively overturns small stones or digs in the

TABLE 57.—Food of *Coris gaimard*.

Rank	Items	No. fish with this item (*n* = 9)	Mean percent of diet volume	Ranking index
1	Mollusks	9	72.2	72.20
2	Echinoids	3	9.8	3.27
3	Crabs	1	2.2	2.44
4	Didemnid tunicates	1	0.6	0.07
5	Gammaridean amphipods	1	0.2	0.02
Also, crustacean fragments		5	15.0	8.33

TABLE 58.—Food of *Macropharyngodon geoffroy*.

Rank	Items	No. fish with this item (*n* = 8)	Mean percent of diet volume	Ranking index
1	Prosobranch gastropods	8	37.8	37.80
2	Foraminiferans	8	35.3	35.30
3	Harpacticoid copepods	2	0.4	0.10
4	Gammaridean amphipods	1	0.1	0.01
Also, crustacean fragments		2	0.6	0.15
	Sand and algae	5	8.4	5.25
	Unidentified fragments	6	17.4	13.05

sand, exposing hidden prey. It is not seen at night, when presumably it is buried in the sand, or secreted in reef crevices.

All nine specimens (117: 81-164 mm), speared during daylight, contained relatively fresh material, but items longer than a few millimeters were crushed so extensively that precise identifications were difficult. The gut contents are itemized in Table 57.

CONCLUSION.—*Coris gaimard* is a diurnal predator that mostly excavates mollusks and other prey that are buried in the sand.

Macropharyngodon geoffroy (Quoy and Gaimard)

This solitary little wrasse is widespread on Kona reefs, but is nowhere numerous. It swims close among coral and rocks during daylight, but is not seen after dark, when presumably it secretes itself in reef crevices, or under the sand.

All eight specimens (99: 74-120 mm) collected during the day had the gut full of the items listed in Table 58, almost all crushed.

The exceptionally large pharyngeal teeth of this wrasse obviously are adapted to a diet of heavily shelled organisms. The specimens examined, which had fed mostly on gastropods and foraminiferans, are undoubtedly representative. The foraminiferans were almost all *Marginospora vertebralis,* which is an abundant benthic form on shallow reefs in the Marshall Islands (Cushman, Todd, and Post, 1954).

CONCLUSION.—*Macropharyngodon geoffroy* is a diurnal predator that feeds mostly on benthic gastropods and foraminiferans.

Gomphosus varius Lacépède—bird wrasse, *hinalea 'i'iwi*

This wrasse is numerous on shallow surge-swept reefs, especially where the coral *Pocillopora meandrina* abounds. During daylight solitary individuals swim among the coral heads, probing with their elongated snouts among the coral branches. At night the species lies quietly in reef crevices.

All 12 specimens (142: 114-180 mm) collected during the day had their guts full of the items listed in Table 59. Most of this material was crushed. The xanthid crabs were mostly *Trapezia* sp. They and the alpheids are species that live among the branches of *P. meandrina.* Hiatt and Strasburg (1960) noted that this labrid's major prey in the Marshall Islands are xanthids and alpheids that live in the interstices of ramose corals. Randall (1955) similarly reported alpheid shrimps and also stomatopods in the diet of this species (as *G. tricolor)* in the Gilbert Islands.

Gomphosus varius takes relatively large motile prey, and with its large mouth does not pluck them from the substratum in the manner characteristic of the many other wrasses that prey on relatively tiny or sessile organisms. Rather, this wrasse vigorously wrests its prey from the reef crevices in which they are secreted.

TABLE 59.—Food of *Gomphosus varius*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Xanthid crabs	7	37.9	22.11
2	Alpheid shrimps	2	6.7	1.12
3	Pelecypods	1	4.2	0.35
4	Gastropods	2	2.1	0.35
Also, crustacean fragments		8	25.8	17.20
	Unidentified fragments	4	23.3	7.77

CONCLUSION.—*Gomphosus varius* is a diurnal predator that takes relatively large crustaceans from reef crevices.

General Remarks on Wrasses

Kona reefs, like tropical reefs the world over, are populated by a diverse array of wrasses, most of them with strong pharyngeal teeth adapted to crush hard-bodied prey. *Macropharyngodon geoffroy,* for example, preys on more heavily armored prey—in this case mollusks and foraminiferans. Others, like *Anampses cuvier,* have the pharyngeal teeth less developed and prey mostly on tiny crustaceans. Some of the wrasses, especially *Thalassoma duperrey,* are highly opportunistic, and these tend to be the most widespread and have the most varied diets.

It is well known that wrasses are active only during the day; at night they rest in reef crevices and under the sand (Longley and Hildebrand, 1941; Gosline and Brock, 1960; Hobson, 1965, 1968a, 1972; Starck and Davis, 1966; Collette and Talbot, 1972). They are among the first diurnal fishes on the reef to seek cover at day's end, and among the last to leave cover in the morning (Hobson, 1965, 1968a, 1972; Collette and Talbot, 1972).

Family Scaridae: parrotfishes

Scarus sordidus **Forskål**—*uhu*

This is one of the more numerous parrotfishes in Kona, especially over coral-rich reefs. During the day, it swims actively close to the substratum, often in groups. With its parrotlike beak, it scrapes away the fine filamentous algae that grows over the surface of dead coral, especially *Porites.* Although frequently it scrapes up to the edge of living coral, it stops there (Figure 34). During twilight, this species migrates in schools from one part of the reef to another, but the migratory pattern remains unclear (Hobson, 1972).

At night *S. sordidus* rests solitarily in reef crevices. Because some parrotfishes are known to secrete a mucous envelope around themselves at night (Winn, 1955), during a series of night observations over 3 mo I estimated the standard length of each resting parrotfish, and noted whether or not it was encased in mucus. During these observations, 20 individuals of this species were seen, estimated to be between 150 and 350 mm long. All eight that appeared to be shorter than 300 mm were in mucous envelopes, whereas all six without envelopes were judged to be longer than 300 mm. The other six, all estimated to exceed about 300 mm long, were in envelopes. Thus, all the smaller individuals, but only some of the larger ones, were in envelopes.

The guts of all seven *S. sordidus* (195: 150-213 mm) that were speared during midday were full of bits of algae, mixed with calcareous powder, organic slurry, and sand (proportions undetermined, but the algae constituted less than 20%). No evidence was found in these specimens of coral tissues or mucus (the latter is prominent in the gut contents of fishes known to feed on coral), even though Hiatt and Strasburg (1960) reported that coral polyps constituted the major food of this parrotfish in the Marshall Islands. These authors stated (p. 103): "Scraping living coral heads seems to be its predominant mode of feeding." This observation contrasts with mine in Kona, where *S. sordidus* avoids the living coral when feeding.

CONCLUSION.—*Scarus sordidus* is a diurnal herbivore that feeds mostly by scraping fine benthic algae that have overgrown the surface of dead coral.

Scarus taeniurus **Valenciennes**—*uhu*

My observations of their social interactions render it clear that the two forms Schultz (1969) distinguished in Hawaii as *S. taeniurus* and *S. forsteri* are conspecific and that his "*S. forsteri*" represents the large male of the species.

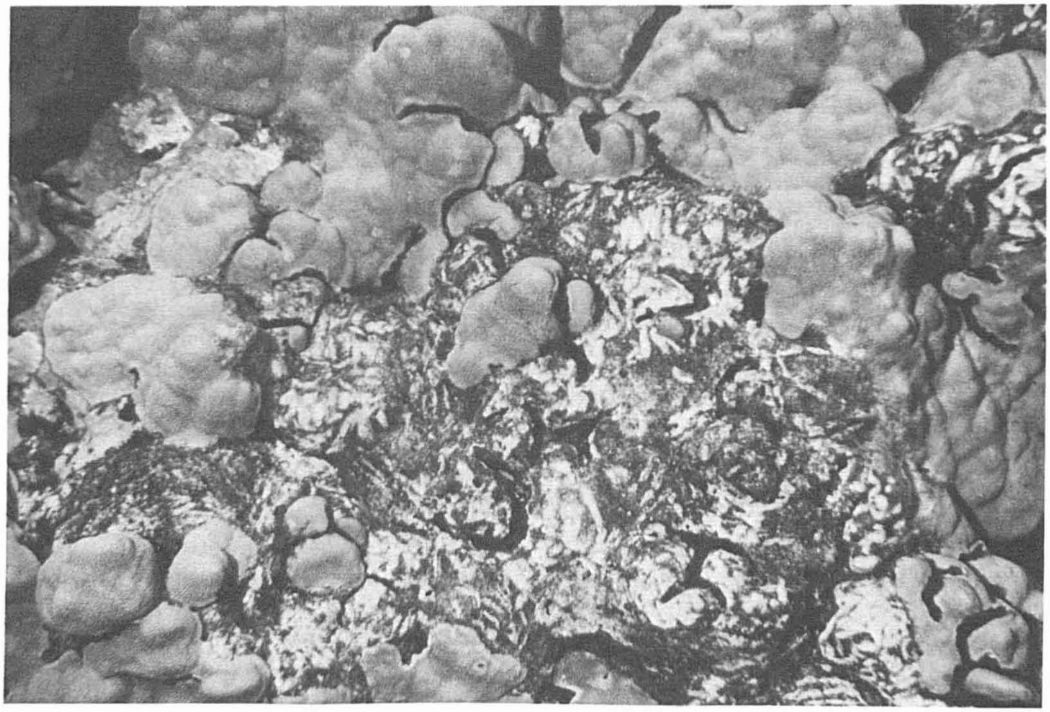

FIGURE 34.—Area of the reef showing scrape marks made by the teeth of grazing parrotfishes, mostly *Scarus sordidus*. Note that grazing has occurred only where dead coral is overgrown with algae—no living coral has been scraped.

This, the smallest Hawaiian species of *Scarus* (not exceeding a length of about 300 mm), is by far the most numerous parrotfish over exposed basalt on shallow reef flats and adjacent reef faces. The smaller juveniles and females, usually in aggregations, tend to occupy the shallow flats, the larger, distinctively hued males, which are usually solitary, tend to occupy the reef faces. This species is like *S. sordidus* in grazing during the day; however, whereas *S. sordidus* usually scrapes algae from the surface of dead coral, *S. taeniurus* ordinarily scrapes algae from the surface of rocks.

At night *S. taeniurus* rests in reef crevices. During the series of night observations in which I checked the incidence of mucous envelopes, all 11 *S. taeniurus,* which were less than 300 mm long, were in envelopes (Figure 35).

The two individuals (150 and 243 mm) that were collected during midday were full of bits of algae, mixed with calcareous powder, organic slurry, and sand (proportions undetermined, but the algae made up less than 20%), with no evident trace of coral tissue or mucus.

CONCLUSION.—*Scarus taeniurus* is a diurnal herbivore that usually feeds by scraping benthic algae from rock surfaces.

Scarus rubroviolaceus Bleeker—*uhu palukaluka*

During the day this parrotfish ranges over the reef, usually in mixed groups of several males and females. It occurs on all the inshore reefs, but mostly on rock substrata. Generally, using the sides of its jaws, it takes one bite and then withdraws a few centimeters before approaching for another bite.

At night *S. rubroviolaceus* rests in reef crevices. While surveying the incidence of mucous envelopes in resting parrotfishes (see accounts for *S. sordidus* and *S. taeniurus* above), of the nine *S. rubroviolaceus* that were observed, including both males and females approximately 200 to 500 (mean 394) mm long, none were in envelopes (Figure 36). Because the large and distinctive males of *S. rubroviolaceus* are not numerous, I came to recognize some individuals. These often returned

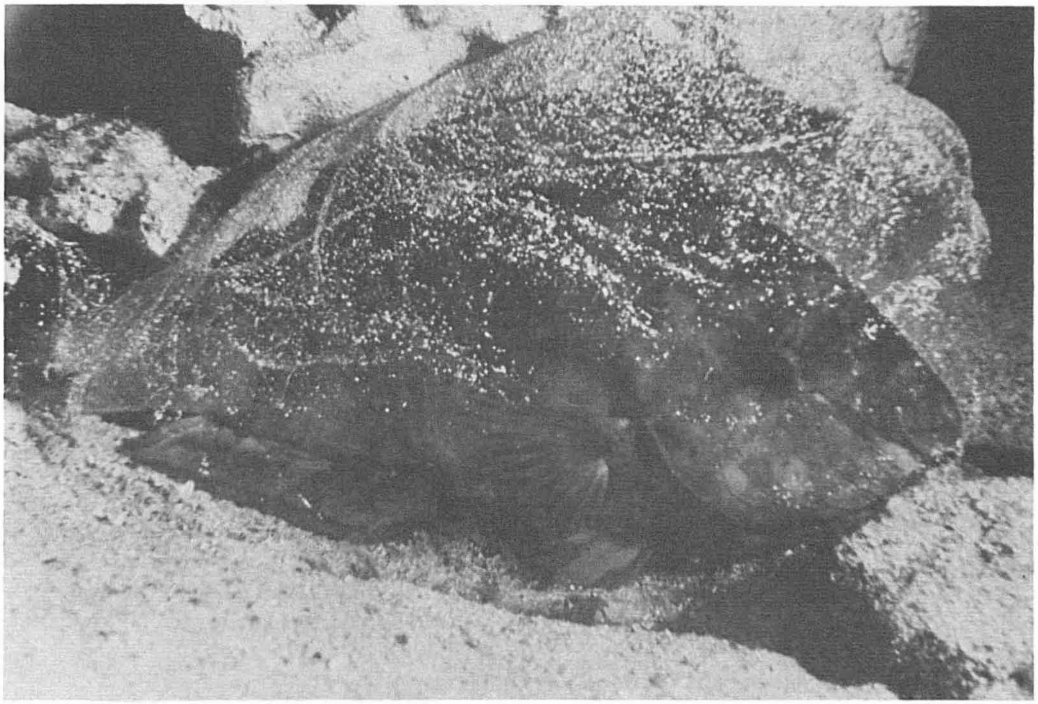

FIGURE 35.—*Scarus taeniurus,* a parrotfish, resting in a mucous envelope at night, a habit apparently shared by all members of this relatively small species.

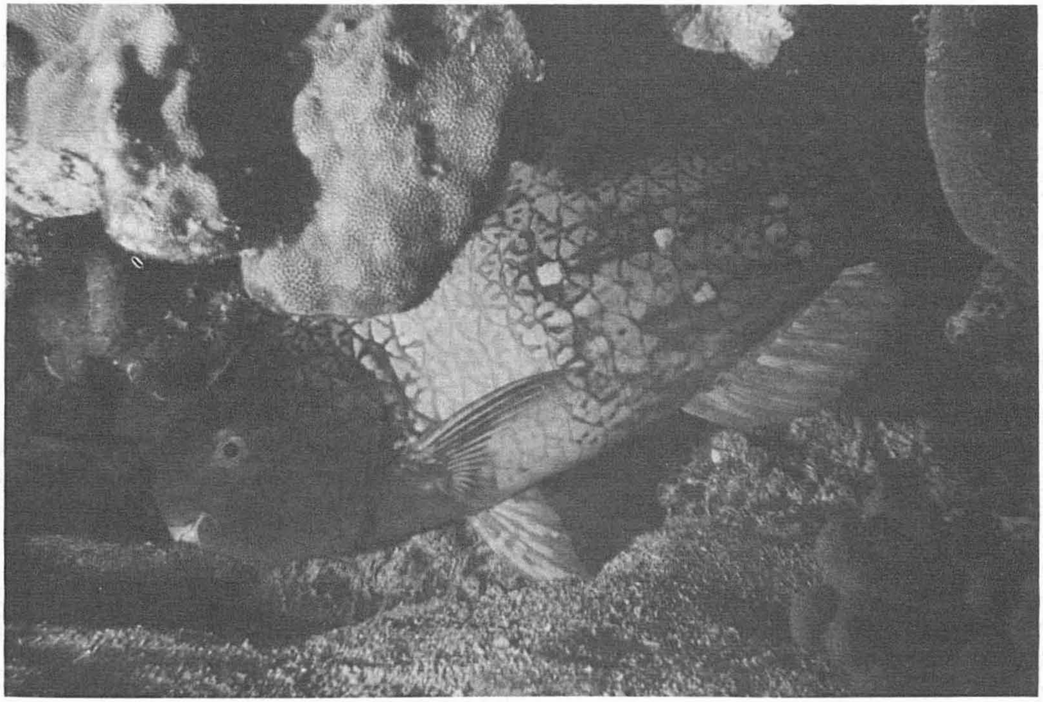

FIGURE 36.—*Scarus rubroviolaceus,* female, a parrotfish, resting under a ledge at night. Members of this species were never seen in mucous envelopes.

night after night to caves in the same areas, but not necessarily to the same cave, as has been reported for some parrotfishes elsewhere (e.g. Winn and Bardach, 1960; Starck and Davis, 1966).

The guts of two males (340 and 410 mm) that were speared during midday were full of bits of algae mixed with calcareous powder, organic slurry, and sand (proportions undetermined, but the algae constituted less than 20%), with no evident trace of coral tissue or mucus.

CONCLUSION.—*Scarus rubroviolaceus* is a diurnal herbivore that typically scrapes benthic algae from rock surfaces.

General Remarks on Parrotfishes

It is well known that parrotfishes are quiescent at night. They have been thus described in the tropical Atlantic (Winn, 1955; Winn and Bardach, 1959, 1960), eastern Pacific (Hobson, 1965; Rosenblatt and Hobson, 1969), Hawaii (Hobson, 1972), and elsewhere. Earlier (Hobson, 1965), I suggested that mucous envelopes in resting parrotfishes at night are characteristic of certain small individuals, or of individuals suffering injury or stress. The relation between small size and envelope secretion was also noted by Starck and Davis (1966) and by Casimir (1971). Winn and Bardach (1959) believed that the envelope is a defense against nocturnal predators, especially those that sense prey by olfaction or gustation, as do certain moray eels (Bardach, Winn, and Menzel, 1959). Because the threat from predators increases with decreasing size, obviously the smaller individuals are in greatest need for protection. Similarly, it is known that injured or distressed fishes are particularly attractive to predators (e.g. Hobson, 1968a), so envelope secretion by parrotfishes suffering these conditions is consistent with the idea that the envelopes provide protection. The survey of mucous envelopes in Kona shows a decreasing incidence with increasing size. Nevertheless, Winn and Bardach (1960), working with *Scarus vetula* at Bermuda, found that certain individuals in aquaria produced the envelope irregularly, and Smith and Tyler (1972) found that one individual of that species observed on a reef in the Virgin Islands formed an envelope on some nights, but not on others. Probably this variation within individuals occurs in other species too, but the question was not examined in Kona, where only certain males of *S. rubroviolaceus* were recognized as individuals, and these were never seen in envelopes.

There is controversy over the diet of parrotfishes. Hiatt and Strasburg (1960) reported a diet of living coral not only in *S. sordidus*, as noted above, but also in all other scarids they examined in the Marshall Islands. I found no evidence that any of the species in Kona, including *S. sordidus*, feed on living coral. Randall (1967) similarly concluded that parrotfishes in the West Indies do not feed on living coral; he noted the large amount of sand in the guts of parrotfishes, and suggested that this material, taken purposefully, aids in grinding plant tissue—the primary food —in the pharyngeal mill.

Although I classify all parrotfish species in Kona as herbivores, their large gut loads of calcareous powder, organic slurry, and sand seem too great a proportion of the total contents to have been taken only incidentally, or to be adaptive only because it aids in grinding up plant tissue. There is need to look closer at how parrotfishes utilize the material they ingest.

Family Blenniidae: combtooth blennies

The combtooth blennies are most numerous in tide pools and close to rocky shores, where frequently they are the dominant fishes. However, this report considers only those species that occur regularly in water deeper than 5 m.

Exallias brevis (Kner)—*pao'o kauila*

Because *E. brevis* is distinctively hued and habitually perches in exposed positions during the day (Figure 37), it is frequently noticed even though it is not especially numerous. It rarely leaves the sea floor and usually rests immobile except when scraping the surface of living coral with its comblike teeth. After dark, it is secreted in reef crevices and seen only occasionally.

Of the 10 specimens (94: 70-106 mm) examined, 2 that were taken from under partial cover at night (between 4 and 5 h after sunset) contained only well-digested fragments, whereas only 1 taken during the day was empty, and the other 7 were full of food, including fresh material. The major item in all seven (over 90% of the contents in each) was scleractinian corals—both skeletal and tissue fragments, along with much mucus. The remaining identifiable items in the diet were fine filamentous algae and diatoms.

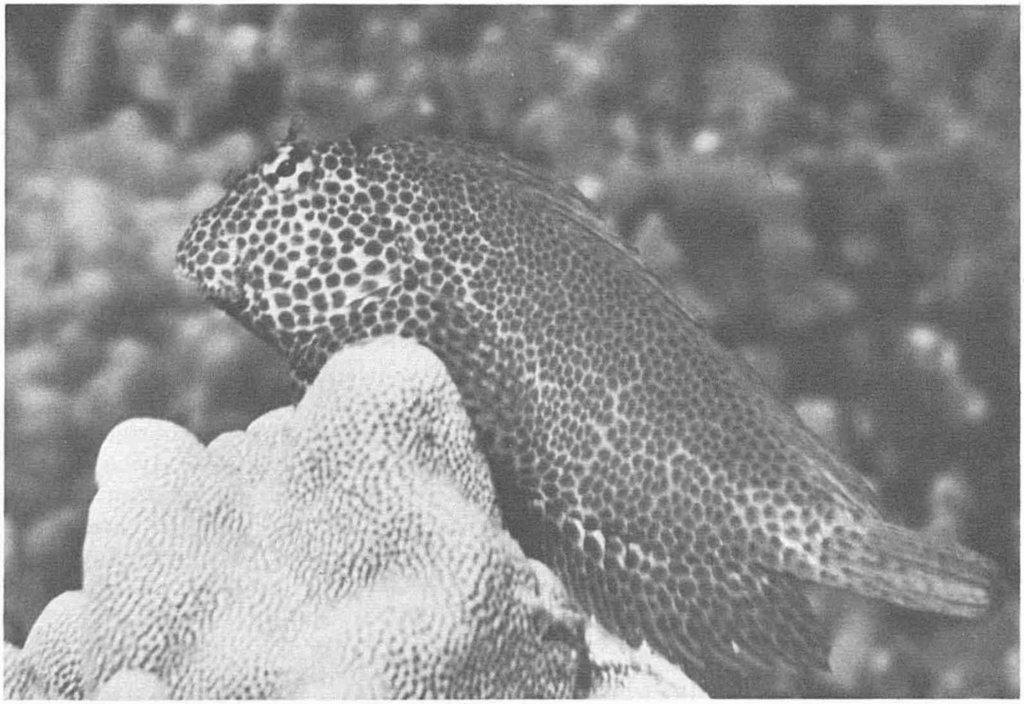

FIGURE 37.—*Exallias brevis,* a blenny, showing typical diurnal attitude.

In contrast to these food data, Hiatt and Strasburg (1960) found only filamentous algae and detritus in the single *E. brevis* (80 mm) that they examined in the Marshall Islands.

CONCLUSION.—*Exallias brevis* is a diurnal species that feeds largely on scleractinian corals, both tissue and mucus.

Cirripectus variolosus (Valenciennes)

During the day, this relatively small blenny moves about close to cover on the reef, remaining in contact with the substratum. Though numerous, it is not seen after dark, when presumably it is secreted in reef crevices.

The guts of both specimens (66 and 80 mm) collected during midday contained filamentous algae (about 40% of the diet volume) and what appeared to be detritus (50 to 60%). In addition, one contained a few scleractinian coral fragments (5%). Except for the coral fragments, the diet of these two individuals was the same as that of one specimen of this species examined by Hiatt and Strasburg (1960) in the Marshall Islands.

CONCLUSION.—*Cirripectus variolosus* is a diurnal species that feeds mostly on algae and detritus.

Plagiotremus goslinei (Strasburg)—sabre-toothed blenny

During the day, *P. goslinei* hovers a meter or so above the reef, from which position it attacks larger fishes that incidentally pass by, striking them unseen from below and behind, much as does *P. azalea* in the eastern Pacific (Hobson, 1968a, 1969). But whereas *P. azalea* usually aggregates when hovering above the reef, *P. goslinei* usually is solitary. No specimens of *P. goslinei* were collected, but presumably it feeds on the mucus and dermal tissue of its victim, as do other species of this genus, including *P. rhinorhynchus* (Wickler, 1960), *P. azalea* (Hobson, 1968a), and *P. townsendi* (Springer and Smith-Vaniz, 1972). These species are called sabre-toothed blennies because each carries in its lower jaw a pair of enormous fangs. Eibl-Eibesfeldt (1955) and Strasburg (1960) believed that these fangs are used in feeding, but Wickler (1960) concluded from work in aquaria that *P. rhinorhynchus* uses its fangs not to feed, but rather to defend its territory.

Plagiotremus goslinei hovers above the reef during only part of the day. Much of the time it occupies abandoned mollusk and worm tubes on the rocks, and these retreats also serve as resting places at night. In the eastern Pacific, *P. azalea* uses similar tubes in the same way (Hobson, 1968a, 1969).

CONCLUSION.—*Plagiotremus goslinei* is a diurnal predator that feeds on mucus and dermal tissue of larger fishes.

General Remarks on Combtooth Blennies

The combtooth blennies are generally regarded as diurnal. For example, Starck and Davis (1966) did not see members of the family, known to be present, during many night observations on Florida reefs, and Randall (1967) reported the group to be diurnal in the West Indies.

Although food habits remain unknown or uncertain for most combtooth blennies, reportedly many feed by scraping filamentous algae and detritus from rocks. These items predominated in the diet of all four blenniid species that Randall (1967) examined in the West Indies, and in all five studied by Hiatt and Strasburg (1960) in the Marshall Islands. In Kona, this mode of feeding occurs in *Cirripectus variolosus,* but *Exallias brevis* may be exceptional in feeding mostly on the tissue and mucus of scleractinian corals. The significance of coral mucus as food of *E. brevis* may relate to the significance of fish mucus as food for blennies of the genus *Plagiotremus.* Böhlke and Chaplin (1968) suggested that at least some combtooth blennies which scrape algae from rocks may gain most of their nourishment from small organisms living on or around the algae. Clearly, much about blenniid feeding remains unknown. Because these small fishes scrape their food from various substrata, their gut contents are difficult to analyze. One can easily see that species of *Plagiotremus* have a mode of feeding that differs from those of other blenniids, because their manner of taking food is uniquely spectacular. In comparison, differences distinguishing the feeding modes of other combtooth blennies are relatively subtle.

Family Acanthuridae: surgeonfishes

The surgeonfishes are the predominant fishes over most Hawaiian inshore reefs, but this report treats only the two species that feed on zooplankton in the water column. The habits of these two were only superficially touched on by Jones (1968), who provided a thorough treatment of the many species occurring in Kona that take their food directly from the substratum (see general remarks on surgeonfishes, below).

Acanthurus thompsoni (Fowler)

Acanthurus thompsoni (Figure 38) swims in stationary aggregations in the water column above the reef in several locations along the outer drop-off, 20 to 30 m deep. Often mixed with this surgeonfish in these groups are several other species, especially *Chromis verater, C. ovalis,* and *Naso hexacanthus.* At nightfall, *A. thompsoni* descends to the reef below where, inactive but alert, it remains under cover until morning.

Fourteen individuals (141: 128-185 mm) were speared at different times of day and night. All six that were taken from crevices during the hour before daybreak had empty stomachs, whereas, all seven collected from aggregations in the water column at various times during afternoons had full stomachs, including fresh material. Finally, one solitary individual speared during midafternoon close among the coral in about 6 m of water, approximately 200 m from the nearest feeding aggregation, had its stomach empty. The seven individuals with material in their stomachs contained the items listed in Table 60.

The data show a strong trend in the diet toward relatively large, semitransparent, and often gelatinous prey. Some planktivorous fishes from other families feed heavily on one or another of these prey, as does the pomacentrid *Chromis verater,* which feeds heavily on larvaceans (see species account, above). But in none of these others is the diet similarly dominated by an array of such prey. However, the sparse information on the food habits of *A. thompsoni* given by other authors does not show this trend. Gosline and Brock (1960) reported only mollusk eggs and copepods, whereas Jones (1968) noted copepods, crab zoea, crab megalops, and mysids. But these reports did not indicate how many specimens were examined, nor the relative proportion of each type of prey in the diet. Most important, they did not indicate how much of the gut contents remained unidentified. The major food items that I found in *A. thompsoni* are types quickly rendered unidentifiable by digestion, and thus easily missed if the sample is not fresh.

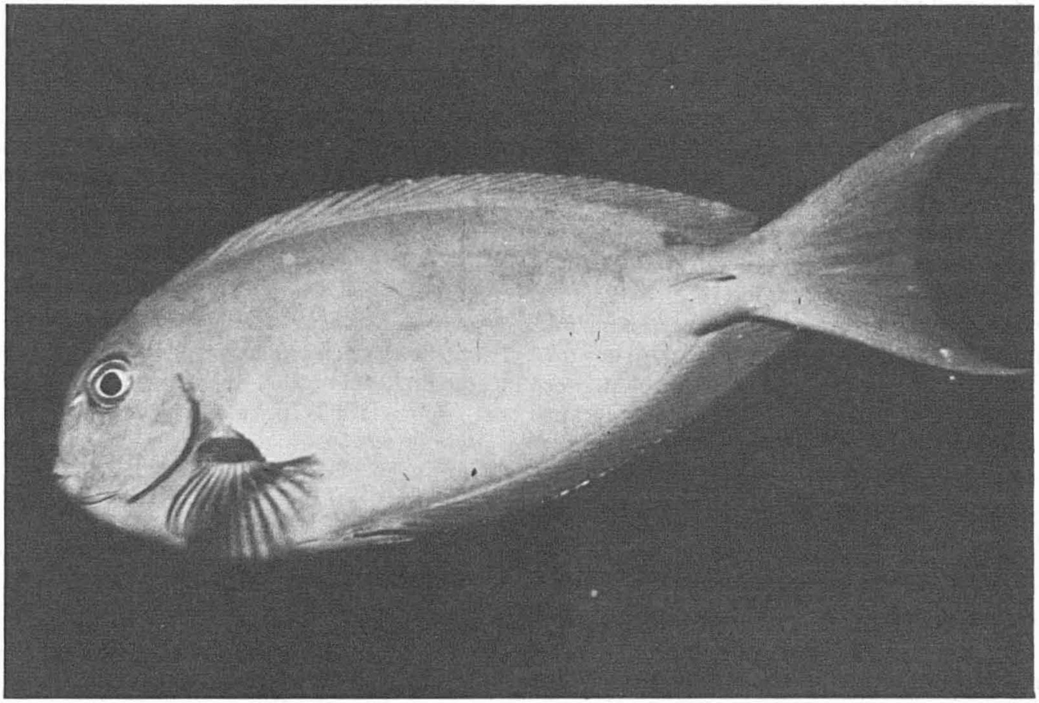

FIGURE 38.—*Acanthurus thompsoni,* a zooplanktivorous surgeonfish. In comparison with its bottom-feeding congeners, this species carries its more upturned mouth higher on its head, its body is more fusiform, and its tail is more deeply lunate. These morphological tendencies occur in many unrelated zooplanktivorous fishes.

CONCLUSION.—*Acanthurus thompsoni* is a diurnal planktivore that feeds mostly on semitransparent, often gelatinous, organisms—especially chaetognaths, salps, siphonophores, and larvaceans.

Naso hexacanthus **(Bleeker)—*kala***

During daylight, this relatively large surgeonfish swims above the outer drop-off in schools that periodically range farther offshore to yet unknown distances. Brock and Chamberlain (1968) found this species at depths below 120 m when diving in the research submarine *Asherah,* but it is not known whether these fish had migrated from shallower water or are of deepwater populations, although the latter possibility seems the more probable. Generally, individuals in less than 10 m of water over inshore reefs during the day are relatively small, and swim in groups of

TABLE 60.—Food of *Acanthurus thompsoni.*

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Chaetognaths	6	37.1	31.80
2	Salps	7	18.6	18.60
3	Siphonophores	4	10.0	5.71
4	Larvaceans	5	7.4	5.29
5	Calanoid copepods	4	8.6	4.91
6	Gelatinous egg masses	2	1.7	0.49
7	Gelatinous clumps of blue-green algae	2	1.6	0.46
8	Fish eggs, planktonic	2	1.3	0.37
9	Hyperiid amphipods	3	0.7	0.30
10	Polychaetes	2	0.9	0.26
11	Decapod shrimps	1	0.3	0.04
12	Harpacticoid copepods	1	0.1	0.01
Also, unidentified fragments		4	11.7	6.69

only a few individuals, often close to the substratum. Most representatives seen inshore are not feeding, but rather move uniformly together closely spaced in schools. When they do feed, the schools are abandoned for aggregations in which loosely spaced individuals act independently.

During evening twilight many individuals move in from deeper water over the shallower parts of the reef. Larger representatives are in the shallows only after dark. On dark nights, the species is scattered close among rocks and corals, relatively inactive, but alert. However, on moonlit nights some swim above the reef in small groups.

Sixteen individuals (261: 202-392 mm) were speared at various times of night and day. Because larger individuals are less accessible, especially during the day, the sample is biased toward smaller members of the species. All four solitary individuals taken close among rocks or coral at night (later than 4 h after sunset and before daybreak) had empty stomachs, whereas only one of nine others taken from schools above the reef at various times of day had material in its stomach, and this one came from a school that had just appeared over the reef from offshore during midafternoon. Finally, all three that had been observed feeding when speared above inshore reefs (on three afternoons over 2 mo) had full stomachs. Items in the four individuals whose stomachs contained food are listed in Table 61.

Like *Acanthurus thompsoni,* this acanthurid feeds mostly on semitransparent, often gelatinous, prey. Of the four that contained food, the three taken from inshore feeding aggregations were relatively small fish (233-238 mm) whose major food was planktonic fish eggs. Perhaps significantly, there were no fish eggs in the fourth specimen, which had just appeared over the reef from offshore. This individual was larger than the others, about 300 mm long, but was collected within 30 min of one of them. The major item in its stomach was filamentous red algae, which did not occur in the smaller three. Only chaetognaths and larvaceans occurred in the stomachs of all four specimens. These limited data suggest there may be distinctive differences in diet and feeding grounds over the size range of individuals sampled.

The high incidence of empty stomachs among individuals over the inshore reefs during the day, as well as at night, suggests that many may feed offshore, and be relatively inactive, or at least not feeding, when they are inshore.

Jones (1968) included *N. hexacanthus* with *A. thompsoni* when reporting the diet of copepods, crab zoea, crab megalops, and mysids noted above. My comments concerning the reported diet of *A. thompsoni* (see above) apply equally here.

CONCLUSION.—*Naso hexacanthus* is a diurnal planktivore that takes mostly semitransparent, often gelatinous, prey—especially chaetognaths, larvaceans, and fish eggs. Limited data suggest that drifting pieces of filamentous algae may also be important.

General Remarks on Surgeonfishes

Surgeonfishes are widespread on tropical reefs, and usually are described in a general way as herbivores (e.g. in the Bahamas by Böhlke and Chaplin, 1968; and in the West Indies by Randall, 1967). Jones (1968) grouped the many Hawaiian surgeonfishes according to their habitats and methods of foraging. In categorizing the bottom-foraging species, not studied by me, he defined three types of habitats, and listed the surgeonfishes characteristic of each: 1) The turbulent

TABLE 61.—Food of *Naso hexacanthus*.

Rank	Items	No. fish with this item (n = 4)	Mean percent of diet volume	Ranking index
1	Chaetognaths	4	21.3	21.30
2	Fish eggs, planktonic	3	25.0	18.75
3	Larvaceans	4	16.3	16.30
4	Filamentous red algae	1	18.4	4.60
5	Decapod shrimps	3	2.3	1.73
6	Calanoid copepods	2	2.3	1.15
7	Siphonophores	2	2.0	1.00
8	Polychaetes	1	1.3	0.33
9	Hyperiid amphipods	1	0.5	0.13
10	Mollusk veligers	1	0.3	0.08
11	Gammaridean amphipods	1	0.3	0.08
Also, unidentified fragments		2	10.0	5.00

waters of the surge zone are frequented by four species of *Acanthurus* (*achilles, glaucopareius, guttatus,* and *leucopareius*). 2) The sand patches on deeper, more tranquil reefs are home to four species of *Acanthurus* (*dussumieri, mata, olivaceus,* and *xanthopterus*). 3) Finally, basalt and coral substrata on reefs below the surge zone (to a depth of about 90 m) are inhabited by three species of *Acanthurus* (*nigrofuscus, nigroris,* and *sandvicensis*); two species of *Ctenochaetus* (*hawaiiensis* and *strigosus*); two species of *Zebrasoma* (*flavescens* and *veliferum*; the adults of the latter often occur in the surge zone); and three species of *Naso* (*brevirostris, lituratus,* and *unicornis*).

In erecting categories according to foraging types, Jones (1968) classified the bottom feeders either as browsers or grazers. The browsers are described as "strictly herbivores that bite and tear off bits of multicellular benthic algae, generally without ingesting any of the inorganic substratum." Browsing surgeonfishes include those characteristic of the surge zone and those characteristic of subsurge reefs, except for the two *Ctenochaetus*. The browsing species of *Acanthurus* and *Zebrasoma* feed chiefly on fine filamentous algae, whereas the browsing species of *Naso* tend to feed on the leafy and fleshy forms.

Surgeonfishes classified by Jones (1968) as grazers are described as "Fishes that purposely pick up large quantities of the substratum while feeding. . . irrespective of whether the material is rasped away from rocks, or picked up as loose sand." This category includes the surgeonfishes characteristic of the sand patches, all of which are species of *Acanthurus,* and the two reef-dwelling species of *Ctenochaetus.* The sand-patch *Acanthurus* species pick up mouthfuls of sand, whereas the reef-dwelling *Ctenochaetus* species ingest sediment that has accumulated over rocks and dead coral. In examining these sediment-packed guts, Jones found material from the two groups distinguishable by particle size—being coarse and grainy in the sand-patch *Acanthurus,* fine and silty in the reef *Ctenochaetus.* He concluded that the major food of both groups are diatoms and detritus that have accumulated around the particles in the surface layers of the sediment.

Surgeonfishes are widely recognized to be active by day and relatively inactive at night (e.g. in the Gulf of California by Hobson, 1965; and in the Florida Keys by Starck and Davis, 1966). Although quiescent, these nocturnally resting acanthurids are most often described as alert; however, Collette and Talbot (1972) reported that *Acanthurus coeruleus* sleeps while sheltered among coral at night in the Virgin Islands. In the Gulf of California, *Prionurus punctatus* aggregates above the reef on bright moonlit nights (Hobson, 1965), as does *Naso hexacanthus* in Kona.

Family Zanclidae: moorish idol

Zanclus canescens **(Linnaeus)—**
moorish idol, ***kihikihi***

The moorish idol (Figure 39a) is closely related to the surgeonfishes, and some ichthyologists (e.g. Greenwood et al., 1966) consider it to be a member of that family. It lacks the caudal spine common to all surgeonfishes, however, and most classifications assign it to the monotypic family Zanclidae.

This fish is numerous in all Kona inshore habitats, where it swims over the reef during the day, usually in groups of four to six individuals. When feeding, it regularly probes the narrow cracks and crevices of the reef with its elongated snout. At night it is relatively inactive, but alert, close among rocks or coral, and at this time its coloration differs strikingly from that displayed in daylight (compare Figure 39a and b).

Of 21 specimens (108: 74-137 mm) speared at various times of day and night, all 9 that were collected at night (later than 4 h after sunset and before sunrise) had empty stomachs, whereas all 12 that were taken during the day (between mid-morning and late afternoon) had full stomachs that included fresh material. Items in the specimens containing identifiable material are listed in Table 62.

The sponges, which greatly predominate in the diet, were all small species that presumably live in narrow reef crevices. This fish appears to be specialized in this diet, although Randall (1955) reported only algae in two specimens from the Gilbert Islands.

CONCLUSION.—*Zanclus canescens* is a diurnal species that feeds mostly on small sponges.

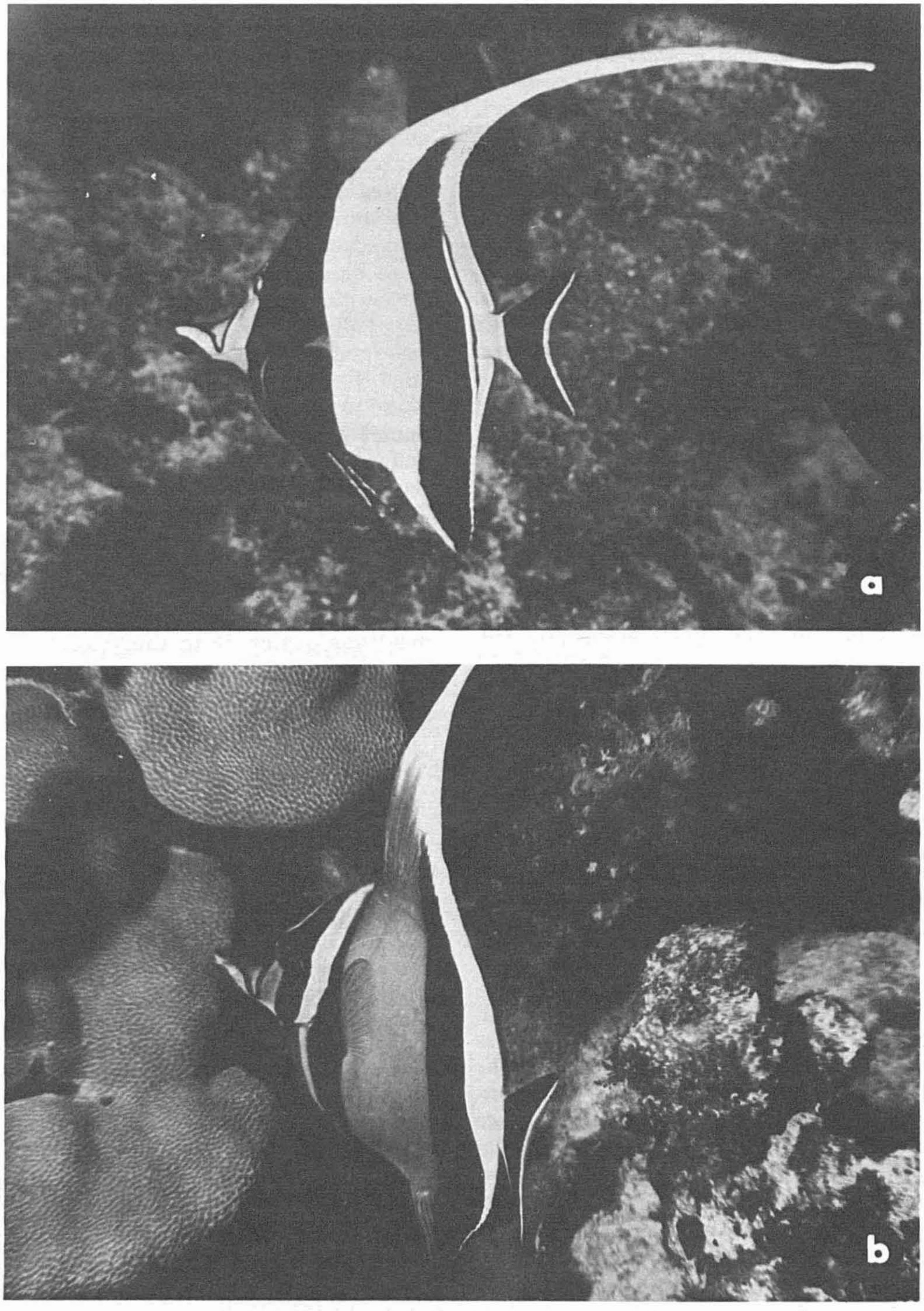

FIGURE 39.—*Zanclus canescens*, the moorish idol: a, showing diurnal coloration while swimming over the reef during the day; b, showing nocturnal coloration while close to the reef at night.

TABLE 62.—Food of *Zanclus canescens*.

Rank	Items	No. fish with this item (n = 12)	Mean percent of diet volume	Ranking index
1	Sponges	12	84.5	84.50
2	Coralline algae	12	5.7	5.70
3	Other algae	12	5.6	5.60
4	Bryozoans	8	1.1	0.73
5	Pelecypod mollusks	8	0.9	0.60
6	Gammaridean amphipods	6	0.5	0.25
7	Polychaetes	4	0.6	0.20
8	Foraminiferans	3	0.3	0.08
9	Hydroids	2	0.2	0.03
10	Barnacle cirri	2	0.2	0.03
11	Didemnid tunicates	1	0.2	0.02
12	Tanaids	1	0.1	<0.01
13	Decapod shrimps	1	0.1	<0.01

ORDER PLEURONECTIFORMES

Family Bothidae: left-hand flounders

Bothus mancus (Broussonet)—*paki'i*

This flatfish is most numerous lying immobile where rocks are interspersed with small patches of sand. It changes its coloration to match closely that of whatever substratum it happens to lie on, rocks or sand. When on sand, it is frequently buried except for its eyes. No change was noted in the overt behavior of this fish between day and night.

Eight specimens (223: 137-277 mm) were speared at various times of the day. Both individuals collected within an hour after sunrise were empty, whereas of six taken during afternoons, two were empty and four contained well-digested fish remains that appeared to have been in the stomachs at least several hours when collected.

Hiatt and Strasburg (1960) reported this flounder on both rocks and sand in the Marshall Islands and noted a diet comprised primarily of fishes that live in sandy areas adjacent to coral. Most prey species listed by them are fishes (balistids, labrids, pomacentrids, and blennies) that probably are active in exposed positions only during daylight. They believed that *B. mancus* responds only to moving prey; if so, at least most of its prey, which rests at night, would not be available after dark. The prey listed by Hiatt and Strasburg also included two species of apogonids, members of what seems to be a universally nocturnal group; however, during daylight these particular apogonid species congregate in exposed positions close among the coral, where they would seem available to diurnal predators.

CONCLUSION.—*Bothus mancus* preys on small fishes during the day. Its nocturnal habits remain uncertain.

General Remarks on Left-hand Flounders

Bothids are the most numerous flatfishes on tropical reefs. In the West Indies, Randall (1967) found fishes the major prey of *Bothus lunulatus* and *B. ocellatus,* both of which occur on sand patches around coral reefs, often largely buried. In the Florida Keys, Starck and Davis (1966) found *B. ocellatus* in sandy areas of all reef zones, and although they did not examine its food habits, they inferred from its behavior that it preys after dark on the various small nocturnal invertebrates active on the sand at night.

ORDER TETRAODONTIFORMES

Family Balistidae: triggerfishes

Melichthys niger (Bloch)—*humuhumu 'ele'ele*

During the day, *M. niger* typically hovers in loosely spaced aggregations several meters above the reef. Each individual independently picks material drifting in the mid-waters. It is a wary animal that dives to holes in the reef when alarmed. It enters these same holes at nightfall and rests there on its side until morning.

All seven individuals (165: 122-195 mm) speared from among those active above the reef during the day were full of food, as listed in Table 63. The major food items are fragments of fleshy algae—filamentous and foliaceous—probably most of which are drifting in the mid-waters when taken. This triggerfish feeds at least occasionally on the sea floor, as indicated by the relatively high

TABLE 63.—Food of *Melichthys niger*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Fleshy algae	7	52.3	52.30
2	Coralline algae	7	18.7	18.70
3	Calanoid copepods	5	2.7	1.93
4	Caridean shrimps	4	1.1	0.63
5	Harpacticoid copepods	4	0.6	0.34
6	Scleractinian coral	1	2.1	0.30
7	Insects	2	0.4	0.11
8	Foraminiferans	2	0.3	0.09
9	Heteropods	2	0.3	0.09
10	Cyclopoid copepods	1	0.6	0.09
11	Crab megalops	1	0.4	0.06
12	Mollusk veligers	1	0.1	0.01
13	Naticid gastropods	1	0.1	0.01
14	Ostracods	1	0.1	0.01
15	Gammaridean amphipods	1	0.1	0.01
16	Fish eggs, planktonic	1	0.1	0.01
Also, sand		1	2.9	0.41
	Unidentified fragments	6	17.1	14.66

proportion of coralline algae in its diet and also by the stony coral, bitten off in chunks, in one individual; nevertheless, most of its food is planktonic. Certainly the relatively minor status of the many zooplankters in the above list far understates their relative significance to this fish. The ranking is biased toward the more bulky items; thus, one algal fragment, in terms of volume, may be equivalent to a hundred or more copepods. And yet the effort expended in taking the algal fragment may have been no greater than that expended in taking a single copepod. A given volume of copepods (and many other zooplankters) probably is far more nutritious than the same volume of algae.

In the West Indies, this circumtropical triggerfish similarly feeds on algae and zooplankton in the mid-waters, taking the algae from the benthos, or as drifting fragments (Randall, 1967).

CONCLUSION.—*Melichthys niger* is a diurnal omnivore that feeds mostly on drifting algal fragments and zooplankton, along with some benthic vegetation.

Xanthichthys ringens (Linnaeus)

This triggerfish (Figure 40) is one of the most numerous fishes at depths below 25 m along the outer drop-off. Like so many fishes that concentrate in this location, it aggregates in the water column and picks plankton, an activity that is limited to daylight; at nightfall, it shelters in reef crevices, where it rests on its side until morning.

Of the 11 specimens (125: 98-145 mm) speared during day and night, 2 that were collected from reef crevices during the last hour before daybreak were empty, whereas all 9 that were taken from mid-water aggregations at various times during the day were full of food, as listed in Table 64.

I found no evidence that this triggerfish takes food from the sea floor. Like *Melichthys niger, X. ringens* is circumtropical (Böhlke and Chaplin, 1968); perhaps the planktivorous habits of these two triggerfishes permit survival over long periods in the open sea where their bottom-feeding relatives would perish. Gosline and Brock (1960), whose data were mostly from relatively shallow water, reported *X. ringens* uncommon in Hawaii. The large numbers of this species occurring along the outer drop-off in Kona, however, indicates a habitat in Hawaii similar to that in the West Indies, where it rarely occurs in less than 35 m of water, but is one of the most numerous fishes below that depth (Randall, 1968).

CONCLUSION.—*Xanthichthys ringens* is a diurnal planktivore that feeds mostly on calanoid copepods.

Rhinecanthus rectangulus (Bloch and Schneider)—*humuhumu nukunuku a pua'a*

This triggerfish is most common on shallow, surge-swept, basalt reefs. It is a solitary fish that swims close to the reef top during the day, picking at organisms on the bottom. A wary animal, it quickly takes refuge in the reef when threatened.

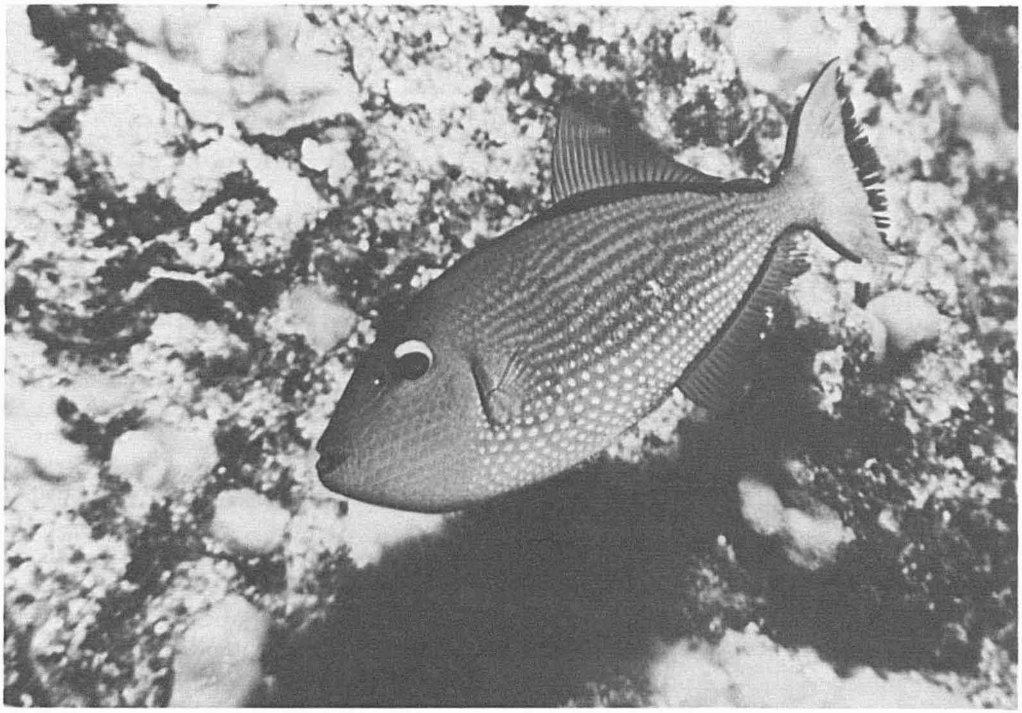

FIGURE 40.—*Xanthichthys ringens,* a zooplanktivorous triggerfish. In comparison with bottom-feeding triggerfishes, this species has a more upturned mouth that is higher on its head, and its body is more fusiform. Both features are widespread among zooplanktivorous fishes.

Its shelters, like those of *Melichthys niger,* above, are small enough so that the fish can wedge itself in by locking its large dorsal spine erect. Each individual fish seems to resort to a specific hole that serves as a refuge by day, and also as a resting place at night when the species is inactive.

All nine individuals (142: 114-170 mm) speared at various times of the day from among those active close to the reef were full of food, as listed in Table 65. Food items were mostly small organisms between 1 and 6 mm in their greatest dimension, taken intact; the few exceptions are fragments of about this size from larger organisms.

Hiatt and Strasburg (1960) found this species numerous on shallow reefs in the Marshall Islands and reported a crustacean and algal diet similar to that of the species in Kona.

TABLE 64.—Food of *Xanthichthys ringens.*

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Calanoid copepods	9	43.9	43.90
2	Mollusk veligers	6	0.8	0.53
3	Fish eggs, planktonic	2	1.4	0.31
4	Chaetognaths	2	1.3	0.29
5	Siphonophores	2	1.2	0.27
6	Pteropods	2	1.2	0.27
7	Ostracods	4	0.6	0.27
8	Cyclopoid copepods	1	0.8	0.09
9	Heteropods	2	0.3	0.07
10	Hyperiid amphipods	2	0.2	0.04
11	Gammaridean amphipods	1	0.2	0.02
Also, crustacean fragments		4	4.6	2.04
	Unidentified fragments	9	43.5	43.50

TABLE 65.—Food of *Rhinecanthus rectangulus*.

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Gammaridean amphipods	9	19.4	19.40
2	Didemnid tunicates	9	8.6	8.60
3	Filamentous algae	6	7.8	5.20
4	Xanthid crabs	4	6.7	2.98
5	Polychaetes	4	6.3	2.80
6	Decapod shrimps	5	4.2	2.33
7	Tanaids	4	2.9	1.29
8	Coralline algae	4	2.6	1.16
9	Prosobranch gastropods	4	2.4	1.07
10	Echinoids	3	2.9	0.97
11	Isopods	3	2.6	0.87
12	Bryozoans	2	0.7	0.16
13	Caprellid amphipods	1	0.6	0.07
14	Pelecypods	1	0.3	0.03
15	Crab megalops	1	0.2	0.02
Also, crustacean fragments		4	6.2	2.76
	Unidentified fragments	7	25.6	19.91

TABLE 66.—Food of *Sufflamen bursa*.

Rank	Items	No. fish with this item (n = 9)	Mean percent of diet volume	Ranking index
1	Echinoids	9	9.1	9.10
2	Gammaridean amphipods	7	8.3	6.46
3	Polychaetes	8	4.6	4.09
4	Prosobranch gastropods	9	3.8	3.80
5	Brachyurans	5	4.8	2.67
6	Sponges	8	2.6	2.31
7	Tanaids	6	2.8	1.87
8	Opisthobranchs	6	2.3	1.53
9	Cyclopoid copepods	9	1.2	1.20
10	Isopods	7	1.3	1.01
11	Ostreid pelecypods	7	1.0	0.78
12	Caridean shrimps	3	0.8	0.27
13	Foraminiferans	4	0.4	0.18
14	Ostracods	4	0.4	0.18
15	Crab megalops	2	0.3	0.07
16	Bryozoans	1	0.1	0.01
17	Sipunculid introverts	1	0.1	0.01
18	Harpacticoid copepods	1	0.1	0.01
19	Barnacle cirri	1	0.1	0.01
20	Mites	1	0.1	0.01
Also, crustacean fragments		5	3.8	2.11
	Algal fragments	5	1.2	0.67
	Unidentified fragments	9	50.8	50.80

CONCLUSION.—*Rhinecanthus rectangulus* is a diurnal omnivore, feeding mostly on gammaridean amphipods and other small organisms.

Sufflamen bursa* (Bloch and Schneider)—*humuhumu umauma lei

This is the most numerous and widespread triggerfish on Kona reefs. A solitary species, active by day close to rocks and coral, it picks at organisms on the sea floor. It is less inclined to seek cover in reef crevices than are *Melichthys niger* and *Rhinecanthus rectangulus*, above, but nevertheless is a wary animal that shys away from humans. At night it is inactive, resting on its side under cover on the reef until morning.

Thirteen individuals (140: 109-164 mm) were speared at various times of day and night. The four that were collected in darkness as they rested in reef crevices during the last 2 h before daybreak were empty, whereas the nine that were collected at various times during the day as they swam over the reef were full of food, as listed in Table 66. As was true of the food of *R. rectangulus*, these food items, including the echinoids, are mostly small animals between 1 and 6 mm in their greatest dimension, taken intact; the exceptions are fragments of about this size from larger organisms. Unlike the omnivorous *R. rectangulus*, however, *S. bursa* seems to be strictly carnivorous (the few algal fragments among its gut contents probably were taken incidentally along with prey). No single item greatly predominates in its diet, a circumstance that may relate to its widespread occurrence in a variety of habitats.

CONCLUSION.—*Sufflamen bursa* is a diurnal predator that feeds on a variety of benthic animals.

General Remarks on Triggerfishes

The balistids are known for their powerful jaws and sharp cutting teeth, which enable them to prey on a variety of armored invertebrates denied as food to most other fishes (Randall, 1967). Most triggerfishes seem to make full use of this equipment: in the Virgin Islands *Balistes vetula* preys on the large echinoid *Diadema* (often attacking this sea urchin from its oral surface, where the spines are shortest) and on relatively large queen conchs, *Strombus,* which it crushes upon ingestion (Randall, 1967). Similarly, in the Marshall Islands several triggerfishes use their powerful feeding apparatus to crush mollusks and hard-shelled crustaceans, as well as to break off the tips of cespitose corals (Hiatt and Strasburg, 1960). *Rhinecanthus rectangulus* and *Sufflamen bursa* in Kona may be exceptional among bottom-foraging balistids in that they feed so heavily on small organisms, ingested intact. On the other hand, it may be that the high proportion of unidentified fragments in the guts of both species are the crushed remains of larger organisms not properly ranked among the data. Nevertheless, the capacity to feed on tiny organisms is probably well established among the balistids, as demonstrated by the exclusively zooplanktivorous habits of *Xanthichthys ringens.*

Triggerfishes are well known to be active by day and to rest under cover at night, usually lying on their sides. Diurnal habits were reported in balistids of the Gulf of California (Hobson, 1965, 1968a) and the West Indies (Randall, 1967). Collette and Talbot (1972) described *Balistes vetula* sleeping at night in exposed positions on reefs in the Virgin Islands, and Earle (1972) reported that in the Virgin Islands *B. vetula* frequently returns nightly to the same hole in the reef. There is at least some activity among triggerfishes on moonlit nights, however, as for example in *B. polylepis* in the Gulf of California (Hobson, 1965), but it is unknown whether this activity involves feeding.

Family Monacanthidae: filefishes

Cantherines dumerili (Hollard)—*'o'ili*

During daylight, this filefish swims several meters above coral-rich reefs, usually in loosely associated pairs that move, often on their sides, back and forth in restricted, well-defined areas. Because it swims in the water column and because it is relatively large, this filefish is a conspicuous component of the fauna, even though relatively few occur on the reef. Despite the time it spends in mid-water, *C. dumerili* was observed feeding only on the sea floor, where it bites off the tips of coral branches. During evening twilight it settles into holes in the reef, where it remains inactive until morning.

All eight individuals (200: 171-240 mm) speared from among those hovering above the reef during midday were full of food. Scleractinian corals were the major food items, occurring in seven of the eight specimens (mean percent of diet volume: 80; ranking index: 70), always as chunks of *Pocillopora* and *Porites,* about 4 mm in diameter. Other food items were: echinoids, all tips of the clublike spines of *Heterocentrotus mammillatus*, in two (mean percent of diet volume: 7.4; ranking index: 1.85), a variety of bryozoans, both encrusting and arborescent, that were almost the total contents of one (mean percent of diet volume: 12.5; ranking index volume: 1.56), and pelecypods in one (mean percent of diet volume: 0.1; ranking index: 0.01).

Hiatt and Strasburg (1960) found that of the two specimens of this species (reported as *Amanses carolae)* that they examined in the Marshall Islands, one had fed on scleractinian corals exclusively, whereas the other had mixed a coral diet with sponges and algae. Apparently this species does not feed during the considerable time that it spends in the water column, as its diet seems to comprise only benthic organisms.

CONCLUSION.—*Cantherines dumerili* is a diurnal predator that feeds mainly on scleractinian corals.

Cantherines sandwichiensis (Quoy and Gaimard)—*'o'ili lepa*

This, the most numerous filefish in Kona, especially on basalt reefs in less than 10 m of water, is a solitary fish that swims close over the reef during

TABLE 67.—Food of *Cantherines sandwichiensis.*

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Filamentous algae	7	35.7	35.70
2	Coralline algae	7	32.1	32.10
3	Didemnid tunicates	7	6.1	6.10
4	Gammaridean amphipods	6	4.0	3.43
5	Scleractinian corals	2	5.0	1.43
6	Sponges	2	2.2	0.63
7	Diatoms	3	1.1	0.47
8	Bryozoans	2	1.0	0.29
9	Hydroids	2	0.4	0.11
10	Polychaetes	1	1.4	0.20
11	Ostreid pelecypods	2	0.6	0.17
12	Caprellid amphipods	2	0.6	0.17
13	Gastropod eggs	1	0.3	0.04
14	Prosobranch gastropods	1	0.3	0.04
15	Tanaids	1	0.1	0.01
16	Ophiuroids	1	0.1	0.01
Also, unidentified fragments		5	8.3	5.93
	Sand	1	0.7	0.10

TABLE 68.—Food of *Pervagor spilosoma.*

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Scleractinian corals	5	35.8	29.83
2	Filamentous algae	4	19.3	12.87
3	Coralline algae	6	7.7	7.70
4	Sponges	1	3.3	0.55
5	Polychaetes	2	1.5	0.50
6	Echinoids	3	0.8	0.40
7	Gammaridean amphipods	3	0.7	0.35
8	Tanaids	2	0.5	0.16
9	Diatoms	2	0.3	0.10
10	Fish eggs	1	0.5	0.08
11	Hydroids	2	0.3	0.10
12	Opisthobranch gastropods	1	0.2	0.03
13	Ostracods	1	0.2	0.03
14	Cyclopoid copepods	1	0.2	0.03
15	Crab megalops	1	0.2	0.03
16	Ophiuroids	1	0.2	0.03
Also, unidentified fragments		5	28.1	23.41
	Sand	1	0.2	0.03

the day, picking at objects on the bottom. During evening twilight, it moves from sight and is not visible at night when presumably it rests in reef crevices.

All seven individuals (116: 84-132 mm) speared from among those active close to the reef during the day were full of food, much of it fresh, as listed in Table 67.

CONCLUSION.—*Cantherines sandwichiensis* is a diurnal omnivore that feeds on a wide variety of benthic algae and invertebrates.

Pervagor spilosoma (Lay and Bennett)—*'o'ili 'uwi'uwi*

This, the most colorful filefish in Kona, as well as the smallest of the three considered there, is most numerous on coral-rich reefs. It is a solitary fish, active close among the corals in daylight, but not seen after dark when presumably it rests in reef crevices.

Of the seven specimens (85: 64-120 mm) collected, one that was speared close to coral just before sunrise (the first individual of the species to appear that morning) had an empty gut, whereas all six that were speared from among those active on the reef between midmorning and midafternoon were full of food, as listed in Table 68.

As is true of *Cantherines dumerili,* above, the major food of this filefish is scleractinian coral; however, whereas *C. dumerili* bites off relatively large chunks of coral, each containing many polyps, *P. spilosoma* seems to pluck at only one polyp at a time, as do certain chaetodontids. Nevertheless, judging from its gut load of skeletal fragments, *P. spilosoma* does not neatly snip off the polyps so much as coarsely gouge them from their thecae.

CONCLUSION.—*Pervagor spilosoma* is a diurnal omnivore that feeds mainly on scleractinian corals, to a lesser extent on algae and other benthic invertebrates.

General Remarks on Filefishes

In summarizing their treatment of monacanthids in the Marshall Islands, Hiatt and Strasburg (1960:105) stated: "There is no question that filefishes derive the bulk of their nutriment from living corals." All of the *Oxymonocanthus longirostris* (a widespread Indo-Pacific species that does not occur in Hawaii) examined by them contained only coral polyps, with no skeletal material. Their account indicates that this species, which has a very long, narrow snout, with teeth protruding from its mouth as long, cupshaped incisors, may be among the most highly specialized of coral-feeding filefishes. On the other hand, Randall (1967) found corals to be insignificant as food for West Indian filefishes; of the six species he examined, corals were in the diet of only one, and only as a minor component. According to Randall, the West Indian filefishes take a diverse array of benthic organisms: Algae and sea grasses are major items, along with a variety of benthic invertebrates. Thus, *Cantherines sandwichiensis* in Kona has a diet much like the West Indian species described by Randall, whereas *C. dumerili* takes largely corals in Kona, just as Hiatt and Strasburg reported it and other filefishes doing in the Marshall Islands. Clearly, many filefishes, especially certain Indo-Pacific species, feed heavily on corals, whereas various other filefishes find their food from among other elements of the benthos.

Filefishes are recognized as being diurnal. For example, Starck and Davis (1966) described *C. pullus* as resting at night wedged in rocky holes on reefs in Florida.

Family Ostraciontidae: boxfishes

Ostracion meleagris (Shaw)—*pahu*

This boxfish is widespread on nearshore reefs in Kona, but is nowhere numerous, except occasionally in some parts of the boulder habitat. During the day it swims, slowly, close among rocks and coral, now and then picking at the substratum. I saw several in the same places at night, but at the time felt they had been disturbed from resting places by my activity. It was difficult to appraise the nocturnal behavior of this species, owing to its relatively low numbers on the reef and the reduced visibility after dark, and because the few observations were somewhat ambiguous.

Of the six individuals (65: 43-80 mm) collected, one speared within 15 min after sunrise as it swam close to the reef had an empty gut, whereas all five taken under similar circumstances, except later in the day (between late morning and late afternoon) had food throughout the gut. The items in the foregut are listed in Table 69.

CONCLUSION.—*Ostracion meleagris* feeds on benthic invertebrates during the day. Its nocturnal status remains uncertain, although tenuous data indicate relative inactivity after dark.

General Remarks on Boxfishes

Boxfishes in the tropical Atlantic generally are described as active during both day and night (Starck and Davis, 1966; Earle, 1972; Collette and Talbot, 1972). Tunicates, the major prey of *Ostracion meleagris* in Kona, were ranked either

TABLE 69.—Food of *Ostracion meleagris*.

Rank	Items	No. fish with this item (n = 5)	Mean percent of diet volume	Ranking index
1	Didemnid tunicates	3	42.8	25.68
2	Polychaetes	2	13.0	5.20
3	Algae	2	7.4	2.96
4	Sponges	1	2.0	0.40
5	Pelecypods	1	1.0	0.20
6	Prosobranch gastropods	1	1.0	0.20
7	Copepods	1	0.4	0.08
Also, sand and debris		1	6.0	1.20
	Unidentified fragments	2	26.4	10.56

first or second as prey of three of the five West Indian boxfishes studied by Randall (1967). Furthermore, polychaetes and sponges also were found to be important prey in the Atlantic species just as they are in *O. meleagris* from Kona. In the Marshall Islands, the major foods of *O. cubicus* are mollusks, polychaetes, and algae (Hiatt and Strasburg, 1960).

At least some boxfishes, including *O. meleagris* in Hawaii (Gosline and Brock, 1960; Thomson, 1964), release a substance that is toxic to other fishes. This may give them some immunity from predation, as suggested for some tropical Atlantic species by Randall (1967).

Family Tetraodontidae: balloonfishes

Arothron hispidus (Linnaeus)—*'opu hue, keke*

This solitary balloonfish is widespread on Kona reefs, but is nowhere numerous. In daylight it frequently hovers inactively several meters above the reef, although just as often it swims slowly among the rocks and coral. After dark it continues to swim actively, close to the reef.

Nine individuals (253: 187-332 mm) were speared during day and night. The guts of two were empty: one of these was hovering high in the water column during early afternoon when collected; the other was swimming close among rocks during the hour immediately before first morning light. All of the other seven, taken as they swam close to the reef—five during midday, two during midnight—contained identifiable material, as listed in Table 70. The tunicates taken by this balloonfish include several benthic species, both compound and simple forms; the echinoids are the crushed tests and spines of echinometrids and cidarids; the asteroids are mostly tips of the appendages from *Linckia*.

Generally the items are hard-bodied forms that remain recognizable for a relatively long time after ingestion; nevertheless, material from the two individuals collected at night appeared fresher overall than that from the individuals collected during midday.

In the Marshall Islands, the single *A. hispidus* examined by Hiatt and Strasburg (1960) had fed on much the same material as listed above, except that it also had ingested some living scleractinian corals.

CONCLUSION.—*Arothron hispidus* preys on a variety of benthic invertebrates, especially those having a hard or leathery external covering. Limited evidence indicates it is active during both day and night.

Arothron meleagris (Bloch and Schneider)—*'opu hue, keke*

Like its congener *A. hispidus*, above, the solitary species *A. meleagris* (Figure 41) is widespread on Kona reefs, but is nowhere numerous. It does not hover inactively above the reef during the day as *A. hispidus* often does, and on the few occasions when it was seen at night—always under ledges or in crevices—*A. meleagris* seemed inactive. During daylight it swims slowly among the rocks or corals.

Eleven individuals (221: 146-393 mm) were collected during the day. Of three whose guts were empty, two were speared as they swam close to the reef within an hour after sunrise, and one was taken from a small cave during midafternoon. The remaining eight, taken as they swam close to the reef during midday, all contained identifiable material. Seven of these had taken scleratinian corals (mean percent of diet volume: 43.1; ranking index: 37.71), mostly small chunks of encrusting

TABLE 70.—Food of *Arothron hispidus*.

Rank	Items	No. fish with this item (n = 7)	Mean percent of diet volume	Ranking index
1	Tunicates	5	33.7	24.07
2	Echinoids	5	28.1	20.07
3	Ophiuroids	3	13.4	5.74
4	Asteroids	3	8.3	3.56
5	Brachyurans	2	6.4	1.83
6	Sponges	1	2.9	0.41
7	Hydroids	1	2.9	0.41
8	Prosobranch gastropods	1	0.1	0.01
9	Pagurid crabs	1	0.1	0.01
Also, algae		1	0.3	0.04
	Unidentifiable fragments	3	3.8	1.63

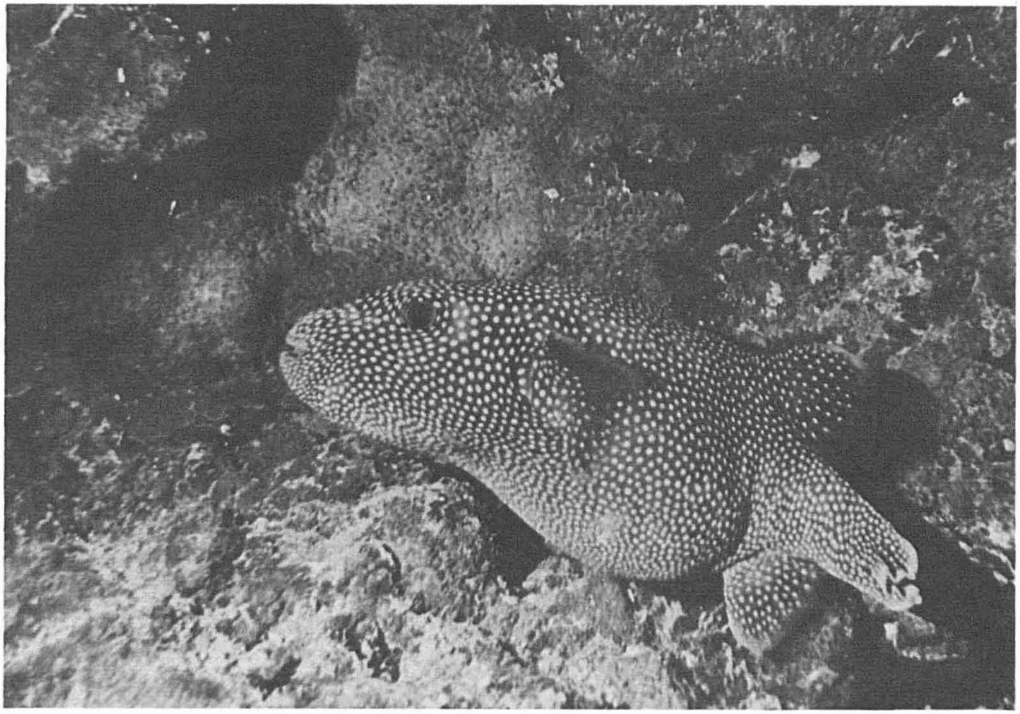

FIGURE 41.—*Arothron meleagris,* a balloonfish. By inflating its saclike body with water, this slow-swimming fish increases its size, which presumably decreases its vulnerability to predators.

Porites, whereas six had taken tunicates (mean percent of diet volume: 44.4; ranking index: 33.3), all of them a large colonial form with a heavy black integument that, like the coral, encrusts on rocks. The only other recognizable items were pectinid pelecypods in one (mean percent of diet volume: 0.6; ranking index: 0.08). Three contained unidentifiable fragments (mean percent of diet volume: 11.9; ranking index: 4.46). Thus, these data indicate that, compared with *A. hispidus, A. meleagris* is a relatively specialized feeder. The three *A. meleagris* that Hiatt and Strasburg (1960) examined in the Marshall Islands had fed almost exclusively on living corals.

CONCLUSION.—*Arothron meleagris* is a diurnal predator that feeds mostly on corals and tunicates which encrust on rocks.

General Remarks on Balloonfishes

The dentition of tetraodontids consists of heavy plates, two in each jaw, that form a sharp beak. With this exceptionally strong apparatus, these fishes crush an array of armored organisms that are unavailable as prey to most other fishes (Hiatt and Strasburg, 1960).

Family Canthigasteridae: sharpbacked puffers

Canthigaster amboinensis Bleeker — *pu'u ola'i*

This pufferfish occurs chiefly in relatively shallow water where there is much exposed basalt. It is a solitary fish, active close to the sea floor during the day, but only infrequently in view after dark, when, presumably, it generally retires to reef crevices.

All 11 individuals (69: 31-91 mm) that were speared at various times during daylight contained identifiable material (much of it fresh), as listed in Table 71.

CONCLUSION.—*Canthigaster amboinensis* is a diurnal omnivore that feeds mostly on coralline algae and various hard-bodied invertebrates.

TABLE 71.—Food of *Canthigaster amboinensis*.

Rank	Items	No. fish with this item (n = 11)	Mean percent of diet volume	Ranking index
1	Coralline algae	10	42.5	38.64
2	Filamentous algae	8	9.4	6.84
3	Scleractinian corals	6	7.7	4.20
4	Pectinid pelecypods	2	7.8	1.42
5	Brachyurans	2	7.3	1.33
6	Ophiuroids	2	4.9	0.89
7	Echinoids	4	2.4	0.87
8	Sponges	5	1.3	0.59
9	Prosobranch gastropods	4	0.6	0.22
10	Bryozoans	2	0.6	0.11
11	Sipunculid introverts	2	0.3	0.05
12	Foraminiferans	3	0.2	0.05
13	Gammaridean amphipods	2	0.2	0.04
14	Didemnid tunicates	1	0.3	0.03
15	Polychaetes	1	0.2	0.02
Also, unidentified fragments		6	14.3	7.80

TABLE 72.—Food of *Canthigaster jactator*.

Rank	Items	No. fish with this item (n = 6)	Mean percent of diet volume	Ranking index
1	Coralline algae	3	15.7	7.85
2	Prosobranch gastropods	4	11.2	7.47
3	Sponges	3	6.8	3.40
4	Scleractinian corals	2	10.0	3.33
5	Filamentous algae	5	3.7	3.08
6	Didemnid tunicates	3	6.0	3.00
7	Sipunculid introverts	3	4.3	2.15
8	Echinoids	2	5.5	1.83
9	Bryozoans	2	1.3	0.43
10	Brachyurans	2	1.3	0.43
11	Diatoms	3	0.7	0.35
12	Foraminiferans	2	0.3	0.10
13	Ophiuroids	1	0.3	0.05
14	Ostracods	1	0.2	0.03
15	Gammaridean amphipods	1	0.2	0.03
16	Isopods	1	0.2	0.03
17	Caridean shrimps	1	0.2	0.03
Also, crustacean fragments		1	5.0	0.83
	Sand	3	1.5	0.75
	Unidentified fragments	5	25.6	21.33

Canthigaster jactator (Jenkins)

This small pufferfish lives mostly where corals are well developed. Like its congener *C. amboinensis*, above, it is mostly solitary, although sometimes several occur together. It swims close among the coral during daylight, but is only occasionally in view at night, probably because it usually rests in reef crevices after dark. Once during the predawn hours, as noted above, I observed a nocturnally active moray eel, *Gymnothorax petelli*, grasping one of these puffers between its jaws.

Thirteen individuals (50: 40-70 mm) were speared at various times of day and night. Four were taken during daylight, and these were the only ones that had material in the anterior third of their gut, much of it relatively fresh. In two others taken at night (one 4 h after sunset, the other during the last hour before daybreak), food was confined to the posterior two-thirds of their guts, but much of it was still largely identifiable. In comparison, the remaining seven, collected either at night (more than 4 h after sunset), or during morning twilight, were empty. Items in the six specimens that contained identifiable material are listed in Table 72.

CONCLUSION.—*Canthigaster jactator* is a diurnal omnivore that feeds mostly on coralline algae and various hard-bodied benthic invertebrates.

Remarks on Sharpbacked Puffers

The canthigasterids are widely recognized as omnivorous fishes that feed on benthic plants and invertebrates (e.g. in the tropical Atlantic by Randall, 1967; and in the western Pacific by Hiatt and Strasburg, 1960). Most investigators have considered them diurnal. Smith and Tyler (1972) described *Canthigaster rostratus* sleeping at night on reefs in the Virgin Islands; Collette and Talbot (1972) also suspected *C. rostratus* to be nocturnally inactive, and suggested that some they saw swimming at night had been disturbed by their lights. To Starck and Davis (1966), however, at least some individuals of *C. rostratus* appeared to be nocturnally active in the Florida Keys; however, they recognized that this species is active in daylight as well.

Family Diodontidae: spiny puffers

Diodon holocanthus Linnaeus — *kokala*

This spiny puffer is numerous in Kona, where it frequently swims close above the reef at night; nevertheless, I never saw one there in daylight. Undoubtedly, it is under shelter during the day, probably deep within the coral caverns that honeycomb much of the reef. In the Gulf of California, where the rocky sea floor offers mostly ledges and relatively shallow caves, one often sees the nocturnally active *D. holocanthus* resting in these places during the day.

All five individuals (211: 175-239 mm) that were speared as they swam in exposed locations on the reef after dark contained identifiable material in their guts, much of it relatively fresh. Prosobranch gastropods, which occurred in all five specimens, were the major food item (mean percent of diet volume and ranking index: 54.1), with pagurid crabs also important prey of all five (mean percent of diet volume and ranking index: 24). Other food items were: echinoids, all *Echinometra mathaei,* in four (mean percent of diet volume: 18; ranking index: 14.4), and ophiuroids in two (mean percent of diet volume: 3.9; ranking index: 1.56). Although this material had been crushed by the powerful jaws and beaklike dentition of the fish, it was apparent that at least many of the gastropod shells actually had housed pagurid crabs; thus the pagurids, not the gastropods themselves, may have been the major food. It remains uncertain how many living gastropods are in fact taken, although opercula among the gut contents showed that living gastropods are important prey.

This circumtropical species has a similar diet in the Atlantic Ocean, as determined by Randall (1967), who also listed prosobranch gastropods as the major food item. He listed pagurid crabs too, but did not suggest that some of the gastropods on his list may have been shells that housed these crabs.

Diodon holocanthus is nocturnal in the Florida Keys, where it stays under ledges or in holes during the day, but emerges at night to feed on various invertebrates, particularly larger shelled forms (Starck and Davis, 1966).

CONCLUSION.—*Diodon holocanthus* is a nocturnal predator that feeds mostly on prosobranch gastropods and pagurid crabs.

Diodon hystrix Linnaeus—*kokala*

During the day, *D. hystrix* either is secreted under ledges, or hovers inactively high in the water column, often several together. At night, solitary individuals (Figure 42) swim in exposed locations close above the reef, especially among basaltic boulders.

Of the 16 individuals (263: 244-333 mm) speared during day and night, only 4 had empty guts, and these were collected during late afternoon, either from holes under rocks, or as they hovered in the water column. The only ones that carried food in the anterior third of their gut were taken at night—two during the hour before midnight and one 2 h before daybreak. Although the anterior third of the gut was empty in the other nine, all carried material posteriorly, which, composing entirely shelled organisms, was readily identifiable: two of these specimens were collected at night—one at midnight, the other just before daybreak; the remaining seven were taken during the day—four of them in the morning, three early in the afternoon. In all, 12 specimens contained identifiable prey.

Echinoids, including both cidarids and echinometrids, occurred in 11 of the 12 specimens and were the major food item (mean percent of diet volume: 55; ranking index: 50.42). Prosobranch gastropods, present in 11 (mean percent of diet volume: 27.1; ranking index: 24.84), were ranked second, and pagurid crabs, also present in 11 (mean percent of diet volume: 12.9; ranking index: 11.83), were ranked third. Thus, the diet includes items similar to those taken by *D. holocanthus,* above, but ranked in a different order. As is true of the material from *D. holocanthus,* many of the gastropod shells had housed pagurid crabs, but the

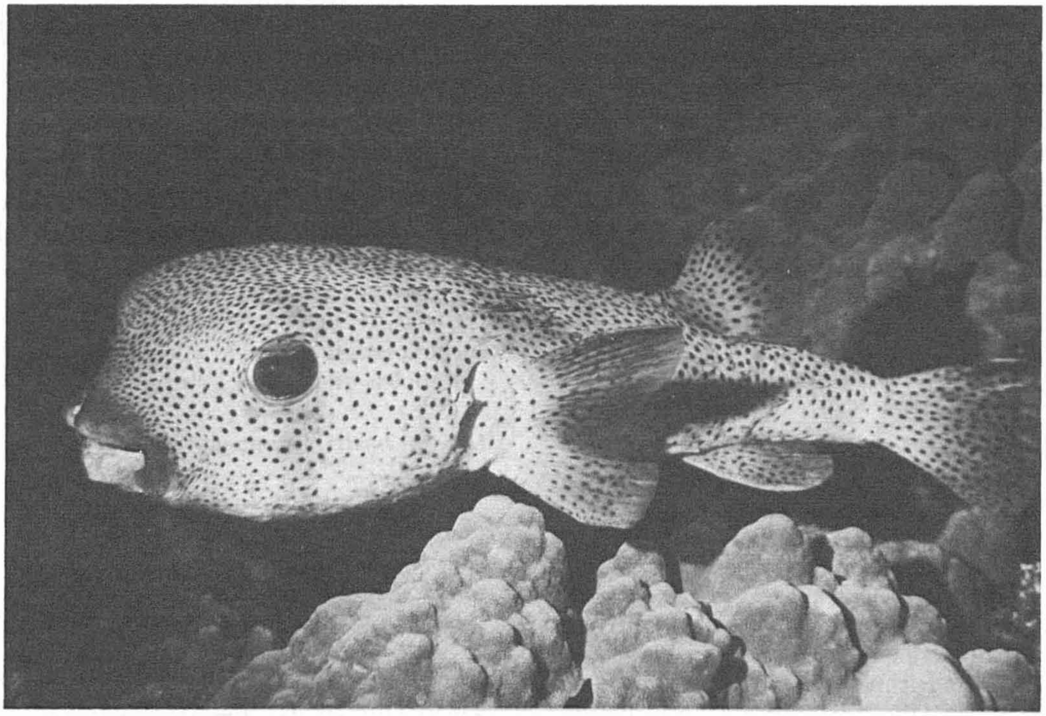

FIGURE 42.—*Diodon hystrix,* a spiny puffer, swimming above the reef at night. With its heavy, beaklike dentition, this fish crushes its shelled prey.

number remains unknown. Nevertheless, the pagurids may actually rank second as prey even though the opercula among this material show that living gastropods are important prey. One *D. hystrix* also contained ostreid pelecypods (mean percent of diet volume: 0.8; ranking index: 0.07), and one contained unidentified fragments (mean percent of diet volume: 4.2; ranking index: 0.35).

Randall (1967) similarly found echinoids the major food of this circumtropical species in the West Indies. For this species as well as *D. holocanthus,* Randall listed gastropods and pagurids separately, without suggesting that some of the gastropods may have been only shells which housed pagurids. Randall recognized that *D. hystrix* feeds partly by night, but believed it to be primarily diurnal. Starck and Davis (1966), however, reported strictly nocturnal habits for *D. hystrix* in the Florida Keys.

The strong, sharp spines that cover *D. hystrix* and *D. holocanthus* are perhaps their most distinctive morphological characteristic. These spines lie flat against their bodies most of the time, but when the bodies inflate with water—a regular response to threats—the spines stand straight out. Although this formidable defense probably deters most predators, the slow-moving *Diodon* would be ready prey for those predators able to tolerate the spines and inflated body. In Hawaii, the tiger shark, *Galeocerdo cuvieri,* regularly preys on full-grown adults of *D. hystrix* (Tester, 1963).

CONCLUSION.—*Diodon hystrix* is a nocturnal predator that feeds mostly on echinoids, and to a lesser extent on prosobranch gastropods and pagurid crabs.

General Remarks on Spiny Puffers

The teeth in both upper and lower jaws of the diodontids are fused together to produce a solid, heavy beak, and this apparatus enables them to crush some of the larger, heavily shelled prey that are beyond the capacity of other fishes—even their relatives the balloonfishes.

The nocturnal habits of the two species of *Diodon,* described above, may be a family characteristic. Starck and Davis (1966) reported that two species of *Chilomycterus* in Florida—*antillarum* and *schoepfi*—are active at night and inactive during the day.

DISCUSSION

The habits of fishes on Kona reefs exemplify the habits of fishes on coral reefs around the world. The following discussion relates these habits to the evolution of fishes on modern tropical reefs, stressing the selective pressures that have shaped the diverse array of forms coexisting on these reefs today. I refer to some of these forms as more advanced, or specialized than others, even though all are products of an equally long evolution, and each is well adaptated to its own specific way of life. Some, nevertheless, have diverged more than others from the generalized carnivores that gave rise to them all, and in this fact lies the basis for the discussion.

The categories erected for presentation have indistinct, overlapping limits, and some species are discussed under one category, rather than another, quite arbitrarily. Nevertheless, the synthesis presented, though an oversimplification, provides a frame of reference within which new information may be assessed. Reemphasizing a point made above, this report deals only with individuals of the various species that behave as adults.

Coral Reefs as a Habitat for Fishes

Most fishes that inhabit coral reefs are among the more recently evolved teleosts (Schaeffer and Rosen, 1961; and others). Indeed, much of the diversity among higher teleosts expresses adaptations to reef habitats. Of the fishes observed along Kona transect lines (Table 7), 98.5% are acanthopterygians.[8]

To properly appreciate the relation of modern coral-reef fishes to their habitat, one should be familiar with the history of tropical reefs. The following outline is based on Newell (1971).

The evolution of tropical reefs can be traced through a fossil record that reaches back into the Precambrian. By the Mid-Ordovician, over 400 million years ago, animal communities had become associated with coral-algal reefs. A succession of reef communities then evolved during subsequent geological history, each with its own characteristic assemblage of animals, and each achieved marked stability before crashing into oblivion during worldwide environmental upheavals. Between each of these periods of stable reef communities, a long time passed without known reefs.

The scleractinian corals, which dominate modern reefs, first appeared during the Triassic, and by Jurassic times, about 150 million years ago, the lithothamnion-scleractinian reef community was well established. Significantly, the teleostean radiation also began during the Jurassic (Gosline, 1971), indicating that their history may closely interrelate with that of the lithothamnion-scleractinian reef community. But Smith and Tyler (1972) suggested that the preacanthopterygian teleosts and their forebearers were maladapted to reef conditions. They contended that fishes entered reef habitats only upon acquiring certain of the morphological advances that marked the first appearance of acanthopterygians early during the Cretaceous, over 100 million years ago. Newell (1971), on the other hand, believed that fishes have had a much longer history as reef inhabitants. He attributed their absence in the fossil record of early reefs to their skeletal remains having been "destroyed by scavengers that abound in this strongly oxidizing environment."

It is unquestioned, nevertheless, that early acanthopterygian fishes—the Beryciformes—were better adapted than were their predecessors for reef habitats. Their increased success probably was based mostly on increased maneuverability and a more adaptive feeding mechanism—the features which Smith and Tyler (1972) felt were especially suited for coral reefs. Patterson (1964) underscored this point when he concluded that most skeletal differences between acanthopterygians and their primitive elopidlike ancestors resulted from changes that permitted the fish better maneuverability: most significant, the fins, given increased rigidity by replacing the anterior soft rays with spines, were more effectively positioned, and the body was shortened and deepened. The advances these fishes made in their feeding mechanism was especially significant, as attested by Schaeffer and Rosen (1961), who stated: "It is primarily the acanthopterygian

[8]Because most of the transect counts were made in daylight, there is a bias toward the more advanced forms in numbers of species (the greater incidence of diurnally secretive habits among the more primitive forms, and of diurnally exposed habits among the more highly evolved forms, is discussed below). Even so, however, the preponderance of acanthopterygians is overwhelming, especially if one also considers numbers of individuals. On Kona reefs such advanced groups as the labrids, pomacentrids, and acanthurids are among the species with the largest numbers of individuals. And although among the nonacanthopterygians the numerous muraenid eels are not properly represented in the counts, neither are such nocturnal acanthopterygians as the numerous holocentrids.

mouth that has given rise to the enormous variety of specialized feeding mechanisms for which teleosts are so well known. Presumably, the evolution of the acanthopterygian jaw mechanism promoted the successful exploitation of food sources that previously were largely unavailable to actinopterygian fishes." They referred to the protrusible premaxillary of acanthopterygians, which permits them to project their upper jaw at food. Fishes with this mouth construction can accommodate the shape and size of the mouth opening more appropriately to the shape of the food item than can fishes without a protusible premaxillary (Alexander, 1967; Gosline, 1971).

During the Cretaceous, in which the beryciforms flourished, the ecological role of the scleractinian corals was challenged by a group of bivalved mollusks, the rudists, which underwent an extraordinary radiation and became the center of a highly successful and widespread reef community. But at the end of the Cretaceous, about 70 million years ago, these and other reef communities collapsed in sweeping extinctions associated with the worldwide biological revolution that marked the close of the Mesozoic (Newell, 1971).

Tertiary seas over most of the world were without known coral-reef communities until lithothamnion-scleractinian reefs underwent a second major radiation during the Eocene, about 50 million years ago (Newell, 1971). The communities that developed in association with these reefs are essentially those of our time. And in what would seem a related phenomenon, the explosive radiation of acanthopterygians into the types that inhabit modern reefs also occurred during the Eocene (Patterson, 1964). Of the families living on reefs today, only a relatively few can be traced back in time earlier than the Eocene (Berg, 1940), and yet by the end of that period, which spanned about 15 million years, representatives of almost every major type of modern fish had appeared (Romer, 1966).

This most recent proliferation of acanthopterygians probably radiated from a line of generalized percoidlike carnivores that had arisen from among the Beryciformes during the late Cretaceous (Gosline, 1966). Above, I note that 98.5% of the fishes seen on Kona transect lines are acanthopterygians; more specifically, 90.4% are acanthopterygians that have reached, or passed, the percoid level of structural development, and 75.5% belong to the order Perciformes (see footnote 7). Only the holocentrids represent the ancestral Beryciformes. In fact, worldwide the Holocentridae, and a few species of Anamalopidae, are the only representatives of this once prolific order that have survived on nearshore reefs.

Obviously the percoid level of development has been highly successful. Gosline (1971) pointed out: "In no single way does it seem to differ from that of the now unimportant, perhaps relic Beryciformes from which it was presumably derived. Possibly the percoids have developed some distinct and as yet unknown biological advantage over the Beryciformes, but for the moment one can only assume that the percoids represent a successful integration of minor advances." The minor advances which Gosline cited include increased maneuverability and adaptability of the protrusible jaw mechanisms, which are refinements on those same features adaptive to reef living that probably gave the Beryciformes an advantage over their progenitors.

Generalized Carnivores: Main Line of Teleostean Evolution

From early Mesozoic times the main line of actinopterygian evolution has progressed through a series of generalized carnivores; with each step forward, the basic feeding mechanism has improved, and the potential for adaptive radiation has increased (Schaeffer and Rosen, 1961). Although this progression has been marked by periodic bursts of specialized offshoots, the primary stem, the generalized carnivore, has remained relatively conservative (Gosline, 1959).

The generalized predator, in simplified form, has a large mouth and is adapted to directly approach, and seize, prey that are fully exposed to the attack. Its prey are small enough to be manipulated, yet large enough to be grasped; moreover, the prey are not sealed in heavy armour, nor do they carry strong spines, spicules, or other noxious components for which the unspecialized digestive tract of the generalized predator is maladapted. Although even the most primitive of today's predators have acquired at least some feeding specializations, the closer one approximates this simplified form, the closer its feeding habits fit this description.

With the generalized predaceous feeding mechanism being a relatively conservative morphological link between periods of adaptive radiation in actinopterygian fishes, one would expect conservative predatory behaviors to be associated with this morphology, and just such behaviors are centered around nocturnal and crepuscular feeding habits. The nocturnal habit involves mostly predation on small, motile crustaceans, the crepuscular habit mostly predation on smaller fishes. Together, crustaceans and fishes are the two major types of prey taken by the generalized predator.

Nocturnal and crepuscular habits among generalized carnivores are discussed separately in the following sections. The separation is artificial, as is the delimitation of a third category, that dealing with generalized carnivores that feed regularly by day. In fact, as illustrated below, the behavior patterns associated with these three types of activity are closely interrelated.

Generalized Carnivores as Nocturnal Predators

Early in the evolving relation between fishes and their prey, the evolutionary lines of many small, vulnerable organisms probably increasingly shifted activity to periods of darkness. There scarcely could be a more elementary solution for animals threatened by active, visually orienting predators. And because effective defense adjustments in prey pressure predators to modify their offense, it seems certain that various predators early aquired means to follow their prey into the night. Thus, in predatory fishes the nocturnal habit itself would be a specialization, but a specialization probably adopted in early preteleostean times that has permitted much of the continued widespread success of the generalized predaceous feeding mechanism.

The smaller generalized carnivores on reefs today find their major prey among the abundant crustaceans, which, as follows from the above, are mostly nocturnal animals that expose themselves at night (Longley, 1927; and others). Many generalized predators that would feed on these organisms have found nocturnal habits adaptive, because only after dark does their straightforward attack find suitable prey in the required exposed position. In this feeding relation, the relatively small size of the crustaceans undoubtedly has influenced the size of the predatory fishes, most of which are of small to medium size (less than about 300 mm long).

Most nocturnal fishes in Kona prey on benthic crustaceans, especially xanthid crabs; however, a number are adapted to take crustaceans and other forms from the water column. The prey of these fishes are mainly relatively large zooplankters (a broad, perhaps loose concept of the term "zooplankton" is used in this report), like crab megalops, that are most abundant in the water column at night. Adults of most nocturnal planktivorous fishes in Kona do not feed significantly on the many small plankters, like calanoid copepods, that predominate in the water column during both day and night.

The extent to which the more primitive reef fishes feed at night seems not properly appreciated. Nocturnal habits are widespread among basal percoids, whereas diurnal habits tend to be characteristic of certain more specialized offshoots. Even if one considers only families that occur in Kona, all nearshore species of the Kuhliidae, Priacanthidae, and Apogonidae seem to be nocturnal, as are many species among the Serranidae, Carangidae, Lutjanidae, Sparidae, and Mullidae.

Probably the nocturnal habits of these more generalized percoids were inherited from ancestral beryciforms. The Holocentridae are the major representatives of this once diverse order on nearshore reefs today, yet as illustrated by their prominence in Kona, they nonetheless are numerous, widespread, and obviously successful. All of them for which there are data are nocturnal, and there is no reason to believe that this is not a primitive characteristic. The anamalopids, which are the only other beryciforms on nearshore reefs, also are nocturnal (e.g. Harvey, 1922). Presumably these modern beryciforms have competed successfully with nocturnal forms among the more advanced teleosts by having refined certain features that are highly adaptive to feeding in the dark. Thus, although much of their anatomy is essentially that of their ancestors, they have acquired highly specialized features—at least many of them sensory—that have permitted more effective use of this equipment. All other present-day beryciforms live in the twilight zone of middepths or in the deep sea, and their suitability to the diminished light of this habitat suggests that their shallowwater ancestors perhaps were nocturnal (Richard H. Rosenblatt, Scripps Institution of Oceanography, pers. commun.). Perhaps during the Cretaceous certain more specialized beryciforms possessed diurnal habits, much as many specialized perciforms do today. But if so, these probably did not survive the widespread extinctions that decimated reef communities at the close of the Mesozoic.

If, as suggested, many reef fishes close to the main line of actinopterygian evolution long ago assumed nocturnal habits in answer to the nocturnal habits of their prey, then one is not surprised to find that widespread predator-prey relations are centered around the nocturnal habit and that the participants are mostly among the more generalized members of the reef community. One especially widespread activity pattern is displayed by the many fishes that assemble in schools on or close to nearshore reefs during the day, then disperse at nightfall and feed on small organisms that become exposed after dark. This is the basic activity pattern of many carangids, lutjanids, pomadasyids, and sciaenids—all among the more generalized perciforms (Hobson, 1965, 1968a, 1972, 1973).

In addition to these basal percoids, it is significant that of the relatively few fishes of preacanthopterygian groups associated with modern reefs, many either follow this pattern themselves, or closely relate as predators to other fishes that do (see next section). A diurnally schooling-nocturnally active pattern is especially widespread, if not universal, among the inshore clupeids, order Clupeiformes—as described earlier for *Harengula thrissina*, an exceedingly numerous fish close to shore in the Gulf of California (Hobson, 1965, 1968a). Starck and Davis (1966) found this same pattern in all five clupeids that they studied on reefs in Florida, and I observed it in *Herklotsichthys punctatus* in the Marshall Islands (unpubl. data). Pertinent information on nearshore clupeids is limited because so few investigators have distinguished between diurnal and nocturnal activity; nevertheless, there are at present no data refuting the generalization that these fishes feed at night.

There are fewer of these diurnally schooling, nocturnally active fishes on Kona reefs than on most other tropical reefs, perhaps for reasons discussed earlier (Hobson, 1972). Still, the pattern is well defined there in certain of the mullids, genus *Mulloidichthys,* and in the lutjanid *Lutjanus vaigiensis,* and is especially apparent in the atherinid *Pranesus insularum,* just as in its congener *P. pinguis* of the Marshall Islands (Hobson and Chess, 1973)—both of the preacanthopterygian order Atheriniformes.

Generalized Carnivores as Crepuscular Predators

In the same way that many generalized predators are nocturnal because suitable prey are most available to them after dark, other generalized predators—those that prey mostly on smaller fishes—are primarily crepuscular because that is when these prey become most vulnerable to their mode of attack (Hobson, 1968a). Moreover, just as is true of the nocturnal forms, the crepuscular piscivores, which also are among the more generalized of the reef fishes, experience certain long-established predator-prey relations. Significantly, many of these crepuscular piscivores are members of the same basal percoid families, the Serranidae, Carangidae, and Lutjanidae, that have produced some of the nocturnal predators discussed above. Many of the crepuscular piscivores, however, tend to be larger than the nocturnal species, which might be expected, inasmuch as the nocturnal fishes are among their major prey (Hobson, 1968a). Schools of nocturnal carangids, pomadasyids, mullids and, especially, clupeids, are well-known targets of such piscivores.

During the twilight periods of greatest piscivorous activity (Hobson, 1968a, 1972), these nocturnal fishes are still in their diurnal schools. And although the schools effectively protect them from predators during most of the day (Manteifel and Radakov, 1961; Eibl-Eibesfeldt, 1962; Hobson, 1968a), this protection is reduced during twilight (Hobson, 1968a). At this time of maximum danger from predators, most other smaller reef fishes, both diurnal and nocturnal, are under cover; thus, the schooling fishes, which are still in the water column, become the most numerous prey of proper size exposed to the space-demanding attacks of the generalized piscivores (Hobson, 1968a). After dark, the smaller fishes seem relatively safe from at least most such predators (Hobson, 1973), but during the changeover between day and night, they are vulnerable (Hobson, 1968a; Munz and McFarland, 1973).

The large piscivores are exceptionally abundant in certain parts of the Gulf of California where the diurnally schooling, nocturnally active fishes are numerous (Hobson, 1968a). As suggested earlier (Hobson, 1972), the relatively few such large predators on Hawaiian reefs, compared with most other tropical areas, may relate to the relative dearth in Hawaii of schooling prey.

Thus, a major activity pattern of these large piscivores closely interrelates with a major activity pattern of the smaller nocturnal predators. For this reason, and because so many members of the two groups are closely related taxonomically, it is apparent that the crepuscular pattern probably has had a longevity comparable to that of the nocturnal pattern. A good indication of this long history exists in the Gulf of California, where the day-night activity pattern of the nocturnal clupeid *Harengula thrissina* closely interrelates with the crepuscular activity not only of certain basal percoids, but also of *Elops affinis*, order Elopiformes, a member of the most primitive of all extant teleostean genera (Hobson, 1968a).

Generalized Carnivores as Diurnal Predators

Thus, nocturnal or crepuscular habits are adaptive for many generalized carnivores. Others with basically the same feeding mechanism, however, have acquired morphological and behavioral characteristics suited to capture small, motile crustaceans and, especially, fishes in daylight. Despite the fact that crustaceans are most exposed to direct attacks at night, and smaller fishes generally are most vulnerable to such attacks during twilight, various predators are equipped to exploit the exceptions to these generalizations.

True, selective pressures applied by generations of visually orienting predators have refined the defense mechanisms that protect so many prey organisms during daylight. But there are occasional lapses in all these defenses when the prey are briefly vulnerable. For example, nocturnal organisms resting under a thin layer of sand occasionally betray their presence by moving. And small fishes that usually are within retreating distance from cover sometimes stray too far into the open; or others, enjoying the security of a school, occasionally drift too far from their fellows. Still others, normally alert to surrounding danger, are momentarily distracted. At such times, these organisms are open to attack. But normally such events fail to occur in the presence of large, free-swimming predators that are actively hunting. Potential prey are sensitive to cues that mark the hunting predator, and take defensive action when a hunter appears—cryptic forms stop moving, others move closer to cover, and schooling forms draw themselves closer together (Hobson, 1965, 1968a). Above all, in this alerted state the prey are less likely to make a defensive mistake. This does happen occasionally, of course, as when large carangids swim slowly among schooling prey for hours during the day without an aggressive move, and then suddenly attack —presumably having sensed a vulnerable target (Hobson, 1968a). Probably this offensive tactic depends on the prey eventually becoming conditioned to the predator's presence, and finally making a mistake. But it seems unlikely that such predators could depend on these relatively infrequent successes. They remain best suited for crepuscular attacks.

The problem of being within striking range when prey are momentarily available during the day because of a defensive lapse is probably best solved by those predators that lie in wait under concealment—the ambushers—or by those that stalk. Both tactics have produced some highly specialized forms that are more appropriately considered in the next section. However, many of those that use concealment to ambush their prey look much like the nocturnal or crepuscular predators discussed above, and so are considered here.

This is especially true among certain basal percoids, like the serranids. For example, many species of *Epinephelus* ambush prey from a concealed position, and much of this activity occurs in daylight (Hiatt and Strasburg, 1960; and others). Most of these predators are cryptically hued for a sedentary existence among rocks or coral—usually they are brown or grey, with the hues often arranged in blotches or spots. Such predators rest unseen until a small organism within striking distance makes a defensive error.

Generalized predators adapted for this tactic are well known to feed regularly during both day and night, as exemplified by certain species of *Epinephelus* (Longley and Hildebrand, 1941; Starck and Davis, 1966; Hobson, 1968a). There is evidence, however, that feeding habits of these predators differ between day and night. In the Gulf of California, *E. labriformis* preys almost entirely on crustaceans at night, but heavily on fishes during the day (Hobson, 1968a). I have already commented on the increased vulnerability of small crustaceans at night; apparently fishes are more vulnerable to the predatory tactics of this fish in daylight. The diurnal piscivorous habit of *Cephalopholis argus* (*Epinephelus argus* of some authors, e.g. Smith, 1971) in Kona is consistent with this probability.

Predators having obvious morphological and behavioral specializations that increase their proficiency as ambushers or as stalkers are considered in the next section.

Specialized Offshoots from the Main Line of Teleostean Evolution

Most fishes inhabiting tropical reefs today, as exemplified by species in Kona, represent specialized offshoots from the main teleostean line.

Predators Specialized to Ambush Prey

As emphasized in the introductory remarks, the categories erected in this discussion overlap. This is especially true of predators that ambush their prey. By using this tactic, predators with the generalized feeding mechanism increase their capacity to capture prey in daylight. But many ambushers, like certain species of *Epinephelus,* are so similar in both morphology and habits to many of the nocturnal and crepuscular forms discussed above that one can only arbitrarily distinguish them as being specialized in this activity. Nevertheless, some forms have retained the generalized feeding mechanism while diverging widely from the primitive form in other respects. And the divergence is based on features that better adapt these fishes for the ambushing tactic.

The synodontids, order Myctophiformes, which are prominent ambushers in Kona, as they are on most other tropical reefs, are products of an evolutionary offshoot that diverged from the main line at a preacanthopterygian level. Thus, the ambushing tactic has had a long history. The scorpaenids, order Scorpaeniformes, and the bothids, order Pleuronectiformes, both of whose Kona representatives include specialized ambushers, belong to groups that diverged from the mainstream near the percoid level (Gosline, 1971; and others). Significantly, the adults of all these forms seem to be primarily piscivorous during the day.

The synodontids, scorpaenids, and bothids that ambush their prey have acquired characteristics that camouflage them as they lie on the sea floor. Clearly, it is important for these predators to go unseen by their victims. In this respect, many of the cirrhitids, order Perciformes, might seem a puzzle. An example from Kona is *Paracirrhites forsteri* (Figure 32), which preys mostly on smaller fishes during the day. Although attacking prey in much the same manner as other ambushers, this colorful fish is clearly visible as it rests in exposed positions on the reef. Selection, in this case, may have in fact favored coloration that attracts attention. Conceivably this could be an effective offensive characteristic, just so long as its use among predators is limited. It is well known that certain small fishes are attracted to conspicuous objects on the sea floor—one needs only to place a small, shiny artifact on the bottom to see this. Perhaps *P. fosteri* actually finds prey among small fishes that approach to investigate its conspicuous features.

Predators Specialized to Stalk Prey

Many predators specialized to stalk prey in the water column belong to groups whose ancestors diverged from the main teleostean line below the percoid level. Characteristically, they have long, attenuated bodies. Among species whose behavior in Kona is described above are the trumpetfish, *Aulostomus chinensis*, and the cornetfish, *Fistularia petimba*—both of the order Gasterosteiformes.

Two other highly specialized stalkers on Kona reefs were not included in the species accounts above because observations on them were infrequent; these are the needlefish, *Strongylura gigantea,* order Atheriniformes, and the barracuda, *Sphyraena barracuda,* order Perciformes. The various species of needlefishes and barracudas are widespread on tropical reefs, and their stalking habits are well documented. Hiatt and Strasburg (1960) reported that *Strongylura gigantea* feeds on small fishes in the Marshall Islands by "drifting up to them and suddenly lashing out with its jaws." On the basis of similar observations in the tropical Atlantic, Randall (1967) reported that needlefishes are almost exclusively piscivorous, and that they "drift slowly into range of one of their prey before making a quick rush." Regarding barracudas, Hiatt and Strasburg (1960) told of *Sphyraena genie* in the Marshall Islands "drifting solitary near the surface stalking its prey" and stated that "it surprises its victim with a sudden lunge." Randall (1967) noted that barracudas in the tropical Atlantic feed primarily on fishes during the day, a statement probably true of at least most stalking predators.

Predators Specialized to Seek Prey in Reef Crevices

Here I am concerned primarily with muraenid eels, order Anguilliformes, and the brotulids, order Gadiformes. Members of both groups, but the eels in particular, have elongated bodies suited to maneuvering through the crevices that honeycomb coral reefs. Their similar morphologies led early Hawaiians to group eels and brotulids together by the generic term *puhi*. There are a number of other secretive forms on Kona reefs—small inconspicuous fishes like the pseudochromid *Pseudogramma polyaccanthus*, which were occasionally visible at night during this study—but because I have little knowledge of their habits they are not considered here.

The muraenid eels are products of an evolution that has diverged widely from the main teleostean line: today they possess many specialized features that equip them for hunting in reef crevices. The primary specializations, for example their exceptionally solid skulls, are adaptive for wedging through small openings, and they can back out of any hole they enter (Gosline, 1959, 1971). Many of the morays, and at least some of the brotulids, for example *Brotula multibarbata* in Kona, are nocturnal; however, other morays are diurnal. Obviously hunting conditions in reef crevices differ between day and night.

Reef crevices are havens for numerous creatures. Many diurnal forms rest there at night, some of them virtually asleep, and many nocturnal forms shelter themselves there in daylight (Hobson, 1968a, 1972). Moreover, most reef animals find refuge in these crevices when they are injured or distressed; obviously, sheltering in reef crevices is adaptive for prey threatened by the many predators on the surface of the reef. But it is equally obvious from their long successful history on tropical reefs that eels have acquired adaptive means to exploit such prey.

Predators with Sensory Specializations That Detect Concealed Prey

In this category I am concerned with the mullids, order Perciformes, which are prominent on Kona reefs. Their distinctive sensory chin barbels permit them to locate prey that go undetected by other fishes. And, like the muraenid eels, above, their numbers include both diurnal and nocturnal forms, as well as species that hunt effectively during both day and night. This fact, and the great diversity in their prey, shows that mullids, with their distinctive modes of feeding, have available to them a broad range of predatory activity denied most other fishes.

Although seeking refuge under rocks, algae, or sand is adaptive for many small animals approached by a predator, this tactic probably plays to the advantage of some mullids. For example, the diurnal *Parupeneus chryserydros* preys mostly on small diurnal fishes that typically take cover when threatened. This mullid may use its exceptionally long barbels not only to locate such animals, but also to drive them into the open.

Many small organisms that seek cover when threatened rest in the same refuges when they are inactive, and at such times may be prey for other mullids, notably *P. bifasciatus*. This species seems to feed with equal effectiveness day and night, although its food habits differ between these two periods. In this respect, a comparison with the serranid *Epinephelus labriformis* in the Gulf of California is insightful. As noted above, *E. labriformis* also feeds regularly day and night, taking mostly crustaceans after dark and small fishes in daylight; thus, its food habits agree with the generalization that crustaceans are most vulnerable at night, and fishes most vulnerable in daylight. *Parupeneus bifasciatus* seems to be a successful exception to this generalization, because it takes fishes more often at night than during the day and crustaceans more during the day than at night. Apparently, *P. bifasciatus* is specialized to capture prey that rest under cover, safe from predators with generalized feeding equipment.

Thus, at least some mullids find prey among animals that have sheltered themselves in the reef, just as do some of the muraenid eels, so that, like the eels, they have gained advantage from what generally are successful defensive behaviors in their prey. But whereas the eels probe deep into reef interstices, the mullids confine their activity to the superficial covering on the reef.

Predators Specialized to Take Prey Among the Plankton During the Day

There are clear distinctions between diurnal and nocturnal planktivorous fishes on coral reefs, with the diurnal species inactive at night and the nocturnal species inactive during the day (Hobson, 1965, 1968a, 1972; Starck and Davis, 1966). Emery (1968) showed that the composition of plankton over reefs in Florida also differs between day and night, a fact undoubtedly related to the diurnal-nocturnal dichotomy among the planktivorous fishes. As described above, planktivorous fishes that feed in the water column at night, for example *Myripristis* and *Apogon,* have the generalized carnivore's large mouth and prey largely on the relatively large plankters, like crab megalops, that are mostly in the water column above the reef after dark.

Although a large array of plankters inhabit the water column during the day, generally they seem too small for adults of the large-mouthed nocturnal planktivores. Significantly, diurnal planktivores all have a small mouth, and their major prey, calanoid copepods, are generally smaller than the prey of their nocturnal counterparts. Moreover, diurnal planktivores among adult reef fishes generally are among the more advanced teleosts, having attained, or passed, the percoid level of development. There are no basal percoids among the prominent diurnal planktivores in Kona, but in the tropical Atlantic certain serranids, lutjanids, and pomadasyids specialized in this habit are numerous (Starck and Davis, 1966; Randall, 1967). Most diurnal planktivores on coral reefs, however, are among the higher Perciformes. These include the pomacentrids, which probably include a higher proportion of planktivorous species than any other major family of coral-reef fishes. The balistids, order Tetraodontiformes, are among the most advanced teleosts and include several specialized diurnal planktivores: species of *Melichthys* and *Xanthichthys ringens* are prominent on coral reefs over much of the tropical world.

Many unrelated species that forage on zooplankton in the water column during the day display convergent morphologies. Features characteristic of these fishes were identified by Davis and Birdsong (1973), who did not distinguish between diurnal and nocturnal forms, however. Drawing examples from the tropical Atlantic Ocean, they illustrated certain unrelated planktivorous fishes, for example *Paranthias furcifer* (a serranid) and *Chromis cyanea* (a pomacentrid), that, on casual inspection, look more like one another than they do members of their own families that feed on the benthos. The similarity among these unrelated forms is based mainly on their common increased tendency toward a fusiform body, a deeply incised (forked or lunate) caudal fin, and a small, upturned mouth that gives their heads a characteristic appearance. Presumably diurnal planktivores that tend toward a more fusiform body and deeply incised caudal fin—both well-known characteristics of rapid-swimming oceanic fishes—can swim faster than relatives in which these tendencies are less developed. Considering the many active predators at large during the day, increased speed clearly is adaptive for small reef fishes that swim at that time in open water, high above the sheltering reef. The advantage of the upturned mouth may be indirect: Rosenblatt (1967) acknowledged Walter A. Starck II for pointing out that this mouth construction gives the fish a shortened snout, which permits close-range binocular vision—an obvious advantage in capturing tiny organisms in the water column. A number of diurnal planktivorous fishes in Kona possess one or more of these characteristics, as described and illustrated above (e.g. Figures 38 and 40).

Significantly, none of the nocturnal planktivores in Kona tend toward having either a more fusiform body, or a more deeply incised caudal fin. In fact, planktivorous squirrelfishes of the genus *Myripristis* are actually deeper bodied than their bottom-feeding relatives of the genus *Holocentrus,* and the caudal fins of most are less deeply incised (compare, for example, Figures 11a and 14). If, as suggested above, these features gain selective advantage in the planktivores by providing added speed to elude predators in open water, then their absence among forms that rise into the water column after dark is consistent with the contention (above, and Hobson, 1973) that small free-swimming fishes face a much diminished threat from predators at night. Many of the nocturnal species, including species of *Myripristis,* have the sharply upturned mouth; but it is a large structure, as noted above, suited to taking the larger zooplankters that appear in the water column after dark.

Not all of the diurnal planktivores in Kona tend toward fusiform bodies, deeply incised caudal fins, or sharply upturned mouths. None of these features occur in the planktivorous chaetodontids, for example *Hemitaurichthys zoster* (Figure 28a), which nevertheless are well suited to feed on copepods, and other tiny zooplankters in the water column by day. Obviously many conflicting pressures have differentially affected the morphologies of the various fishes that forage on tiny organisms in the mid-waters.

Predators Specialized to Prey on Benthic Invertebrates During the Day

A wide variety of fishes prey on benthic invertebrates during the day. They include most of the labrids, chaetodontids, balistids, canthigasterids, monacanthids, ostraciontids, and tetraodontids, as well as many of the pomacentrids, blenniids, and others—all of them higher perciforms or tetraodontiforms. Their prey are among the more prominent invertebrates on the reef, including such sessile forms as sponges, coelenterates, and tunicates; and also various slow moving animals like echinoids and gastropods. Typically, these prey are fortified with toxic or noxious components, like spines, spicules, nematocysts, or tough, fibrous components; or they are encased in heavy armour. Because of these defensive features, fishes that prey on such forms must have specialized feeding structures or techniques—the unspecialized feeding apparatus of generalized predators is maladapted for this task. Also unavailable to generalized predators are the many very small organisms whose capture requires delicate manipulations or movements for which large-mouthed fishes are unsuited. Moreover, many of these prey are diurnally cryptic or secretive, thus requiring still additional specializations to capture them in daylight.

Thus, fishes that successfully feed on most benthic reef invertebrates during the day are advanced species whose evolution has been mostly one of perfecting means to feed in daylight on prey that are beyond the capacity of fishes with generalized feeding equipment. Certain mullids, discussed above, are adapted to feed on many of these prey, but mullids use nonvisual means, whereas fishes considered here are primarily visual feeders.

These are fishes that have passed the percoid level of development. The evolution of the percoid morphology, especially with its highly adaptive feeding mechanism, gave fishes added potential to adjust to a wide variety of feeding situations. But although percoids appeared first during the Cretaceous (Patterson, 1964), not until modern reef communities appeared during the Eocene (Newell, 1971) does it appear they began to fully realize this potential.

Bakus (1964, 1966, 1969) concluded that the secretive habits and defensive structures of many benthic invertebrates on coral reefs today, including sponges, didemnid tunicates, and others, are the result of predation pressures from fishes. Whether or not this is so, certainly the array of specialized feeding habits and structures that characterize diurnal bottom-feeding fishes on coral reefs are mostly adaptations which cope with specific defensive characteristics of their prey. Because predation pressures lead to defensive adjustments in prey, and these in turn stimulate further offensive modifications in predators, it is not surprising that the diverse array of defenses in benthic invertebrates today is matched in the fishes that feed on them by an equally diverse array of solutions. These solutions to invertebrate defenses are manifest in the extremely varied feeding structures and behaviors that occur among diurnal fishes. Most diurnal fishes specialized for diets of benthic invertebrates have relatively small mouths, but beyond this their feeding morphologies have diverged widely.

Sessile invertebrates seem to be significant prey only during the day, perhaps because an animal must move to be sensed by most predaceous fishes at night (Hobson, 1968a). Thus, the few highly specialized fishes that feed on sponges are strictly diurnal. In Kona, the chaetodontid *Holacanthus arcuatus* feeds on some of the larger sponges that encrust in exposed locations on rocks, whereas the zanclid *Zanclus canescens* uses its elongated snout to feed on some of the smaller sponges that are attached within crevices or depressions on the reef. Randall and Hartman (1968), in studying sponge-feeding chaetodontids and monacanthids in the West Indies, noted that sponges cannot be digested by most fishes, and concluded that these organisms have become available as food for only a few highly specialized teleosts in geologically recent times.

Some diurnal predators, for example *Forcipiger flavissimus*, *Chaetodon auriga*, and *C. fremblii*, among chaetodontids in Kona, habitually tear off pieces of larger sessile invertebrates, including polychaetes, tunicates, and alcyonarians. The analogy drawn above between the snout and jaws of *F. flavissimus* and a pair of needle-nosed pliers underscores the suitability of this fish's feeding morphology for its feeding habit.

One of the most obvious potential foods for carnivorous bottom-feeding fishes on coral reefs would seem to be the corals themselves. Nevertheless only some of the most advanced teleosts exploit this resource. In Kona, coral eaters include certain chaetodontids, pomacentrids, and blenniids (all higher Perciformes) and certain monacanthids and tetraodontids (all Tetraodontiformes). In pointing out that coelenterates are not food for fishes in most marine communities, Hiatt and Strasburg (1960) cited various specialized features of fishes that prey on corals in the Marshall Islands: for chaetodontids and monacanthids that snip off individual polyps, they listed the produced snouts, small terminal mouths, and fine protruding incisiform teeth; for tetraodontids and balistids that bite off larger pieces of coral, they noted very heavy, strong dentition. All fishes that feed on coral, including those that feed heavily on coral mucus, seem to be diurnal. Obviously a predator that bites off large chunks of coral, or which scrapes away mucus, would find diurnal habits adaptive—its food is equally accessible day or night, and its own activity would benefit from daylight. On the other hand, the polyps of some coral species are most expanded at night, suggesting that perhaps predators that would snip them off might find them most accessible after dark; however, the precise manipulations involved in this activity probably require the light of day, because without exception all such predators are diurnal.

Daylight and precise manipulations also seem required of predators that pluck tiny cryptic organisms, notably amphipods, from amid benthic cover. An example from Kona is the labrid *Anampses cuvier,* whose prey are amphipods and other organisms too small for large-mouthed generalized predators of comparable size. Taking such prey requires a specialized tactic and feeding mechanism. Characteristically such predators hover within a few centimeters of the substratum, inspecting the surface. When they spot prey—perhaps through movement or an unusual contour—they take it in a characteristic plucking manner.

Probably this way of plucking tiny prey from a substratum preadapted precursors of those fishes that are specialized as cleaners. Most cleaner fishes, which include certain labrids, pomacentrids, and chaetodontids, pluck various materials, mostly ectoparasitic crustaceans, from the bodies of other fishes. Possessing both the necessary techniques and morphology, certain fishes in this category were prepared to adopt the cleaning habit when their concept of a suitable feeding substratum broadened to include the bodies of other fishes (Hobson, 1971). A few species, like *Labroides phthirophagus* in Kona, are specialized as cleaners, having refined both their feeding morphologies and techniques to more efficiently practice this habit. All known cleaner fishes are diurnal.

Most of the invertebrate prey of diurnal fishes are insignificant as prey of nocturnal fishes. However, the specializations that permit certain diurnal fishes to seek out secretive prey in daylight make available to them at that time some of the forms—motile crustaceans in particular—that are important prey of various generalized predators after dark. For some fishes, the adaptations that permit them to take crustaceans and other forms from under reef cover in daylight are morphological. Thus, the chaetodontid *Forcipiger longirostris* and the labrid *Gomphosus varius* both have elongated snouts with which they reach deep into reef crevices for crustaceans. In other fishes the adaptations that make secretive prey available are more strictly behavioral. Thus, the labrid *Thalassoma duperrey* follows close to the feeding jaws of large herbivores and other fishes that disturb the substratum, and snaps up tiny crustaceans driven from cover. This behavior is widespread, occurring in other wrasses in Kona and also in the Gulf of California (Hobson, 1968a). Some species lower on the evolutionary scale seem to have similar behavior: as suggested above, the carangid *Caranx melampygus* may enjoy this advantage by following the mullid *Parupeneus chryseydros,* as may the aulostomid *Aulostomus chinensis* by accompanying grazing schools of acanthurids—in these two situations, however, the prey seem to be mostly small fishes.

Some diurnal predators excavate buried prey, as when the labrid *Coris gaimard* overturns small stones with its snout and feeds on animals thus exposed. And in the eastern Pacific the balistid *Sufflamen verres* uncovers prey buried in the sand by exposing them with a jet of water from its mouth, or by rapidly undulating dorsal and anal fins while lying on its side, thereby generating currents that sweep the sand away (Hobson, 1965, 1968a). Similarly, the ostraciontid *Lactophrys triqueter* in the tropical Atlantic by jetting water from its mouth uncovers prey buried in the sand (Longley, 1927).

Related Problems of Species Recognition.—The enormous potential for varied feeding adaptations in these advanced teleostean groups has led to the occurrence on most coral reefs of large numbers of closely related species that seem to have diverged from one another chiefly on the basis of differing food habits. For example, 14 species of the genus

Chaetodon occur together on Kona reefs—all very similar in general body form, but with distinctive differences in diet and related morphology. Obviously, such situations can exist only if, in addition to having acquired adaptations suited to specialized diets, closely related forms have also acquired effective barriers to interbreeding. Central to this is the ability of each individual to recognize others of its own kind, which probably relates to the circumstance that most species in this category have highly visible species-specific color patterns.

It is logical that diurnal fishes would employ visual cues to identify one another. But the distinctive nocturnal colorations of many chaetodontids suggest that members of some species need to recognize each other after dark as well. Nocturnal colorations that occur among chaetodontids in Kona tend to accentuate a contrast, thus making them more visible at lower light levels (e.g. Figures 28a and b; 29a and b). Although the nocturnal colorations of some fishes, such as those that become mottled, make them more difficult to see in the dark (Schroeder, 1964), certain chaetodontids in Kona seem to be effecting a nocturnal display. This phenomenon appears most pronounced among fishes in the present category, but others show it as well; for example, in Kona certain of the nocturnal squirrelfishes, *Holocentrus* (Holocentridae: Beryciformes) display characteristic white bars or spots at night that are more visible under reduced light than their daytime colorations would be (e.g. Figure 12a and b). Probably one can generalize only to the extent that distinctive day/night colorations in coral reef fishes reflect distinctive day/night situations.

Fishes Specialized to Feed on Vegetation

Vegetation, which carpets much of the rocky sea floor inshore, would seem ready food for fishes. Yet relatively few species utilize this resource, even though, as in Kona, they often predominate on tropical reefs. The herbivorous habit is an advanced trait among marine fishes, a fact recognized by Hiatt and Strasburg (1960).

In general, herbivorous fishes on coral reefs share many characteristics with the diurnal predators that are specialized to prey on benthic invertebrates, discussed in the previous section. Like the fishes grouped together in that category, at least most coral reef herbivores are active by day and relatively inactive at night; furthermore, they too tend to be colorful animals that have small mouths which are part of highly evolved feeding systems. In fact, several families of fishes span both categories; for example, the Chaetodontidae, Pomacentridae, Blenniidae, Balistidae, Monacanthidae, and others include gradations of species from some that are strictly carnivorous, to others that feed on both plants and animals, to still others that are strictly herbivorous. Within these groups, which have favored plasticity in feeding habits and structures, it seems that characteristics adaptive to plucking benthic invertebrates from the sea floor have been modified in some species for grazing on plants.

Nocturnal Activity Among Advanced Teleosts

Not all the more advanced fishes are diurnal. The chaetodontid *Chaetodon lunula* seems to be nocturnal in Kona, and at least some of its congeners—notably *C. quadrimaculatus* and *C. auriga*—may feed to some extent after dark. But these are exceptional cases in an overwhelmingly diurnal group. As suggested above, nocturnal activity in these instances may relate to competition among the exceptionally large number of *Chaetodon* species that cooccur on Kona reefs.

Nocturnal habits cannot be regarded as exceptional where they occur among the diodontids, however, because night feeding seems to be the rule in this family. And these members of the order Tetraodontiformes are among the most highly evolved of all reef fishes. The prey of *Diodon hystrix* and *D. holocanthus* in Kona —large echinoids, gastropods, and pagurid crabs—are more exposed at night than during the day. And because they are relatively large and move at least intermittently after dark, one can predict they would be suitable quarry for nocturnal predators having means to crush heavy armour. These are large prey, so a predator must carry its crushing mechanism in its mouth, rather than in its throat—as do many of the labrids and other predators that feed on smaller mollusks and echinoids during the day. The highly evolved diodontids accomplish this job with their powerful crushing jaws, but the problem has also been solved at a more primitive level by certain basal percoids. In Kona, the nocturnal sparid *Monotaxis grandoculis*, with its molariform dentition, has feeding habits similar to those of the diodontids, but with less emphasis on heavily armoured forms. Clearly, the diodontids, with more powerful jaws and heavier dentition, are better adapted than the sparids for this particular task. Of even more primitive stock than the sparid, the muraenid eel *Echidna zebra* has crushing dentition, but its prey seem to be primarily large crabs that it takes regularly from reef crevices in daylight. There is no evidence that it can crush the heavy gastropods so prominent in the diets of the more advanced sparids and diodontids.

CONCLUSIONS

1. The feeding relationships of fishes on coral reefs in Kona, Hawaii, follow essentially the same pattern as do feeding relationships of fishes on coral reefs elsewhere.

2. Nocturnal habits have had a long history in teleostean fishes, and are widespread among the more generalized forms, including many of the clupeids, holocentrids, serranids, kuhliids, priacanthids, apogonids, lutjanids, and others. These large-mouthed predators find night feeding adaptive because that is when their prey—mostly small, motile crustaceans—are in exposed locations and thus vulnerable to their straightforward attack.

3. Piscivorous predators that have a generalized feeding mechanism, and which attack with a straightforward charge, for example certain large carangids, are mostly crepuscular.

4. Certain piscivorous predators that have a generalized feeding mechanism feed effectively during the day, as well as during twilight, by ambushing or stalking their prey. The ambushers, which include certain synodontids, serranids, scorpaenids, and bothids, typically have cryptic morphology, coloration, and behavior. The stalkers, which include the aulostomids, fistulariids, belonids, and sphyraenids, typically have long, attenuated bodies.

5. In acquiring features adaptive for hunting in reef crevices, muraenid eels have become highly successful, capitalizing on the otherwise effective shelter-seeking habits of small reef animals. Although many small reef animals become more vulnerable to eels when they shelter in reef crevices, they find these refuges adaptive when resting, injured, or distressed, because they are relatively safe here from the even greater threat from predators that exists on the surface of the reef.

6. The mullids use their distinctive sensory barbels to locate prey that are sheltered under the superficial covering of the reef and adjacent sand. Some mullids are best adapted to capture such prey at night, others to capture such prey in daylight, and some feed effectively during both day and night. At least some use their barbels not only to detect prey, but also to drive them into the open.

7. Most fishes on Kona reefs, like fishes on coral reefs elsewhere, are among the more recently evolved teleosts, having reached, or passed, the percoid level of structural development.

8. The adaptability of the perciform feeding apparatus has given rise to a wide variety of forms that have diverged from one another primarily on the basis of differing food habits. Much of this diversity has resulted from adaptations that cope with specific defensive characteristics of the organisms on which these fishes feed.

9. Just as nocturnal and crepuscular habits predominate among the more generalized coral-reef fishes, diurnal habits predominate among the more advanced, specialized forms, including most of the higher Perciformes, and Tetraodontiformes. Some of the most advanced of all, however, including the diodontids, are nocturnal.

10. Some higher teleosts, including certain chaetodontids, labrids, and balistids, have specializations that permit them to capture, during daylight, nocturnal forms hidden under cover. Such prey include forms like motile crustaceans that expose themselves at night, and at that time become the major prey of generalized nocturnal fishes.

11. Some advanced teleosts, including certain chaetodontids, labrids, and pomacentrids, are specialized to pluck tiny prey, such as amphipods, from among vegetation and other benthic cover. These prey are too small, and too cryptic, to be taken after dark or by predators with a large mouth. This plucking habit preadapted certain species for cleaning ectoparasites and other material from the bodies of other fishes.

12. Fishes that prey mostly on sessile invertebrates, like sponges and coelenterates, are highly evolved diurnal species, including certain chaetodontids, pomacentrids, balistids, and monacanthids. These predators have specialized feeding structures and techniques that handle various noxious or toxic defensive features in their prey, including spines, spicules, nematocysts, tough fibrous tissues, and heavy armour. And they take these sessile animals in daylight because only moving prey are effectively sensed by visually feeding predators after dark.

13. Characteristics developed in feeding on sessile benthic invertebrates have been modified in some fishes for grazing on benthic vegetation. Thus, many families, for example the Chaetodontidae, Pomacentridae, Balistidae, and Monacanthidae, include some strictly carnivorous forms that prey on benthic invertebrates, other forms that feed on both benthic invertebrates and vegetation, and still others, strictly herbivorous, that only graze on benthic vegetation.

14. On coral reefs there is no sharp distinction between fishes that feed on sessile invertebrates and those that graze on benthic vegetation: species in both categories tend to be colorful diurnal fishes with a small mouth that is part of a highly evolved digestive apparatus.

15. The plasticity in feeding habits and structures characteristic of higher teleosts that feed on benthic organisms has led to the multiplicity of closely related, and morphologically similar species that live together on coral reefs. This situation could not have evolved without effective barriers to interbreeding, which in turn requires that individuals recognize others of their own kind from among many very similar forms. This requirement has been met by having developed highly visible, species-specific color patterns. The distinctive nocturnal color patterns of some forms, for example *Zanclus* and certain chaetodontids, indicate that, although they are diurnal, certain of them need identifying features at night, as well as during the day.

16. The small mouth of higher teleosts is adaptive for feeding on the smaller plankters, like calanoid copepods, that compose the vast majority of organisms in the water column. This characteristic distinguishes diurnal planktivores, including certain pomacentrids, chaetodontids, and balistids, from the nocturnal planktivores, which include certain holocentrids and apogonids. Most nocturnal planktivores have the larger mouth of the generalized predators, and most of them feed primarily on the larger plankters, like crab megalops and mysids, that are most numerous in the water column over the reef at night.

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