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General Ecology of Six Species of Hawaiian Cardinalfishes[1]

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ABSTRACT: Six species of cardinalfishes (Pisces: Apogonidae) are found together in shallow marine waters of Hawaii day and night. All six species remain in holes and caves during the day and emerge at night when they feed. The centers of abundance, ecological ranges, and other requirements of the six species differ during their life histories. During the day, *Foa brachygramma* is found in crevices or rubble on shallow, calm reef flats and unlike the other species may enter areas of low salinity and poor circulation. Young *Foa* are found under ledges in deeper water than are adults. *Apogon menesemus* is most abundant in clear, relatively deep water, especially where the substrate is almost completely covered by live coral. It lives at the back of holes or caves. *Apogon erythrinus* frequently inhabits small, dark holes in either dead coral heads or basalt cliff caves. *Apogonichthys waikiki* is most often found in pairs in large, widely spaced living coral heads. *Apogon maculiferus* adults are found under ledges and in caves at depths of over 20 meters. Young *A. maculiferus* aggregations are found in shallow water under ledges or at cave entrances. *Apogon snyderi* has the widest habitat distribution, although it is restricted to substrates with some sand. It lives in the middle of caves close to the floor, and under rubble, coral heads, or ledges.

Each species reacts differently to increasing or decreasing light levels. Generally, a species' response to a given amount of light in the laboratory is similar in the field. In shallow water, adult *Apogonichthys waikiki* is not seen outside holes unless light intensity is less than 1.75 fc. *Apogon erythrinus* emerges or enters holes at about ± 5 fc, *A. menesemus* at about 16 fc, and *A. snyderi* at about 88 fc. Adult *Foa brachygramma* leaves or enters cover at about 2400 fc, young *Foa* at about 700 fc. Adult *Apogon maculiferus* emerge and enter cover at about 100 fc and young *A. maculiferus* at about 2700 fc. Diurnal predators remove more individuals of species living in brighter light intensities; cave-dwelling predators remove those living in lower light intensities.

At night all species are opportunistic carnivores on zooplankton and benthic invertebrates, but there are differences in their foraging locations. *Apogon snyderi* and *A. maculiferus* forage mostly over light-colored substrates, but *A. maculiferus* feeds nearer dawn, higher in the water, in aggregations, and closer to large objects than does *A. snyderi*. *Apogon erythrinus* is found no more than 3 cm from hard substrates, vertical and horizontal. The other three species are found near large underwater objects. *Foa brachygramma* remains near the bottom when there is a current, and groups of fish rise in the water column on quiet nights when there is a half to full moon. *Apogon menesemus* is most often found in midwater and is often located in the shadow of large underwater objects on moonlit nights. *Apogonichthys waikiki* hovers near holes in the isolated coral heads where it is found diurnally. Nocturnal predators take individuals of all species except *A. waikiki*.

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CARDINALFISH, MEMBERS OF THE FAMILY Apogonidae, are easily recognized by their large mouths and eyes; robust, perch-like bodies; and two small dorsal fins. The largest number of species is found in the tropical Indo-Pacific, which is probably the center of distribution for the group (Fraser 1972).

Of eight shallow-water species of cardinalfishes recorded in Hawaii, six species, *Apogon erythrinus*, *A. maculiferus*, *A. menesemus*, *A. snyderi*, *Apogonichthys waikiki*, and *Foa brachygramma*, are common in shallow water. At least three species may be found together on all Hawaiian reefs that I have examined. The presence of six species in some shallow-water areas provides an opportunity to study differences between phylogenetically related fishes both in the field and in the laboratory. The six species have similar behaviors. All activities other than feeding (including courting) occur in holes and caves during the day. Initial observations and collections give the distinct impression that the six species are common and coexist in a harmonious fashion. In this study, observations and experiments were conducted to determine how these species are separated from each other ecologically and morphologically.

METHODS

The field methods employed in this study estimate the distribution of the different cardinalfish species around Oahu. At each station, measurements of salinity, water depth, temperature, light intensity, and turbidity were made.

Light measurements were taken in shallow water from 0.5 to 3 meters in depth between 1100 and 1400 on clear days with Knight (KG-275A) and Spectra Universal (U751) incident light meters. The light meters were initially calibrated with an underwater TSK luxometer. Light intensity was read directly in footcandles when measuring light underwater. The light meters were held horizontally and measurements were taken in four directions and averaged. Light readings were taken at the location where the fishes were first sighted in the field. The distance between each fish and the closest substrate (i.e., coral head, ledge, etc.) was measured. The nearest cover in that substrate was located and the distance from the fish to cover was estimated by triangulation. Cover is defined as a space into which a cardinalfish may swim which is at least a magnitude (10 ×) darker than the spot where it is first observed.

To quantify distribution patterns of the various apogonid species, three permanent 100-meter transects were established in the vicinity of the Waikiki Natatorium near the south end of Waikiki (Figure 1). The transects were run two nights per month from July 1968 to June 1970. Two hundred and eighty cubic meters of water were observed each night. Each transect was divided into five discrete substrate types: sand, reef flat, rubble, undercut reef flat, and boulders. Estimates of their surface areas (in two dimensions) were made to determine whether increased surface area affected the placement of each apogonid. A 3-meter rod was placed in each substrate type and an estimate of relief was obtained by molding a chain with 1-cm links in and around the substrate irregularities beside and along the rod. The ratio of the length of chain to the rod length was taken to be the relative surface area of the substrate type; a ratio of 1 indicates perfectly flat substrate and higher ratios indicate greater surface areas.

The ocean was classified as "rough" when the waves reached 1 meter in height and broke at the south Natatorium wall. Otherwise, it was termed "calm." The tides and moon phases were estimated from a chart issued yearly by the Dillingham Corporation of Hawaii. Visibility estimates were made by shining the transect light against the Natatorium wall at the beginning of the transects and determining the distance at which the wall could be seen.

Initially, an attempt was made to randomize both time of night and time of month for running the transects. However, night dives and tagging experiments (Chave 1971) showed that most cardinalfishes spread out over the substrate just after dark and then move very little. Subsequent transects were

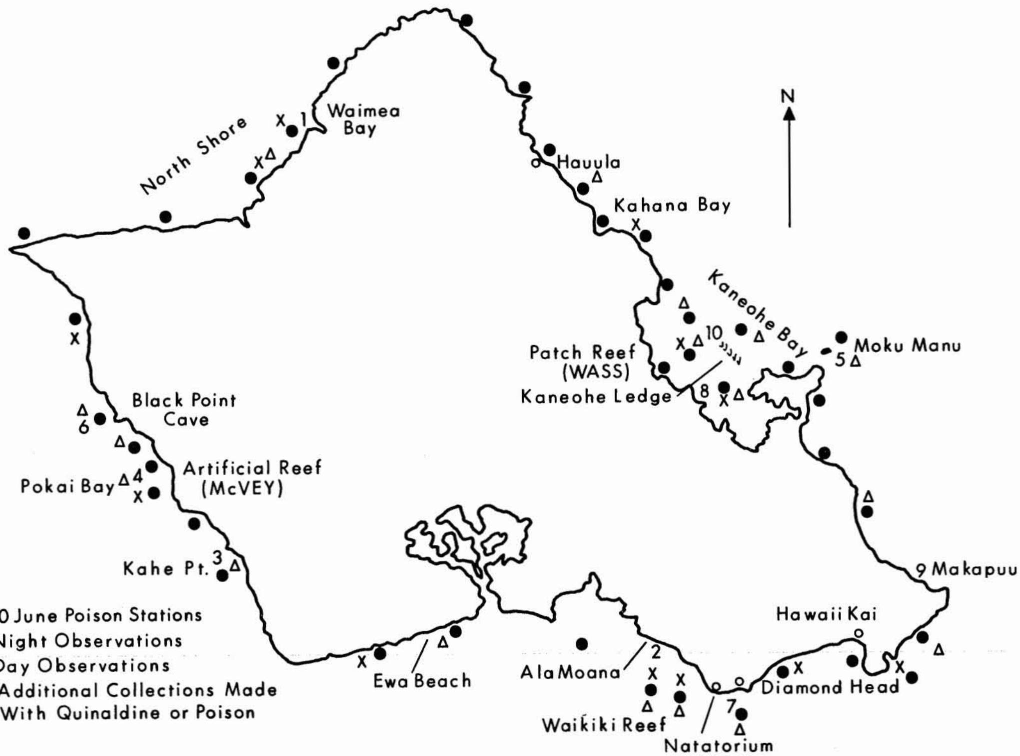

FIGURE 1. Map of Oahu showing the major collection and observation sites. Place names mentioned in the text are also indicated.

run approximately 1 hr after sunset. Because of rough water and ebb tides, visibility on randomly selected nights often fell below 1 meter and, consequently, preselection of nights for high water and flowing tides resulted in good visibility most of the time.

Recording methods along the transects were as follows: The observer swam on the surface with a Dacor light (the 6-V battery was changed every night). The water column and the substrate in the path of the light were examined, as were the large rocks and crevices under the light. Fish observations were tallied on plastic sheets.

To determine the type and abundance of food eaten by cardinalfishes, 1034 individuals were collected in early morning poison stations. All were dissected and 73 individuals had recognizable food items in their stomachs. Each food organism was measured, tallied, and classified as far as possible. Records of where food items were seen at night—in midwater, on hard substrates, or on sand—were also made. Since the algae in the study areas grew on rocky, not sandy or muddy, substrates, animals clinging to seaweeds were counted with the hard substrate group. Most of the shrimp were as likely to be in midwater as on the substrate and were placed in a separate category.

Fishes needed for experiments in the laboratory were placed in 32-liter containers and maintained on a 12-hr light, 12-hr dark cycle, with various light intensities. Light intensity was measured at the level of the top of the experimental tank. The temperature in the tanks varied from 25 to 28°C and salinity from 33 to 36‰.

All fishes were tested in a 120 × 140-cm tank of 60 cm depth. The front of the tank was clear plastic. Cover in the experimental tank consisted of various combinations of PVC pipes with different lengths and aperture sizes, concrete blocks with holes, coral heads, and piles of rock. All diurnal observations were made behind a blind; nocturnal observations were made with red light.

Fish were tested from 1.75 to 7168 fc, the lowest and highest intensities that could be consistently obtained during the day. The light intensity was increased by adjusting the banks of lights and dimming switch; each time, light intensity was doubled. A strong effort was made to use light that had a spectral composition approximately equal to that of the sun. The relative energy of the sun's radiation on the surface of the sea at noon and the fluorescent light chosen for the laboratory studies were both about 800 g-cal/cm^2/hr and between 450 and 600 nm. Above and below this value the fluorescent energy dropped abruptly. The bulbs were designed so that light intensity could be reduced without causing flicker.

A light background was provided in the experimental tanks so that the cardinalfishes could be seen more clearly when in midwater. This method was also used by Hunter (1968) and Whitney (1969). Cover in the light-intensity experiments consisted of a concrete block with six holes approximately the same color and texture as that of parts of the reef at Waikiki from which the animals were collected. Light intensity one-third of the way back in the holes was one or more orders of magnitude lower than that in the rest of the tank.

Twenty fish of each species were placed in the experimental tank in lots of five and subjected to various light intensities. In most experiments they were acclimated to the aquarium for 5 days and to a light intensity of 112 or 448 fc. During this time, they were fed at 6:00 AM and 5:00 PM. On the sixth day, animals were tested in increasing or decreasing light intensities. All measurements were made between 11:00 AM and 2:00 PM, the same time of day the field measurements were taken. The distance from cover was measured (in centimeters) for each of the five cardinalfishes 20 min after a light intensity was switched on. Twenty minutes is adequate for adaption to halving or doubling of light levels (Chave 1971). Each animal was then observed for 1 min.

EXTERNAL MORPHOLOGY AND DISTRIBUTION

Eight shallow-water cardinalfish species are found in Hawaii. Their generic allocations follow Fraser (1972). Two species, *Apogon evermanni* and *Apogon* sp. nov., are rare and are not discussed in this paper.

Apogon erythrinus is small, red, and translucent (Figure 2*B*). It has a forked tail and complete lateral line typical of the other *Apogon* species. It is widely distributed in the Pacific at depths of from 1 to 17 meters (Fowler 1928, Jordan and Evermann 1905, Kami et al. 1968, Lachner 1953, Randall 1955).

Apogon maculiferus is a reddish fish with black spots (Figure 2*C*). It is endemic, with a known range extending from Hawaii to Laysan in the leeward Hawaiian chain (Fowler 1928, Garrett 1863), where it occurs at depths of from 1 to 90 meters. In shallow water it is far less common than either *A. menesemus* or *A. snyderi* (Chave et al. 1973).

Apogon menesemus is brownish-gray, with black fin markings that fade during the day (Figure 2*F*). This species adopts its striking nocturnal coloration when courting. Its current geographical range is restricted to Palmyra in the Line Islands, Johnston Island, and the island of Hawaii to French Frigate Shoals in the leeward Hawaiian chain (Jenkins 1903, Lachner 1953). It is found at depths of from 1 to 40 meters.

Apogon snyderi is brownish-gray, with a black spot on its caudal peduncle and often a stripe running from the tip of the snout to the caudal peduncle (Figure 2*D*). It has been found around Oahu at depths of from 1 to 40 meters. This species occurs throughout the Pacific and Indian oceans (Chave and Eckert 1974, Gosline 1955, Jordan and Evermann 1903, Kami et al. 1968, Lachner 1953, Randall 1955, Smith 1961). Its senior synonym is *Apogon kallopterus* (Fraser, personal communication, 1977).

Apogonichthys waikiki is highly variable in coloration; the lateral line is complete and the tail is round and red (Figure 2*E*). This endemic Hawaiian species ranges from Niihau to Maui and Johnston Island at depths of 1 to 43 meters. It has been dredged

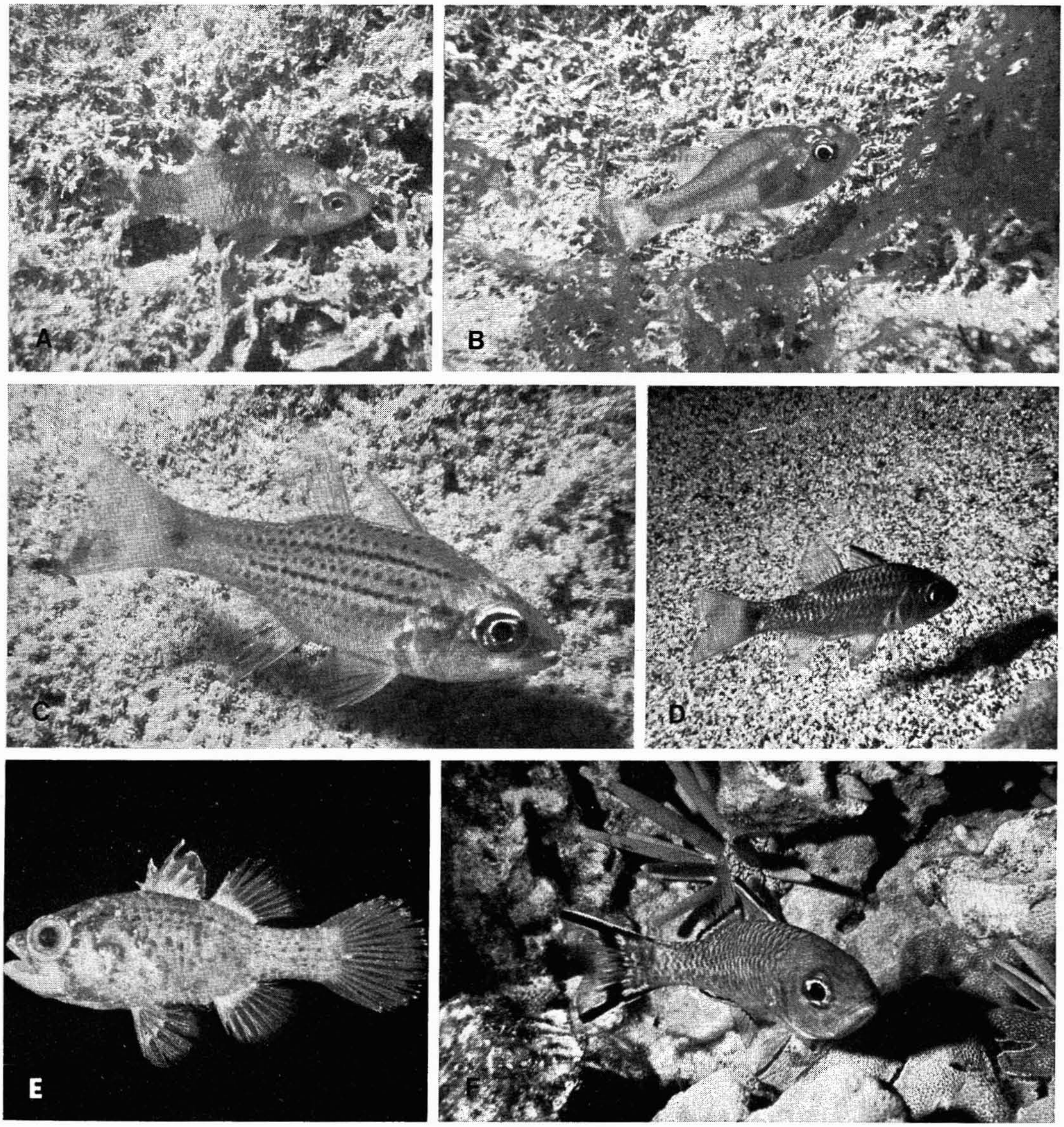

FIGURE 2. Six common apogonid species. *A*, *Foa brachygramma*; *B*, *Apogon erythrinus*; *C*, *Apogon maculiferus*; *D*, *Apogon snyderi*; *E*, *Apogonichthys waikiki*; *F*, *Apogon menesemus*.

in water from 38 to 66 meters in depth (Gilbert 1905). *Apogonichthys waikiki* has not been reported from the island of Hawaii, but it is not very common and may have been overlooked there.

Foa brachygramma is distinguished by its incomplete lateral line and chunky body (Figure 2*A*). Its body color is mottled brown and gray, and its tail is truncate. The lack of a striking color pattern may help camouflage this species during the day, because individuals are in the open more than the other species. *Foa brachygramma* is a small endemic species originally described by Jenkins (1903). It has been taken on Hawaii and Molokai. On Oahu it is found in Kahana Bay, in Kaneohe Bay, and along the southern side of the island from Hawaii Kai to Pearl

Harbor (Figure 1). It is common in the areas where it occurs. At Ala Moana, about 600 individuals were collected (35 percent of the fishes taken in a station with an area of about 1000 m^2).

Based on size alone, two different groups of apogonids may be distinguished. The mean adult standard lengths of *Apogon menesemus*, *A. snyderi*, and *A. maculiferus* are 118, 80, and 84 mm, respectively. *Apogon erythrinus*, *Apogonichthys waikiki*, and *Foa brachygramma* are small forms; the adults average 38, 34, and 44 mm standard lengths. The largest fish in this group of smaller apogonids was 64 mm long, whereas the smallest reproductively mature fish in the larger apogonid group was 67 mm long.

DISTRIBUTION IN VARYING WATER CONDITIONS

Results

Distributions of the apogonid species were correlated with differences in salinity, water movement, and turbidity at the various stations around Oahu. Adults of *Foa brachygramma* and *Apogon snyderi* were found in waters of less than normal salinity during the course of this study. Adults of *Foa* were occasionally found in fresh water, and males were observed brooding eggs in salinities of 5‰. In the laboratory, adult *Foa* acclimated to abrupt changes between saltwater and fresh water. Young animals tolerated changes in salinity to 10‰ in the laboratory and were found in salinities greater than 15‰ in the field. *Apogon snyderi* were occasionally seen in brackish water (20‰) at night. Weber and de Beaufort (1929) have also described several apogonids from fresh or brackish water.

Foa brachygramma tends to be highly concentrated in quiet water areas. For example, collections made at a 1000 m^2 area of inshore reef at Ala Moana near Waikiki in 1968 and again in 1969 yielded over 600 *F. brachygramma* each time. *Foa brachygramma* is also found in large numbers in backreef areas of Kaneohe Bay, but is rare to absent in forereef areas. At Waikiki, this species was found mostly inside the Natatorium pool when storm waves occurred, but was found both inside the pool and along the transects when the sea was calm. One *F. brachygramma* individual per square meter was found in the Natatorium area and six per square meter in the backreef areas of Ala Moana. The Natatorium is more exposed to wave action than the Ala Moana backreef. When waves 1 meter high broke at the Natatorium wall, the Ala Moana backreef area was calm.

Foa brachygramma has not been found on the north shore of Oahu. In the winter when storm waves occur there, *Apogonichthys waikiki*, *Apogon maculiferus*, and *A. menesemus* can be seen only in water about 20 meters and deeper, but a few *A. snyderi* and *A. erythrinus* may be observed in shallow-water caves. *Apogon snyderi* apparently comes out to feed only on calm nights, because when strong surge was present, individuals removed from caves to midwater locations 10 meters away, were unable to return to cover.

Apogon menesemus is found more frequently than *A. snyderi* where there is a good stand of coral and clear, open water. Hobson (1974) reports more *A. menesemus* than *A. snyderi* in the Kona region of Hawaii; this area has extensive coral coverage and clear water. In the Oahu study areas (mainly dead reef flat and sand), there are commonly three times as many *A. snyderi* as *A. menesemus*. R. Wass (personal communication, 1967) collected 12 *A. menesemus* and 212 *A. snyderi* from a living coral patch reef in a turbid area of Kaneohe Bay. However, collections from Moku Manu, a deep, clear-water area only a few miles away but with less living coral, contained five times as many *A. menesemus* as *A. snyderi*. Secchi disk readings indicate that the backreef around the Natatorium has clearer, cleaner water than the Ala Moana backreef. (An average of readings on 10 consecutive nights in August gave 2.8 meters visibility for the Natatorium and 0.8 meter for Ala Moana.) Twenty-eight *A. menesemus* were counted per 1000 m^2 at the Natatorium and none were seen in an equivalent area at Ala Moana on the same night.

TABLE 1

LENGTH OF APOGONID SPECIES AS RELATED TO LENGTH OF FOOD ITEMS EATEN BY INDIVIDUALS OF EACH SPECIES

SPECIES	NUMBER OF FISH	FOOD LENGTH (mm), $\bar{X}$ $\pm$S.D.	FISH LENGTH (mm), $\bar{X}$ $\pm$S.D.	r*
A. snyderi	162	6.5 $\pm$ 0.8	80 $\pm$ 13.1	0.601
A. menesemus	134	8.0 $\pm$ 1.1	70 $\pm$ 15.4	0.840
A. maculiferus	132	7.0 $\pm$ 0.9	65 $\pm$ 7.9	0.729
F. brachygramma	96	4.0 $\pm$ 0.5	45 $\pm$ 6.0	0.747
A. erythrinus	68	3.0 $\pm$ 0.3	30 $\pm$ 4.1	0.722
Apogonichthys waikiki	68	3.0 $\pm$ 1.2	30 $\pm$ 6.8	0.620

NOTE: r = correlation coefficient, $\bar{X}$ = mean, S.D. = standard deviation.
*r is significant at the 1 percent level.

TABLE 2

PERCENTAGE COMPOSITION OF FOOD ITEMS EATEN BY CARDINALFISHES

SPECIES	CRUSTACEA	POLYCHAETA	GASTROPODA	OPHIUROIDEA	PISCES
A. snyderi	74.9	12.3	2.7	4.1	6.0
A. menesemus	73.0	2.8	—	0.3	24.2
A. maculiferus	94.0	1.2	0.5	—	4.3
F. brachygramma	90.7	5.1	0.4	0.6	3.2
A. erythrinus	100	—	—	—	—
Apogonichthys waikiki	91.2	0.9	0.1	—	7.8

Discussion

Differences in salinity, water movement, and turbidity affect the distribution of some of the Hawaiian apogonids. Although *Apogon snyderi* occasionally enters brackish water, *Foa brachygramma* is apparently adapted to living in water with poor circulation during the summer and fall and in freshwater runoff from the streams feeding bays during the winter and spring. This species also appears to be restricted to calm, backreef areas or to bays or estuaries. It is influenced by wave action more than the other species.

All six species of cardinalfishes are found in waters protected by fringing reefs (e.g., the Natatorium). Gosline (1965) suggested that these areas have mixed faunas of surge zone fishes, fishes from quiet deeper waters, and fishes that are restricted to shallow, protected areas. *Apogonichthys waikiki*, *Apogon maculiferus*, and *A. menesemus* are not found in shallow water during seasons when normally calm areas are exposed to storm waves. *Apogon erythrinus* and *A. snyderi* do occur in these areas, but the latter species apparently forages on calm nights.

Since *Apogon menesemus* occurs more commonly in clear-water areas, regardless of the amount of coral cover, it is felt that water clarity is the more important factor in *A. menesemus* distribution.

FOODS AND FEEDING

Al-Hussaini (1947), Bardach (1958), Hiatt and Strasburg (1960), Hobson (1974, 1975), Livingston (1970), Randall (1964), Starck and Davis (1966), Suyehiro (1942), and Talbot (1965) all suggest that cardinalfishes are largely nocturnal generalized carnivores. In Hawaii, all six species were observed from dusk until dawn feeding on small moving organisms. The data shown in Tables 1 and 2 and Figure 3 indicate slight differences in the food eaten among the six species, but the taxonomic levels to which the prey were identified were too high to permit further

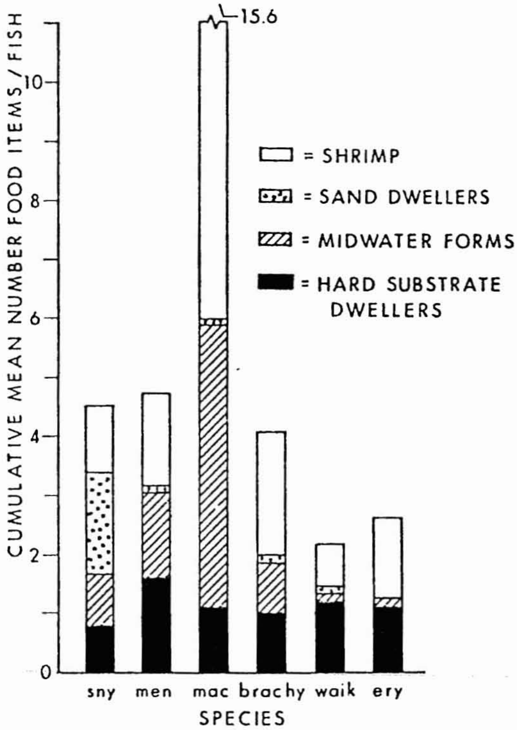

FIGURE 3. Cumulative number of food items of different categories found in apogonid stomachs. sny, *Apogon snyderi*; men, *A. menesemus*; mac, *A. maculiferus*; brachy, *Foa brachygramma*; waik, *Apogonichthys waikiki*; ery, *Apogon erythrinus*.

analysis. Table 1 shows that food size (measured by the longest or widest part of the animals eaten) correlates significantly with the size of different species; that is, small cardinalfishes eat smaller animals than do large cardinalfishes.

Table 2 indicates that *Apogon erythrinus* eats only crustaceans. *Apogon maculiferus*, *Apogonichthys waikiki*, and *Foa brachygramma* eat mainly crustacean food but will take other prey. One-fourth of the diets of *Apogon snyderi* and *A. menesemus* are of animals other than crustaceans. (Hobson [1974] reports diets similar to these for *A. menesemus*, *A. snyderi*, and *A. erythrinus* in the Kona region of Hawaii Island.)

Apogon snyderi eats more sand dwellers than the other species and *A. maculiferus* more midwater forms (Figure 3). Figure 3 also seems to indicate that *A. maculiferus* eats more food items than the other species. However, when the three larger species were collected in lots of 10 each at three different times of night and examined, it was found that *A. maculiferus* eats more food toward dawn. *Apogon maculiferus* had eaten an average of 3.4 food items in the collection made at 8:00 PM, 1.7 food items in the 2:00 AM collection, and 7.9 food items in the 8:00 AM collection. *Apogon snyderi* had eaten 4.9, 3.6, and 4.3 food items at these same times; *A. menesemus*, 3.7, 4.8, and 2.0 food items. Since most fish collections were made early in the day, the food items in *A. maculiferus* stomachs had not yet passed to the intestine as they had in the other species.

NOCTURNAL HABITAT

Results

Most cardinalfishes, including the Hawaiian species, live in holes or caves, or are associated with other organisms during the day and remain in the open near these areas at night (Brock et al. 1965, Collette and Talbot 1972, Fricke 1966, Livingston 1971, Longley and Hildebrand 1941, Randall 1963, Smith and Tyler 1972, Starck and Davis 1966, Strasburg 1966). The Natatorium transects were run to determine whether there were differences in nocturnal behavior of the different species, and whether they were affected by physical or biological fluctuations there. Figure 4 is a graphical presentation of the data, showing the mean number of fishes per 100 m^2 per night.

Apogon snyderi is by far the most numerous species. It is found in all substrates, most commonly in sand and limestone areas close to the substrate and least frequently in boulder areas. Unlike other species, as many individuals are found in areas close to the Natatorium wall as away from it. At the Natatorium, the sand and limestone areas are light in color. On the island of Hawaii, where there is black sand subtidally, this species was found over lighter-colored substrates such as living coral heads. In the laboratory, five groups of four *A. snyderi*

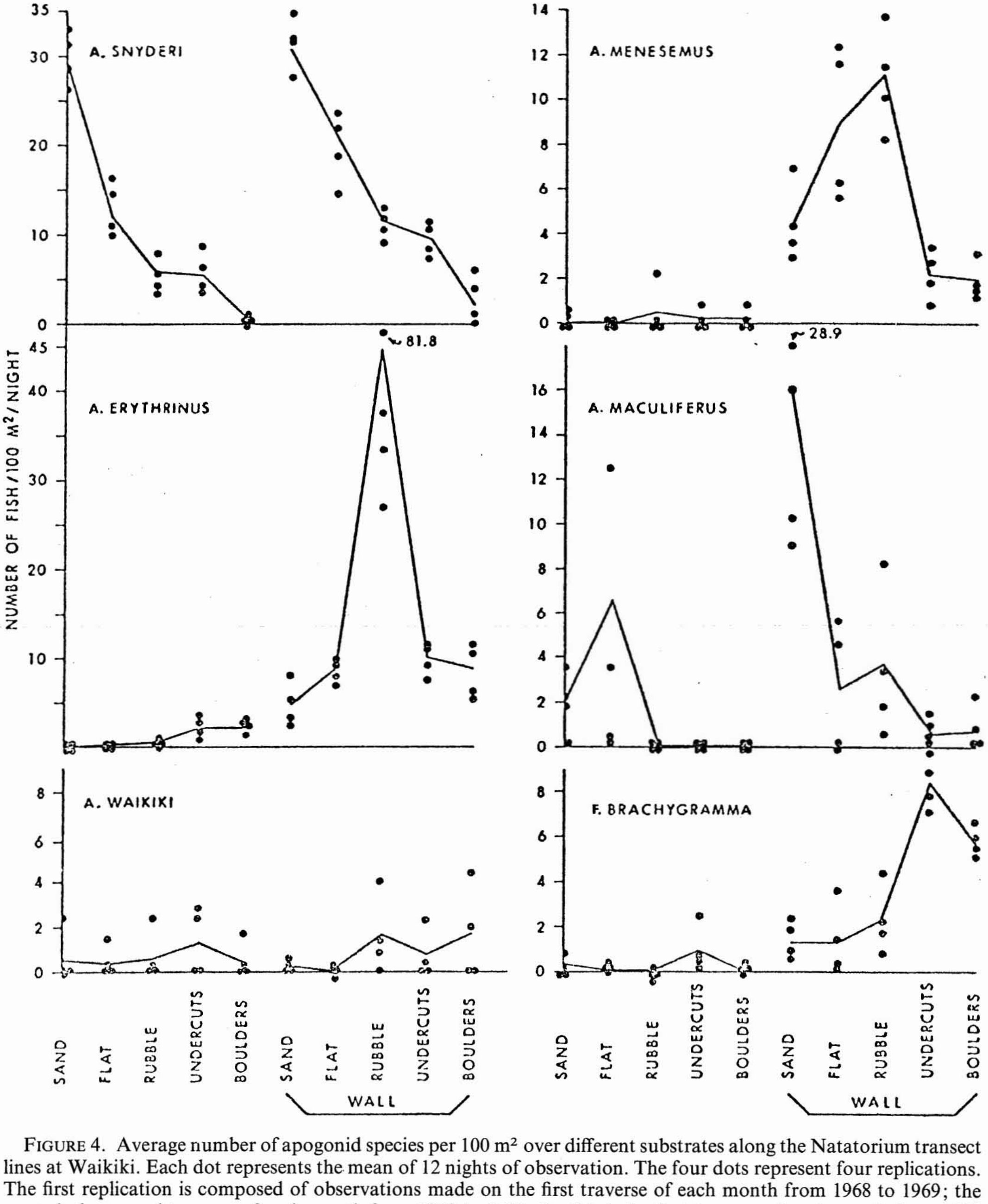

FIGURE 4. Average number of apogonid species per 100 m^2 over different substrates along the Natatorium transect lines at Waikiki. Each dot represents the mean of 12 nights of observation. The four dots represent four replications. The first replication is composed of observations made on the first traverse of each month from 1968 to 1969; the second, the second traverse of each month from 1968 to 1969; the third, the first traverse of each month from 1969 to 1970; and the fourth, the second traverse of each month from 1969 to 1970. Wall is the Natatorium wall. The substrates are ranked from the least relief to the highest relief.

were presented with half light/half dark sand. Of the 20 animals, only 3 were observed on dark sand and were repeatedly chased there by the others. Large concentrations of adult *A. snyderi* are also abundant in other areas that contain large amounts of light-colored sand (Chave 1971, Hobson 1974).

At the Natatorium, juvenile and subadult *Apogon maculiferus* are also found over sand and limestone flats of low surface contouring near the Natatorium wall. Unlike *A. snyderi*, which tends to be spaced out, *A. maculiferus* individuals are aggregated and feed higher in the water than the former. Elsewhere, regardless of depth, *A. maculiferus* aggregations are seen over sand and flat substrates near large underwater objects such as the Natatorium wall. At night, if there is a bright moon, *A. maculiferus* aggregations become tighter.

Apogon menesemus is found almost always near the Natatorium wall. In other areas, *A. menesemus* is found near large coral heads or over substrates of higher relief than the undercut and boulder areas of the transects. In deeper water than I usually traversed, *A. menesemus* feed near coral pinnacles and higher in the water than *A. snyderi* (Hobson 1974).

Apogon erythrinus is the second most common fish along the transects. The species is extremely active and is hardly ever motionless at night, in contrast to the other cardinalfishes which drift along, not moving until prey is spotted. Even the smallest *A. erythrinus* has a territory around its hole which it patrols and in which it feeds. I have never seen one of these fishes more than 3 cm from hard substrate, although they do not ordinarily rest on it. *Apogon erythrinus* also swims with its ventral surface toward the substrate whether the latter is vertical or horizontal. This type of orientation was reported for *A. lachneri* (Collette and Talbot 1972, Livingston 1970). Eighty-seven percent of *A. erythrinus* individuals are seen along the wall just under the surface of the water, snapping at plankters or at crabs in the algae. Most of the remaining individuals are found in limestone areas of high relief.

Apogonichthys waikiki is found most commonly in pairs and associated with solitary coral heads. The Natatorium did not have much living coral, and this may account for the rarity of *Apogonichthys* there. (At Makapuu, Diamond Head, and Kahe Point, which have more living *Porites compressa*, the species was more common.) Since *Apogonichthys waikiki* is quite rare at the Natatorium, not much can be said except that it remains hovering in midwater near its daytime holes in large objects such as boulders and coral heads.

Foa brachygramma is seen near the undercut ledges and boulders among green or brown algae covering them. It is usually found next to the Natatorium wall and in areas of high relief. Individuals were either absent from or fewer in similar areas where there was no wall. Very few *Foa* are found in rubble. *Foa* reacts to light shining on the water. The species is usually near the bottom after dusk and rises during calm nights if there is a half to full moon; otherwise, it remains near the substrate. An average of 20 *Foa* individuals were seen in midwater at the Natatorium per night when there was a half to full moon; 5.9 individuals were seen during the new to half moon phases. There were also more fish per group: 11.5 during the half to full moon: 2.6 during new to half moon. As *Foa* travels upward in the water column, individuals group together to form loose aggregations. The species clusters about fishermen's lights shining on the water and feeds on plankton gathered there. If the light is moved quickly, this cardinalfish dives toward the bottom. Starck and Davis (1966) and Livingston (1970) note that *Phaeoptyx conklini* acts in much the same way at night.

Discussion

Nocturnal behavior and placement of the different species of apogonids differed and is related to their feeding habits.

Apogon snyderi is found over sand where reflected moonlight and starlight from light-colored substrates may help in foraging for sand-dwelling prey. Evidence for *A. snyderi*'s preference for light substrates comes from two sets of data. First, the species is seldom found over black sand on the island of Hawaii. In these areas, it can be found over light-colored hard substrates. Second, in the laboratory, *A. snyderi* preferred light to dark substrates at night.

Apogon maculiferus tended to aggregate at night and fed higher in the water column than *A. snyderi*. This behavior may be a feeding response, since the nekton at the Natatorium were not evenly distributed. The tendency to form tighter aggregations during periods of full moon, is perhaps a response that has evolved to enable *A. maculiferus* to escape predators that target individuals as prey.

The association between *Apogon menesemus* and coral areas was not investigated. Possibly, prey may be more visible in the reflected light over the yellow coral surfaces (Hobson reports both *A. snyderi* and *A. menesemus* striking at his silvery spear point). Or, perhaps the areas of high relief with a number of holes and small caves are suitable cover for *A. menesemus* during the day.

Of the three smaller species, *Apogon erythrinus* and *Apogonichthys waikiki* capture available prey in a small area near their holes. *Foa brachygramma* forages by objects with high vertical profiles on dark nights and aggregates in the water column on moonlit nights. This species is able to change its behavior, taking advantage of benthic and nektonic prey, especially food items that aggregate in lighted areas.

DIURNAL HABITAT

Results

Several studies have been conducted on shelter preferences of fishes. Breder (1950, 1954) initiated some of the first experiments on hole selection in fishes by giving animals substitute shelters. He found that tactile and visual stimuli were of differing importance in different species. Stephens et al. (1970) found that the type and position of holes preferred differed in three sympatric species of *Hypsoblennius*. Fishelson et al. (1974), Sale (1969, 1972, 1975), and Sale and Dybdahl (1975) found that the amount and type of cover was of prime importance to substrate selection in juvenile acanthurids and several pomacentrid species.

Notes on cardinalfish species indicate that they are extremely varied in their selection of diurnal shelters. Some species are found in the open ocean and have no shelter (Haneda et al. 1966). Other species live in association with animals such as basket stars (Fricke 1966), the queen conch (Longley and Hildebrand 1941), sea urchins (Strasburg 1966), and sponges (Collette and Talbot 1972). Randall (1963), Brock et al. (1965), Starck and Davis (1966), Livingston (1971), and Smith and Tyler (1972) found that most cardinalfishes live in a variety of cover such as under cobbles, in holes, or in caves during the day. The Hawaiian cardinalfishes have similar habits. At dawn, all the cardinalfishes in shallow water retreat to caves and smaller holes where they remain until dusk. Often, more than one species are seen living in large caves.

At Waimea, Oahu, a shallow-water cave was studied during the spring and summer for 3 years. During the winter it was exposed to high surf. The *Apogon* species in the cave were observed and then a fine-mesh partition was placed horizontally 1 meter from the top of the entrance, dividing the cave roughly into two halves (Figure 5). The fish were poisoned and collected. Similar field studies in other areas and laboratory experiments were conducted to determine the type of hole preferred by apogonid species. Fishes were placed in tanks that contained PVC pipes of aperture sizes 2, 4, and 10 cm and lengths of 15 and 30 cm. One end was either closed or open. The methods and results of these experiments are described by Chave (1971). Here they are reported in conjunction with field experiments at the Waimea cave and elsewhere.

Apogon erythrinus adults and young live in small holes in dead reef or basalt areas. At Waimea they emerged from small holes at the back of the cave, both over and under the screen. The species was never seen in its natural diurnal habitat (Chave 1971, Hobson 1974). The only time the species was observed in the field during the day was when five

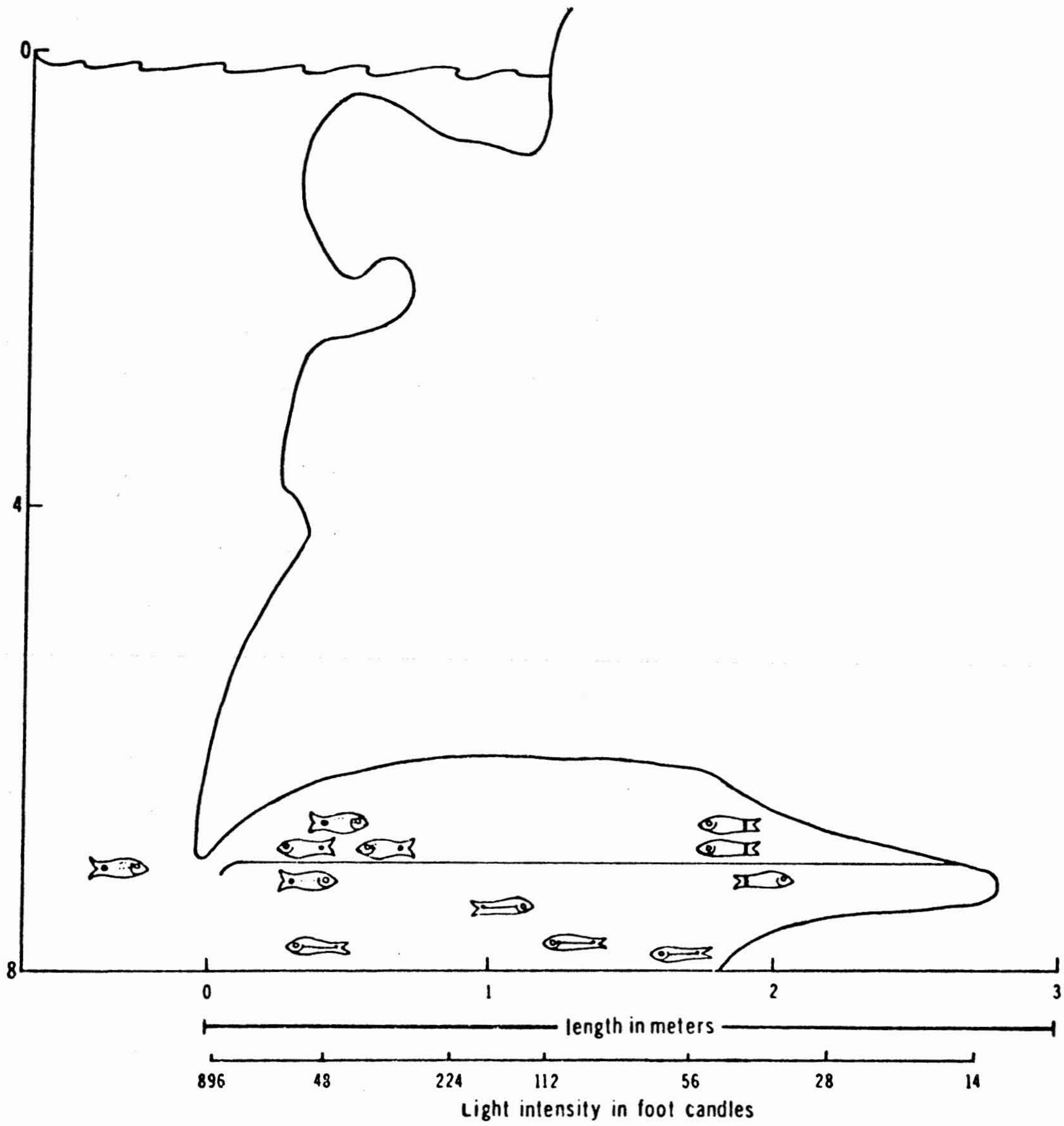

FIGURE 5. Lateral section of the Waimea cave showing the locations of the different species of *Apogon*. The line drawn lengthwise down the middle of the cave represents a screen. The number of fishes illustrated gives the ratio above and below the screen. *Apogon maculiferus* has the caudal spot, *A. menesemus* the caudal band, and *A. snyderi* the stripe.

animals took up residence in three 2 × 30-cm pipes encased in large concrete blocks and closed at one end. This species hovered in midwater in the smallest closed pipes in the laboratory. When similar-sized black or gray pipes were presented, *A. erythrinus* entered black pipes 92 percent of the time. The other species did not discriminate between the two.

At Waimea, *Apogonichthys waikiki* was observed only in water deeper than 20 meters. The species does not emerge from holes during the day but will emerge, usually in pairs, from living or dead *Porites* if a narcotic is applied. In the aquaria, *A. waikiki* individuals wedged themselves between the pipes if two were touching but did not enter

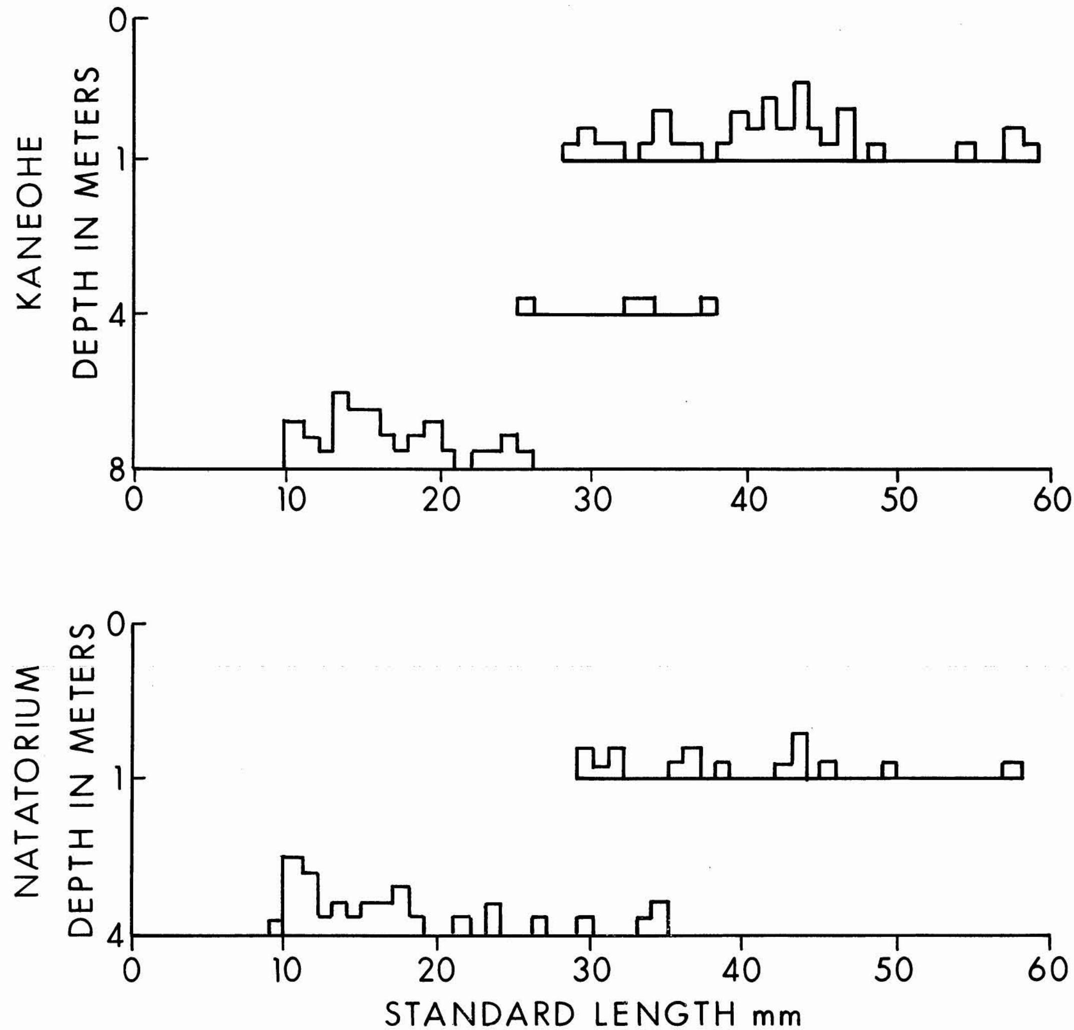

FIGURE 6. Number and lengths of *Foa brachygramma* at the Natatorium and in Kaneohe Bay. 100 ml of quinaldine was used to catch each group of individuals at the depths indicated. The smallest squares = 1 individual.

them. If no cover was available, they dug holes in corners or under bricks, a behavior unique among the cardinalfishes studied. If given piles of rubble or dead coral heads, *A. waikiki* abandoned its station between the pipes and sought cover in these.

Foa brachygramma was also absent from the Waimea cave. Adults are found in shallow quiet water under dead coral reef ledges or on the top of reef flats in crevices. The young can be located under rubble or in isolated coral heads below (Figure 6). The Waimea cave area does not have shallow reef flats, extensive coral growth, or quiet water. In the laboratory, this species hovered near or within most of the larger pipes except the long closed ones.

In the aquaria, *Apogon snyderi* and *A. menesemus* chose the pipes with the largest diameter. Neither 2- nor 4-cm pipes were entered after the fishes backed out of them on the first day. Ninety-seven percent of the *Apogon snyderi* were collected from the lower part of the Waimea cave; adults were toward the back and young were in the middle. They also occurred in the lower part of other caves under ledges or in limestone rubble, and they hovered in long, open 10-cm pipes in the laboratory.

Apogon menesemus, which were found only in the back and usually the upper part of Waimea cave, occur elsewhere at the back of caves or under large coral heads. They chose only large closed 10-cm pipes in the laboratory.

At Waimea cave, three-fourths of the *Apogon maculiferus* juveniles were observed and collected from the top entrance area and one-fourth from the lower entrance. Additional small *A. maculiferus* were found elsewhere under overhangs and along ledges. In the laboratory, young *A. maculiferus* chose the shortest pipes with the largest diameter and open ends, but remained in them only 26 percent of the time. If given concrete blocks, subadult *A. maculiferus* preferred these to pipes. *Apogon maculiferus* adults preferred long, open 10-cm pipes. Adults are usually found near ledges in water deeper than 20 meters. Small adults collected from 3 meters of water and tagged with acrylic dye were observed moving across the reef and to below 20 meters in depth.

Discussion

Diurnal habitat selection of the six *Apogon* species appears to be similar in both the field and laboratory. While the smaller species are able to utilize rubble or small holes, the larger species partition themselves throughout caves or under ledges (Figure 5). Light intensity is a major factor in this partitioning.

LIGHT INTENSITY

Results

Collette and Talbot (1972), Hobson (1972, 1973), Hunter (1968), and Livingston (1971) pointed out that various reef species have varying responses to light. Observations on the habitats of the different Hawaiian apogonid species indicate that light intensity is one of the more important physical factors controlling their location not only at dawn and at dusk but during the day.

During the day, at dusk, and at dawn, light levels were recorded in the field at positions where individuals of different apogonid species were observed. Because of the chance that these positions had been occupied due to factors other than light intensity, experiments were also conducted in the laboratory. When natural or simulated sunlight dimmed sufficiently, the fishes left cover at slightly lower light levels than when they returned to cover in brightening light. This was not statistically significant and probably occurred because retinal accommodation to decreasing light intensities is slower than the response to increasing light levels (Ali 1959, Ali et al. 1961). Figures 7 and 8 graphically present the average of both decreasing and increasing light intensity measurements in the field and in the laboratory. Table 3 gives the means and variances between measurements of light level when the fishes were at the point of leaving and entering cover and also when the fishes were 50 cm from cover.

In both laboratory and field, *Apogonichthys waikiki* adults entered or left cover when light intensities were too low to be measured with my equipment (Table 3). Juvenile *A. waikiki* were not observed or collected.

Foa brachygramma adults were found in brightly lighted areas in the field but they stayed close to cover until low light intensities were reached (Table 3, Figure 7). When light intensity was increased in the laboratory, the response of *Foa* was to back into the closest corner (or cover if nearer) and stay there. Therefore, to test the species' response to light under simulated conditions, the distance of individuals from both cover and corners was measured, rather than to cover alone. No statistically significant difference was found in response to natural and artificial light. During the day, young *Foa* were found at statistically significant, lower light intensities than adults, but they were found in the open at approximately the same light levels as adults (Table 3).

Apogon erythrinus adults and juveniles emerged from and retreated to cover at light intensities too low to be measured in the field and at slightly higher light levels under

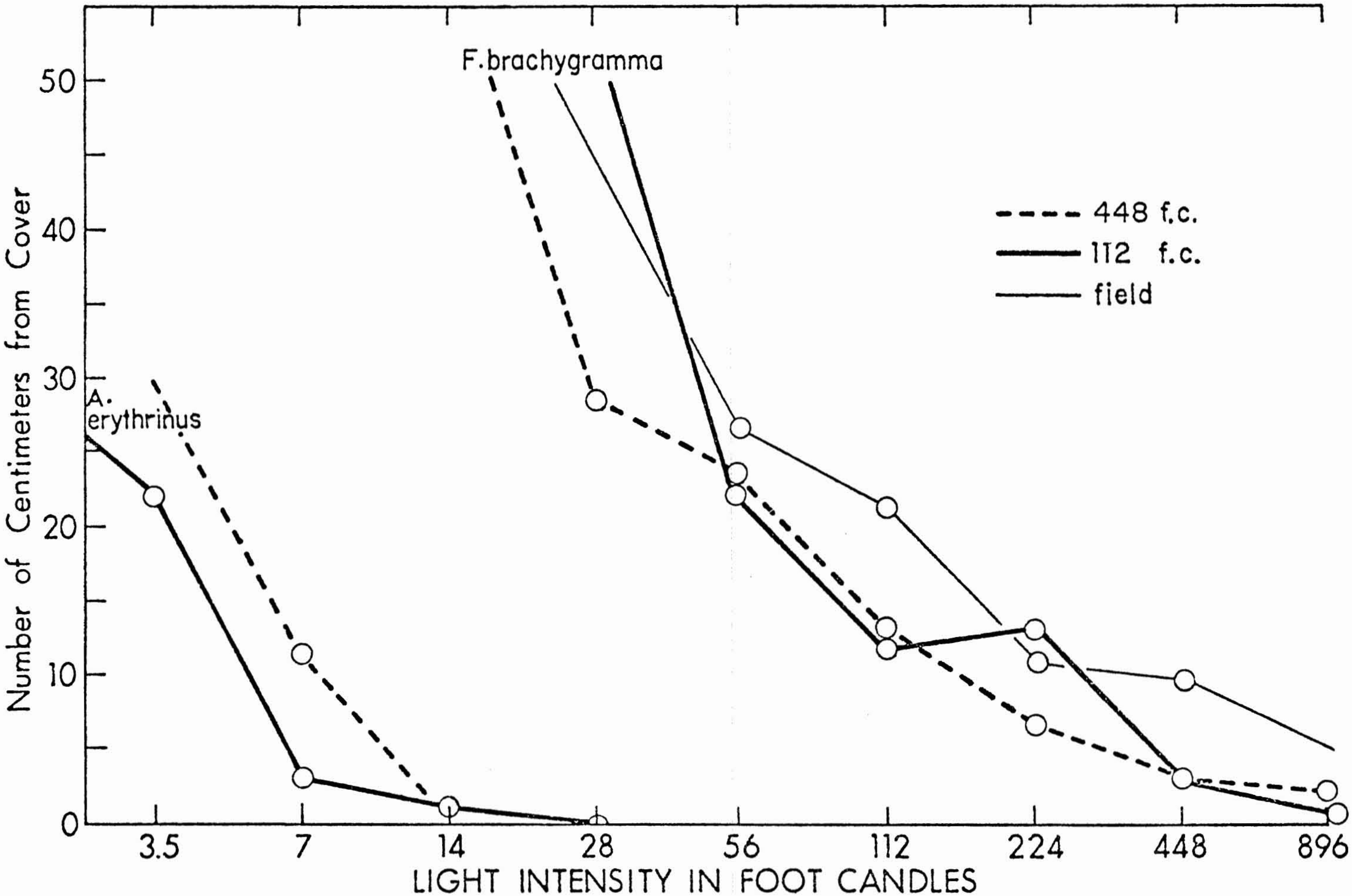

FIGURE 7. Summary of the distance from cover of *Foa brachygramma* and *Apogon erythrinus* in the laboratory and in the field. The thin solid line shows the distance to cover of fish in the field; the thick solid line, fish acclimated to 112 fc; the dashed line, fish acclimated to 448 fc.

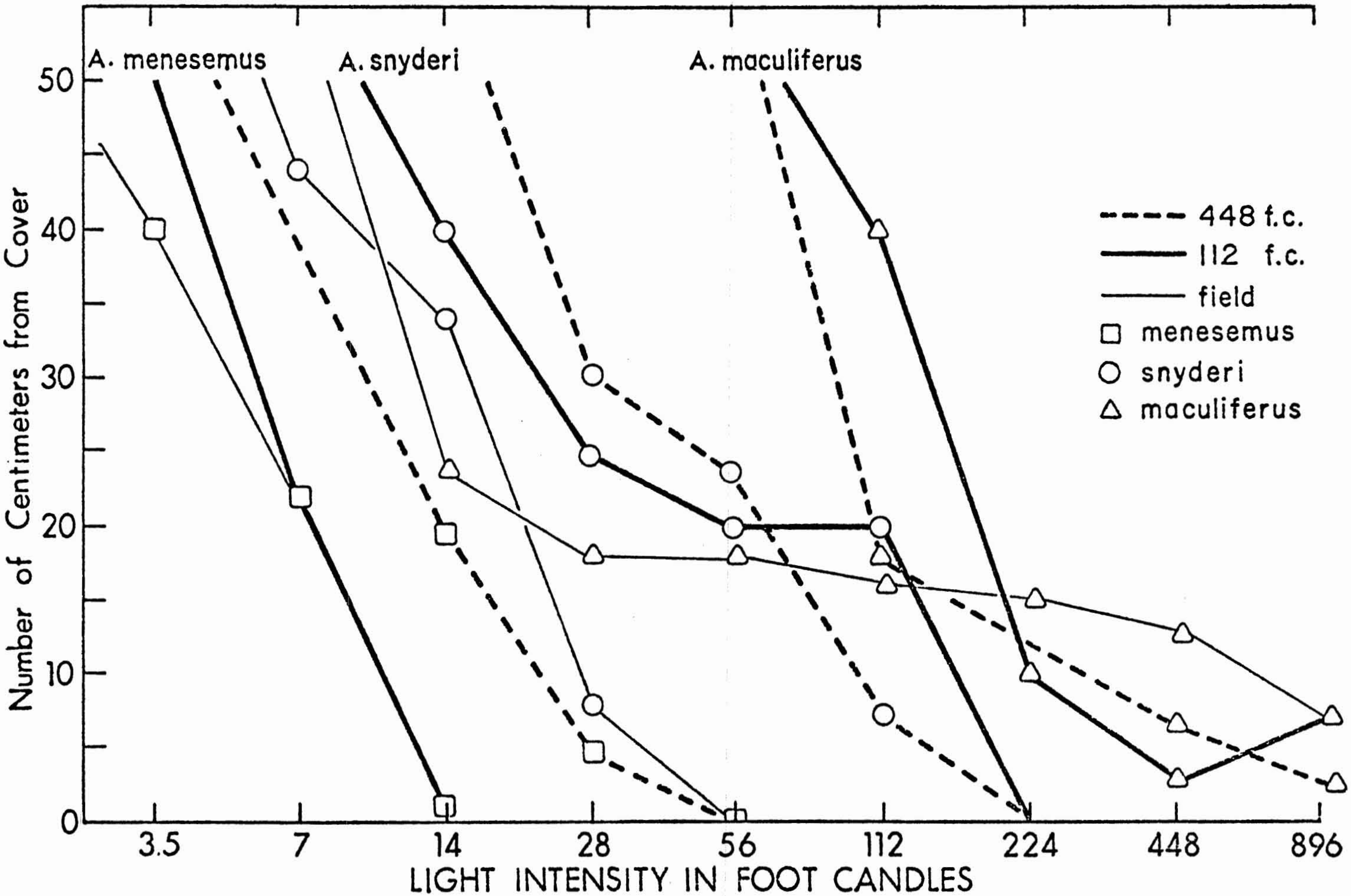

FIGURE 8. Summary of the distance from cover of juvenile *Apogon maculiferus*, adult *A. menesemus*, and adult *A. snyderi* in the laboratory and in the field. The thin solid line shows the distance to cover of fish in the field; the thick solid line, fish acclimated to 112 fc; the dashed line, fish acclimated to 448 fc.

TABLE 3

DIFFERENCES IN LIGHT INTENSITY AND THE POSITIONS OF THE APOGONID SPECIES WITH RESPECT TO COVER

	LIGHT LEVEL (fc) WHEN FISHES LEAVE OR ENTER COVER (mean ± variance)		LIGHT LEVEL (fc) WHEN FISHES ARE 50 cm FROM COVER (mean ± variance)	
SPECIES*	ADULTS	YOUNG	ADULTS	YOUNG
A. snyderi				
Field	56 ± 15	224 ± 56	10 ± 4	14 ± 7
Lab, 112 fc	224 ± 36	238 ± 95	14 ± 5.5	22 ± 13
Lab, 448 fc	224 ± 80	442 ± 212	28 ± 6	30 ± 11
A. menesemus				
Field	14 ± 6	56 ± 20	2 ± 2	4 ± 1
Lab, 112 fc	19 ± 6	44 ± 27	4 ± 0.5	7 ± 6
Lab, 448 fc	56 ± 12	30 ± 32	6 ± 4	12 ± 2
A. maculiferus				
Field	56 ± 56	3584 ± 1200	24 ± 10	36 ± 14
Lab, 112 fc	220 ± 110	1792 ± 612	43 ± 15	60 ± 37
Lab, 448 fc	112 ± 112	1792 ± 448	37 ± 9	65 ± 112
F. brachygramma				
Field	2250 ± 890	896 ± 620	38 ± 70	56 ± 16
Lab, 112 fc	1792 ± 2200	224 ± 80	30 ± 28	34 ± 8
Lab, 448 fc	3584 ± 1780	682 ± 100	18 ± 13	29 ± 30
A. erythrinus				
Field	<1.75	<1.75	<1.75	<1.75
Lab, 112 fc	7 ± 7	9 ± 11	<1.75	<1.75
Lab, 448 fc	14 ± 14	22 ± 20	1.75 ± 1.75	2.0 ± 1.75
Apogonichthys waikiki				
Field	<1.75	—	<1.75	—
Lab, 112 fc	<1.75	—	<1.75	—
Lab, 448 fc	<1.75	—	<1.75	—

*The three categories are the same as the categories described in Figures 7 and 8.

simulated conditions (Table 3, Figure 7).

Juvenile *Apogon maculiferus* emerged from cover in bright light intensities both under natural and simulated illuminations. Like *Foa* adults, *A. maculiferus* juveniles stayed close to cover at intermediate light intensities and were found in midwater only at slightly higher light levels than adult *A. maculiferus* (Table 3, Figure 8). Laboratory-tested adults emerged from or retreated to cover at statistically significant, higher light intensities than those in the field (Table 3). In the field, light levels seldom reached 100 fc, and the animals emerged or retreated to cover at about 56 fc.

Apogon snyderi young and adults were found 50 cm from cover at approximately the same light intensities in the laboratory and field (Table 3, Figure 8). Young emerged or retreated to cover at slightly higher light levels than adults (Table 3).

Of the larger apogonids, *Apogon menesemus* adults and juveniles emerged from or returned to cover at the lowest light intensities.

Since the three large *Apogon* species were commonly found together in the same caves, experiments were conducted to determine what effect the number of hole spaces had on them. Figure 9 illustrates one of the five experiments (all gave the same results). The distance from the same cover items as used in the rest of the light experiments (two 10 × 30-cm open pipes in one concrete block provided only four holes) was measured for six fishes, two of each of the large species. As light levels increased, both *A. menesemus* entered the pipes at 28 fc. *Apogon snyderi* and *A. maculiferus* stayed out longer, but hugged the sides of the concrete block. At 112 fc, both *A. snyderi* approached the pipes. Each *A. menesemus* came partly out of its pipe to

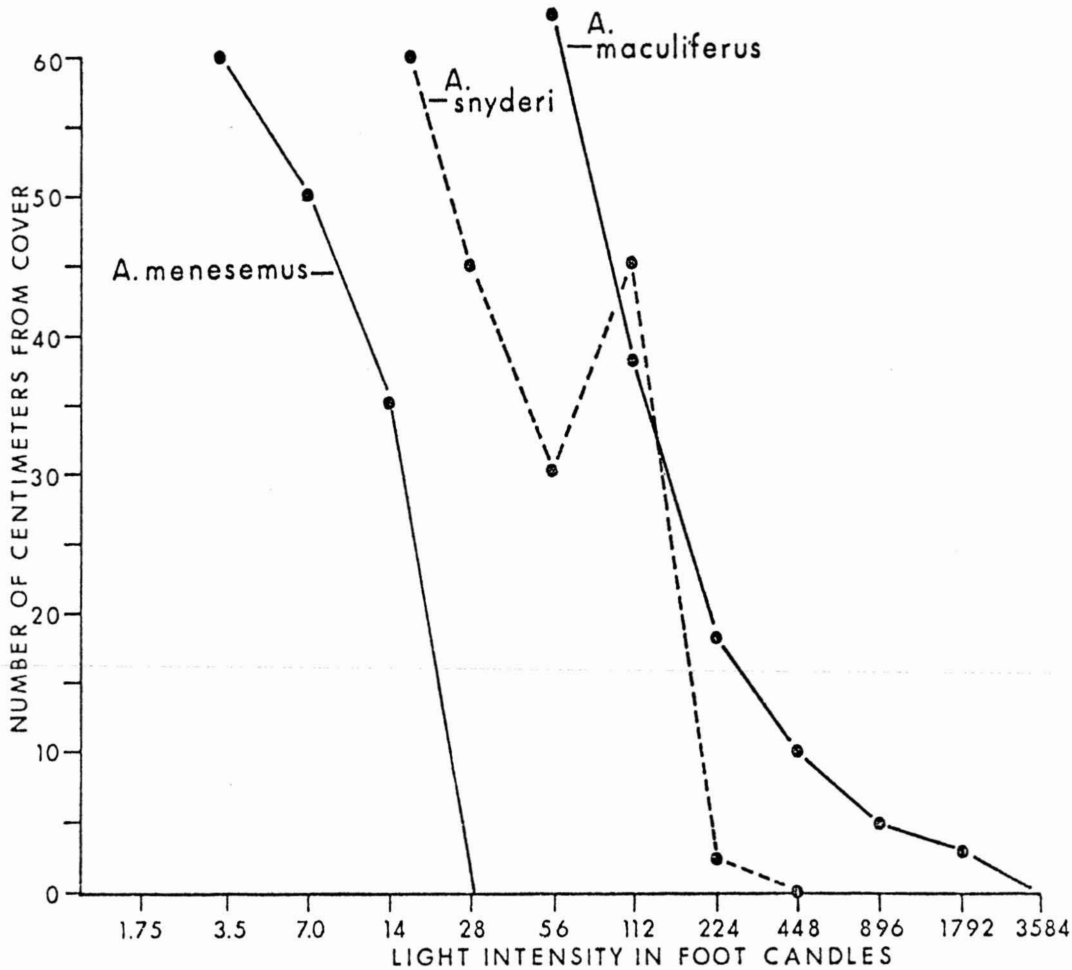

FIGURE 9. Distance from cover of *Apogon snyderi*, *A. maculiferus*, and *A. menesemus* at increasing light intensities. Two *A. snyderi* (65 and 76 mm long), two *A. maculiferus* (62 and 74 mm long), and two *A. menesemus* (65 and 78 mm long) were placed in the experimental tank.

chase them and then retreated. When the light became brighter (224 fc), the *A. snyderi* and *A. maculiferus* darted into the two empty holes to the side of the pipes. *Apogon snyderi* chased *A. maculiferus* out and the two *A. maculiferus* went to the back of the block and stayed there.

Discussion

In theory, the six apogonid species should enter holes or caves during the day. Adult *Foa brachygramma* and juvenile *Apogon maculiferus* are species that do not conform to this postulate.

Nicol (1963), in his review of vision in fishes, states that as far as is known, fishes' spectral sensitivity ranges maximally between 478 and 525 nm. Rod pigments of most species of shallow-water fishes tested have peak absorbences from 490 to 500 nm (Munz and McFarland 1973). Munz (1958*a*, 1958*b*, 1964) has found that maximal retinal absorption in the rod pigments often coincides with the most prevalent wavelength in various water masses and at various depths. Tyler and Smith (1967) have found that a wavelength of 480 nm is the peak band for deep reef areas. The retinal pigment absorption peak of *Apogon maculiferus* adults (484 nm) shows visual adaptation to deeper, bluer water in contrast to tested *A. erythrinus*, *A. snyderi*, *A. menesemus*, and *Foa brachygramma* in which absorption peaks range from 490 to 496 nm (Munz and McFarland 1973). Pigment analysis seems to correlate with the deep-water location of *A. maculiferus* adults in the field.

Although no young *Apogon maculiferus* were available when Munz and McFarland were in Hawaii, *Foa brachygramma* young were tested. Retinal absorption spectra of juvenile *Foa* rod pigments showed peaks of 481 and 484 nm (typical of deep-water fishes), whereas adult rod pigments peaked at 493 nm and were typical of shallow-water cardinalfishes (Munz and McFarland 1973). These authors felt that perhaps the larval pigment is distinct from the adult one. Blaxter (1966, 1968), Blaxter and Holliday (1963), and Blaxter and Pattie Jones (1967) found that the single rods of herring larvae were replaced by multiple rods as the larvae grew. Similarly, *F. brachygramma* larvae under 12 mm in length have single rods and multiple rods appear later. Whether multiple rods alter the pigment or light absorption peak in this species is not known. At any rate, it is interesting that most *Foa* adults live in higher light intensities than their young and that there is a difference in light absorption peaks between adult and young.

Apogon maculiferus adults are abundant around ledges in deeper water, possibly because more food is present (McVey 1970, Smith et al. 1973, L. R. Taylor, personal communication). However, there is a more plausible hypothesis. All Hawaiian cardinalfish species brood, court, and spawn in holes during the day, which perhaps gives the fish added protection from diurnal predators or disturbances such as rough water conditions and high light intensity. Since the other two large species of *Apogon* are common in shallow water and chase *A. maculiferus* out of holes in the laboratory, the behavioral interaction between species might have resulted in the migration of *A. maculiferus* to deep-water holes and ledges where *A. menesemus* is rare and *A. snyderi* hovers in the open over the substrate.

PREDATION

Results

Stomach content analysis of all carnivorous fishes obtained in early morning poison stations was conducted. Cardinalfish predators are listed in Table 4. Diurnal predators were observed in the open during the day and at dawn. Their guts contained either almost intact apogonids or their bones. Nocturnal predators were seen at night and at dusk. Their guts contained partially digested apogonids. Cave-dwelling predators were found in holes and caves both day and night. Almost intact to completely digested apogonids were found in their guts. *Fistularia petimba* was observed feeding both day and night.

Table 5 shows the number of apogonids of each species eaten by three different types of predators, diurnal, nocturnal, and cave-dwelling. A greater percentage of *Apogon maculiferus* are eaten by diurnal predators than other species. Cave-dwelling predators catch the five other species, especially *A. menesemus* and *A. erythrinus*. Nocturnal predators eat all species except *Apogonichthys waikiki*.

Discussion

Hobson (1974) confirms the piscivorous feeding habits of most of the predators collected in the Oahu poison stations (Table 4). Additional species that were not captured, e.g., large jacks and snappers, probably eat apogonids as well (Chave 1971, Hobson 1974).

The predation patterns shown in Table 5 were expected. Since *Apogon menesemus* and *A. erythrinus* live in the darkest regions of caves, most were caught by cave-dwelling predators. *Apogon maculiferus* aggregates in

TABLE 4

NUMBER OF CARDINALFISHES FOUND IN THE STOMACHS OF PREDATORS

PREDATORY SPECIES	NUMBER EXAMINED	NUMBER FOUND IN STOMACHS		
		DIURNAL* PREDATORS	NOCTURNAL* PREDATORS	CAVE DWELLING PREDATORS
Apogon menesemus	572	—	2	—
Aulostomus chinensis	12	2	—	—
Bothus mancus	7	1	—	—
Brotula multibarbata	12	—	—	2
Cheilinus rhodochrous	3	1	—	—
Conger marginatus	2	—	2	—
Dendrocheirus barberi	31	—	4	—
Fistularia petimba	43	1	5	—
Gymnothorax eurostis	63	—	—	2
Gymnothorax flavimarginata	47	—	—	7
Gymnothorax meleagris	31	—	—	1
Gymnothorax petelli	3	—	1	—
Gymnothorax steindachneri	3	—	—	1
Paracirrhites forsteri	2	1	—	—
Parupeneus bifasciatus	20	—	2	—
Parupeneus chryserydros	14	—	1	—
Saurida gracilis	5	1	—	—
Scorpaena balieui	47	8	—	—
Scorpaenodes diabolis	22	—	3	—
Scorpaenopsis cacopsis	2	2	—	—
Synodus variegatus	14	1	—	—
Uropterygius knighti	22	—	—	3

* Diurnal and nocturnal predators may also forage at dusk and dawn.

TABLE 5

NUMBER OF PARTIALLY DIGESTED APOGONIDS FOUND IN THE STOMACHS OF DIFFERENT PREDATORY FISHES (BASED ON ALL POISON STATION SAMPLES)

NUMBER OF APOGONIDS COLLECTED	PERCENTAGE EATEN BY PREDATORS	NUMBER FOUND IN STOMACHS		
		DIURNAL* PREDATORS	NOCTURNAL* PREDATORS	CAVE DWELLING PREDATORS
A. snyderi, $n = 753$	0.9	1	4	2
A. menesemus, $n = 572$	0.9	—	1	4
A. maculiferus, $n = 1841$	1.0	14	5	—
F. brachygramma, $n = 2238$	0.8	2	9	6
A. erythrinus, $n \mp 384$	0.9	—	1	3
Apogonichthys waikiki, $n = 72$	1.3	—	—	1

* Diurnal and nocturnal predators may also forage at dusk and dawn.

the open near the mouths of caves and most were caught by diurnal predators. Nocturnal predators took all apogonid species (except for *Apogonichthys waikiki*) because they were in the open at night. *Apogonichthys waikiki* is not a common animal and results of predation on this species are inconclusive.

CONCLUSIONS

Table 6 summarizes the differences among the six Hawaiian cardinalfish species studied. Smith and Tyler (1972) point out that most coral reef fishes have morphological specializations and precise habitat requirements,

TABLE 6

SUMMARY OF DIFFERENCES AMONG APOGONID SPECIES

A. MORPHOLOGY AND NOCTURNAL DISTRIBUTION

SPECIES	COLOR	MEAN ADULT SIZE (mm)	TAIL SHAPE	NOCTURNAL SUBSTRATE	NOCTURNAL POSITION	NOCTURNAL SPACING	FOOD SELECTION
A. snyderi	Brownish-gray	80	Forked	Smooth, sandy, bright, flat	Near substrate	Solitary	Mostly sand dwellers
A. menesemus	Brownish-gray with black fin markings	118	Forked	Large boulders, coral heads, or undercuts	Midwater	Solitary or loose aggregations	—
A. maculiferus	Red with black dots	84	Forked	Smooth, sandy, bright, flat	Midwater	Aggregated	Mostly midwater forms taken toward dawn
F. brachygramma	Mottled brown and gray	44	Truncate	Algae or undercuts	Variable	Solitary or aggregated	—
A. erythrinus	Transparent red	38	Forked	Flat with small holes	Near substrate	Solitary or paired	Crustaceans only
Apogonichthys waikiki	Variable, with red tail	34	Round	Coral heads and boulders	Midwater	Solitary or paired	—

TABLE 6 (*Cont.*)

SUMMARY OF DIFFERENCES AMONG APOGONID SPECIES

B. RESPONSE TO LIGHT AND COVER

SPECIES	LIGHT LEVEL (fc) WHEN FISHES LEAVE OR ENTER COVER		LIGHT LEVEL (fc) WHEN FISHES ARE 50 cm FROM COVER		DIURNAL SUBSTRATE	PIPE PREFERENCE (LAB.)
	ADULT	YOUNG	ADULT	YOUNG		
A. snyderi						
Field	56	224	7	14	Holes or caves—near mouth or along sides, near bottom	Large, long, open
Lab	112	340	28	26		
A. menesemus						
Field	14	56	2	4	Caves—near back in midwater	Large, long, closed
Lab	18	33	5	9		
A. maculiferus						
Field	56	3584	24	36	Undercuts or caves—near mouth in midwater	Large, open, (adults) long, (young) short
Lab	164	1792	40	62		
F. brachygramma						
Field	2250	896	38	56	Rubble or undercuts	Large, long, open
Lab	2688	453	24	31		
A. erythrinus						
Field	<1.75	<1.75	<1.75	<1.75	Small holes—near back of caves	Small, long, closed, black
Lab	10	15	<1.75	~1.75		
Apogonichthys waikiki						
Field	<1.75	—	<1.75	—	Small holes in coral heads or boulders	Between pipes
Lab	<1.75	—	<1.75	—		

C. DISTRIBUTION AND RESPONSE TO WATER QUALITY

SPECIES	DISTRIBUTION	DEPTH (m)	SALINITY	WATER CONDITION
A. snyderi	Indo-Pacific	0—40	Normal	Rough to calm
A. menesemus	Restricted	0—30	Normal	Rough to calm
A. maculiferus	Endemic	0—20 (young) 20—140 (adults)	Normal	Calm
F. brachygramma	Endemic	4—8 (young) 0—4 (adults)	Fresh to normal	Calm
A. erythrinus	Indo-Pacific	0—17	Normal	Rough to calm
Apogonichthys waikiki	Endemic	0—66	Normal	Calm

leading to strong selective advantages within the preferred habitat. This creates resource sharing with no direct competition for limited resources. Sale (1977), on the other hand, points out that for territorial fishes, colonization is the main role in determining fish community structure. Both concepts apply to Hawaiian apogonids.

Smith and Tyler's hypothesis is applicable to size-limited groups of species in a diverse habitat such as the Natatorium. In a diverse habitat, during the day, the most important difference between species is the ability of each to use dissimilar areas of the reef flat or even the same hole or cave because of differences in behavior, substrate preference, and tolerance to light intensity. At night, the small areas in which all species are found are heterogeneous in ways that enable these opportunistic carnivores to utilize different portions of their environment, i.e., feeding within different substrates, areas of the water column, or times of the night. The six species do not occur in all habitats. Thus, a factor such as calm water is acceptable to all six apogonid species but rough water only to three. On the other hand, if the water is subject to salinity fluctuations, only one species is present.

Sale's hypothesis is particularly applicable to *Apogon maculiferus*, which may colonize, but eventually cannot live, in the same shallow-water holes as *A. menesemus* and *A. snyderi*. It migrates to utilize deeper holes where the other two species are not abundant. The differences between juvenile and adult retinal pigments indicate adaptation to shallow water and then to deep water.

Of the three large species, *Apogon snyderi* is the most generalized. It has a wide geographical range, and is found in many habitats where sand is present. Its coloration is nondescript and it is found in the open at light intensities of less than 56 fc. During the day, it lives in holes or caves at intermediate light intensities where it is found closer to the bottom than the other species. At night, individual *A. snyderi* is mainly found close to light, sandy substrates and eats more sand-dwelling organisms than the other species.

Apogon menesemus and *A. maculiferus* are restricted geographically, and adults are found only in clear water. *Apogon menesemus* is often associated with living coral and *A. maculiferus* is found under ledges over 20 meters in depth. These two species are both striking in their coloration. *Apogon menesemus* has little light tolerance in the field and is found in midwater at the back of caves during the day. It emerges from cover later and may be seen in midwater around objects of higher relief than the other large apogonids. Subadults of *A. maculiferus* are found in high light intensities during the day and aggregate both night and day. Individuals take most of their food closer to dawn, are found over the same substrates but higher in the water than *A. snyderi*, and eat a larger proportion of midwater forms than the other species.

Of the smaller species, *Apogon erythrinus* has the widest geographic range of all the cardinalfishes and may be found in most clear-water areas. It is solitary, lives in small dark holes during the day, and is never found more than 3 cm from hard substrate at night. It eats only crustaceans.

Foa brachygramma, an endemic, perhaps relict species, is specialized in its morphology and tolerance of high light intensities. It differs from other Hawaiian apogonids in that adults are found in shallower water than juveniles and it is abundant in calm but often highly stressed marine environments. It is more highly camouflaged than the other species (Figure 2) and is not eaten by diurnal predators as often as *Apogon maculiferus* (Table 4). *Foa brachygramma's* nocturnal behavior and food is more generalized than the other apogonids'.

Apogonichthys waikiki, an uncommon endemic species, is a specialized form associated with living or dead *Porites* heads. Its striking color pattern and unusual habits (such as mouth digging) are not yet understood.

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