

THE STRUCTURE OF REEF FISH COMMUNITIES IN
THE HAWAIIAN ARCHIPELAGO: INTERIM STATUS REPORT

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ABSTRACT

The structure of reef fish communities in the Hawaiian Archipelago is being studied as part of a broad investigation of marine resources in the Northwestern Hawaiian Islands. To date, communities have been sampled at eight islands or island groups: Kure, Midway, French Frigate Shoals, Necker, Nihoa, Niihau, Oahu, and Hawaii. Other locations will be sampled soon. The following generalizations are evident in the data collected so far, but remain tentative until sampling has been completed. (1) Forces that determine the distribution patterns involve either environmental factors (including biological interactions) or fishing pressures. (2) Northwestern communities show close ties with communities in both the warm temperate and the tropical western Pacific, but southeastern communities show close ties only with communities in the tropical western Pacific. (3) The predominant members of the northwestern communities, as a group, are better attuned to the overall Hawaiian environment than are the predominant members of the southeastern communities. They show this by being more evenly distributed over the archipelago and by including proportionally more endemics. (4) Many species prominent in shallow-water communities in the northwest occur only in deeper water southeastward. (5) The southeastward distributions of species in the northwestern communities are limited by both environmental factors and fishing pressures, but the northward distributions of species in the southeastern communities are limited only by environmental factors.

fishes
Hawaii

fish communities
zoogeography

INTRODUCTION

Our knowledge of reef fishes in Hawaii is based almost entirely on what is known of the inhabitants of reefs surrounding the high islands. We know little of the fishes that live on reefs around those low bits of land and expansive shallows that stretch more than 1,500 km northwestward from the high island of Kauai. These are the Northwestern Hawaiian Islands, a vast region that constitutes less than 1% of the land area in the archipelago, but about 65% of the marine environment between shore and 100 fathoms (Bryan, 1954). Clearly the reef resources here, still virtually untouched by humans, greatly exceed those of the long exploited high islands.

Not only do the reefs of the Northwestern Hawaiian Islands encompass greater area, they also include more varied habitats. Although each of the high islands offers many distinct reefs, it is a mix that tends to be repeated from island to island. Probably this is because each high island presents a similar underwater setting. Being in essence one or more large volcanic peaks that block the prevailing wind and seas, they support distinctive windward and leeward reefs. And the area available for shallow reefs around these islands tends to be limited to relatively narrow shelves, beyond which the seafloor drops sharply to great depths.

In comparison, shallow reefs exist in highly dissimilar circumstances from one end of the Northwestern Hawaiian Islands to the other. In part, this is because they cover almost three times the distance and more than twice the latitude covered by the high islands. Probably more important, however, their topographies are more varied. Nihoa and Necker are most like the high islands, being small volcanic peaks that rise abruptly from the sea. But they offer no appreciable lee, and both rest on broad submerged platforms that provide more suitable depths for shallow habitats than do the comparatively narrow shelves that surround the high islands. Northwestward from Necker, conditions progressively become even more different. At French Frigate Shoals exposed volcanic rock is limited to La Perouse Pinnacle, an anomalous basaltic structure that juts from amid expansive shallows and low sandy islets. This and Gardner Pinnacles--two precipitous volcanic rocks surrounded by a broad submerged platform--are the last bits of exposed basalt to the northwest. Farther on, Maro Reef is the almost totally submerged crest of an oval-shaped seamount, whereas Laysan and Lisianski are low sandy islands surrounded by wide shallows. Finally, Pearl and Hermes, Midway, and Kure are coral atolls, even though they lie at high latitudes.

This great diversity of reef habitats strongly influences how fishes are distributed over the archipelago. Because a species is defined by a combination of characteristics adapted to specific environmental conditions, it should be most successful where those conditions are best approximated. Thus, its distribution should reflect its environmental requirements. The importance of this concept to those that would manage Hawaiian fishes is obvious. If we know both the requirements of a species and the characteristics of a habitat, we should be able to predict that species occurrence in that habitat. And where the occurrence fails to meet the prediction, it should be possible to identify the root of the discrepancy.

So, I believe that study of how Hawaiian reef fishes are distributed over the archipelago will identify many of the forces that shape their communities.

Several other investigations, past and present, contribute to this effort. The project is based on my earlier study of reef fishes at Kona, Hawaii (Hobson, 1972, 1974) and is closely tied to current studies of the reef benthos (see paper by Grigg and Dollar) on the same reefs. And because I believe that trophic relationships are the major forces shaping the structure of reef fish communities, I expect valuable interaction with the current studies of trophic relationships among fishes in the Northwestern Hawaiian Islands (see paper by Parrish et al.).

This is a preliminary report on the project's current status. Anticipated contributions to the scientific literature include the distribution patterns of certain key species done in collaboration with Leighton Taylor, and an analysis of ecological relations in distribution patterns done in collaboration with Richard Grigg.

METHODS

This study is based on direct observations, using SCUBA, of reef communities between shore and depths of 20 to 35 m. Work at each island begins with a general reconnaissance where representative habitats are identified and all species seen are listed. Having acquired a general familiarity with the area and its fauna, 25 x 4 m transect lines are established in the representative habitats. My experience with transect counts to assess fish communities under varied conditions has shown this to be an effective sample area. A longer line too often cannot be contained within a single type of habitat. Cryptic forms escape notice when more than about 2 m from the line. Also, the standard 72 cu. in. diving tank provides just a bit more air than it takes to complete a count at the deeper stations.

The counts are made as follows. The preliminary reconnaissance and previous experience have established species likely to be present, their relative numbers, and their general behavior. As I lay out the line (a fiberglass metric measuring tape), moving rapidly, I count those species that tend to avoid humans. Then I return along the line, counting those species that are attracted to humans, but moving fast enough to avoid repeated counts of those individuals that follow. Finally, I move slowly back along the line, carefully inspecting crevices for cryptic, sedentary forms that readily go unnoticed. I spend 40 min. on each count so that each habitat receives equal attention, and during this time note any fish within the sampled area that I have reason to believe was not counted earlier. The tally generally includes more individuals than are in the area at one time. With the limited number of counts I am able to make, this methodology has proven the most effective way to determine which species frequent the sampled habitat. It does not, however, provide data for projections of biomass.

To make the counts more accurately reflect community structure, it is necessary to make an adjustment for certain species, generally grazing

acanthurids or scarids, that roam over the reef in exceptionally large aggregations. Typically these aggregations include several hundred individuals, and experience has shown that their chance entry--or non-entry--into the sample area will produce a distorted picture of community structure. The problem is exaggerated in this study because there is opportunity for just a relatively few transect counts in any one place. I have concluded that it is best to record these schools (estimates of the number of individuals) as footnotes, whether or not they enter the same area, and not use them in calculating the index used to characterize community structure. This procedure seems to be working out. Generally when such schools are present there are enough conspecifics present apart from these large schools to rank the species among the major components of the community.

The counts are not without inherent bias. Generally, highly cryptic forms like muraenid eel^s are grossly underrepresented. In some habitats the same is true of certain nocturnal species, like holocentrids, that spend the daytime under cover. And although the water was clear enough at all stations to include the entire water column in the counts, certain very small species like atherinids and engraulids that school just under the surface were not included because their numbers, and sometimes their identities, could not be determined consistently in observations made from the seafloor. These problems, however, applied equally to all counts, so do not weaken the comparisons.

Finally, I did not count small juveniles because their numbers vary greatly with the season and from year to year for reasons unrelated to conditions on the reef. Their inclusion would, in fact, obscure, rather than clarify, the adaptiveness of the established adult to the habitat under study.

Following the transect count, I inspect the surrounding area for other species, noting their relative abundance, and any indications that the transect counts might have produced a misleading assessment of the community. These supplemental observations contribute to the interpretations drawn from the transect data and are especially important as added support when a species is noted to be absent.

Eight islands, or groups of islands, have been sampled to date (Table 1).

RESULTS

Temporal variations in community structure

The communities at different locations in the archipelago are being sampled at different times--often one or more years apart. There would be serious problems with the comparisons if the communities change much from year to year. But their major components, at least, remain essentially unchanged over the period of time involved here, as determined by transect counts made at Kona over three years and at Midway over two years. Because space is limited here, I present data from just one site at each location (Tables 2 and 3), but two other sites at Kona and

TABLE 1. STATIONS WHERE THE FISH COMMUNITIES HAVE BEEN SAMPLED WITH TRANSECT COUNTS AND OTHER OBSERVATIONS, JULY 1977 TO SEPTEMBER 1979

Island	Dates	No. Transect Sites	No. Transects	Depth (m)	Depths of General Obs. (m)
Hawaii	7/77; 10/78; 9/79	3	36	2-12	shore to 35
Oahu	7/77; 11/77; 10/78; 5/79; 9/79	2	8	7-10	shore to 35
Niihau	11/78	2	4	7-10	shore to 20
Nihoa	11/78	2	4	8-10	shore to 35
Necker	11/78	1	2	15	shore to 20
Fr. Frig. Sh.	11/78	5	8	9-12	shore to 20
Midway	8/77; 9/79	8	16	2-12	shore to 35
Kure	8/77; 9/79	8	14	2-12	shore to 35

TABLE 2. MAJOR SPECIES ON ONE CORAL REEF AT KONA, HAWAII

1977 Rank	Species	Relative Abundance Index ¹		
		1977	1978	1979
1	<u>Chromis agilis</u>	19.1	18.0 (1) ²	18.5 (1)
2	<u>Ctenochaetus strigosus</u>	12.7	15.8 (3)	15.4 (2)
3	<u>Zebrasoma flavescens</u>	12.1	16.6 (2)	13.8 (3)
4	<u>Chaetodon multicinctus</u>	8.4	10.1 (4)	8.3 (4)
5	<u>Chromis vanderbilti</u>	6.3	0.9	4.7 (5)
6	<u>Thalassoma duperreyi</u>	6.1	4.4 (5)	3.4 (7)
7	<u>Acanthurus nigrofuscus</u>	4.4	1.7 (9)	1.0
8	<u>Plectroglyphidodon johnstonianus</u>	3.3	3.0 (7)	1.8 (8)
9	<u>Centropyge potteri</u>	3.1	3.3 (6)	3.8 (6)
10	<u>Chromis hanui</u>	2.4	2.8 (8)	1.8 (8)
		4 transects	4 transects	4 transects
		\bar{x} no. sp. 34	\bar{x} no. sp. 33	\bar{x} no. sp. 35
		\bar{x} no. ind. 185	\bar{x} no. ind. 159	\bar{x} no. ind. 191

¹Relative Abundance Index is the percent of all individuals counted that were of this species.

²Numbers in parentheses indicate rank that year if in top 10.

TABLE 3. MAJOR SPECIES OUTSIDE WINDWARD REEF AT MIDWAY ATOLL
(ONE LOCATION)

1977 Rank	Species	Relative Abundance Index ¹	
		1977	1979
1	<u>Acanthurus triostegus</u>	16.3	11.7 (3) ²
2	<u>Chromis ovalis</u>	14.2	13.9 (1)
3	<u>Acanthurus leucopareius</u>	12.3	12.8 (2)
4	<u>Myripristis amaenus</u>	7.0	6.1 (7)
5	<u>Stegastes fasciolatus</u>	6.3	8.5 (5)
6	<u>Kyphosus cinerascens</u>	5.4	4.9 (8)
7	<u>Thalassoma duperreyi</u>	4.9	8.5 (4)
8	<u>Acanthurus nigroris</u>	4.7	0.4
9	<u>Abudefduf abdominalis</u>	2.7	7.6 (6)
10	<u>Thalassoma ballieui</u>	1.9	2.9 (9)
		2 transects	2 transects
		\bar{x} no. sp. 33	\bar{x} no. sp. 35
		\bar{x} no. ind. 316	\bar{x} no. ind. 223

¹Relative Abundance Index is the percent of all individuals counted that were of this species.

²Numbers in parentheses indicate rank that year if in top 10

another at Midway produced similar results. Not only do the same species predominate from year to year, but they do so in approximately the same relative numbers. It is important that this condition exists at both ends of the archipelago, because fish community structure can be more changeable at higher latitudes (unpublished data).

Spatial variations in community structure

I have yet to sample certain important locations in the archipelago, e.g., Gardner Pinnacles, Maro Reef, Laysan, and Pearl and Hermes, so many relationships remain unexamined. Nevertheless, data now in hand illustrate certain patterns that probably are significant.

Because the reef habitats change progressively from one end of the archipelago to the other, it is meaningful to compare conditions on the island of Hawaii with those at Midway-Kure. It is striking that the major species at Kona tend to lose dominance northwestward until they are rare or absent at Midway-Kure (Table 4), whereas the major species at Midway-Kure, while they tend to decline somewhat in relative numbers southeastward, nevertheless are generally more evenly distributed over the archipelago (Table 5).

TABLE 4. NORTHWESTWARD OCCURRENCES OF MAJOR SPECIES¹ ON TRANSECT LINES AT KONA, ISLAND OF HAWAII

Species	Hawaii	Oahu	Nihoa	French Frigate S.	Midway-Kure
<u>Chaetodon multicinctus</u>	****	**	**	**	●
<u>Plectroglyphidodon imparipennis</u>	****	●	**	*	0
<u>Chromis agilis</u>	****	●	0	*	0
<u>C. vanderbilti</u>	****	****	****	****	●
<u>Acanthurus nigrofuscus</u>	****	****	****	****	0
<u>Zebrasoma flavescens</u>	****	***	●	*	●
<u>Ctenochaetus strigosus</u>	****	****	**	****	**

¹Listed are the species that represented >10% of all individuals counted on any one of the 36 Kona transect lines. Asterisks represent the largest percent of all individuals counted that were of that species on any one transect line at each location.

**** = >10% *** = 5-9% ** = 1-4% * = <1%
 ● = seen (but not on transect) 0 = not seen

TABLE 5. SOUTHEASTWARD OCCURRENCES OF MAJOR SPECIES¹ ON TRANSECT LINES AT KURE AND MIDWAY ATOLLS

Species	Kure-Midway	French Frigate S.	Nihoa	Oahu	Hawaii
<u>Myripristis kuntee</u>	****	●	●	*	**
<u>Flammeo sammara</u>	****	●	●	●	*
<u>Kyphosus cinerascens</u>	****	**	****	●	**
<u>Mulloidichthys flavolineatus</u>	****	●	●	●	**
<u>Chromis ovalis</u>	****	****	****	●	●
<u>Dascyllus albisella</u>	****	***	●	●	●
<u>Stegastes fasciolatus</u>	****	**	**	***	***
<u>Thalassoma duperreyi</u>	****	***	***	***	***
<u>T. ballieui</u>	****	**	**	**	*
<u>Scarus dubius</u>	****	**	●	0	*
<u>S. sordidus</u>	****	**	●	●	*
<u>Acanthurus leucopareus</u>	****	**	**	●	***
<u>A. nigroris</u>	****	**	**	**	***
<u>A. triostegus</u>	****	**	**	**	***

¹Listed are the species that represented >10% of all individuals counted on any one of the 30 Midway to Kure transect lines. See footnote 1 of Table 4 for explanation of symbols.

I believe that the combination of exploratory reconnaissances, general observations, and transect counts produced reasonable species lists for most locations. If so, the patterns of occurrence of even the relatively minor species in these lists can be meaningful. The data show that 21 of the species seen more than once on transect lines at Kona were not seen on transects or during other observations at Kure or Midway, and 12 of the species that recurred on the transect lines at Kure and Midway were not seen on transects or during other observations at Kona (Table 6).

Generally the comparisons drawn in this report are limited to observations made during this study. This is to reduce the bias that would otherwise stem from my many observations in the high islands, especially Hawaii and Oahu, during previous years. It is significant, however, that during all of my intensive work at Kona, I saw only one of the species listed in part II of Table 6--an occasional Caranx ignobilis. Similarly, two other species--the histiopterid Histiopterus typus and the pomacanthid Genicanthus personatus--seen repeatedly on reefs as shallow as 20 m at Midway and Kure (though not on transect lines) have not been seen in the high islands.

The shift in community structures from one end of the archipelago to the other is not a smooth progression. The various islands, and certain groups of islands, have distinct features that influence their fish communities. This was most evident at French Frigate Shoals. Two relatively common species, Chaetodon trifascialis and Chaetodon citrinellus, were not seen elsewhere in the archipelago during this study. Chaetodon trifascialis invariably occurred with coral of the genus Acropora, which dominated some reefs there, but is rare or absent elsewhere in the archipelago (see paper by Grigg and Dollar). An additional feature of fish communities in the Northwestern Hawaiian Islands is the relatively high incidence in shallow water of the large terminal male phase of many labrid species. Most prominent are: Bodianus bilunulatus, Coris flavovittata, Anampses cuvier, Thalassoma purpureum, and Thalassoma ballieui. These are especially numerous at Midway and Kure.

DISCUSSION

It is premature to draw broad generalizations about the structure of reef fish communities throughout the archipelago because too many critical locations remain unsampled. Nevertheless, the data in hand suggest certain patterns likely to be strengthened by future sampling.

Because conditions differ so from one end of the archipelago to the other, it is not surprising that dominant species vary from place to place. Forces likely to limit distribution of the various species fall broadly in one of two categories: environmental factors (including biological interactions) and fishing pressures.

Undoubtedly, a great variety of environmental pressures exist in the wide range of reef habitats between the island of Hawaii and Kure Atoll. These would be expected to influence both the northwestward distribution of species more prominent in the southeast (such as those at Kona, Tables 4 and 6, part I), and the southeastward distribution of species more

TABLE 6. SPECIES THAT RECURRED ON TRANSECT LINES AT ONE END OF THE ARCHIPELAGO, BUT WERE NOT SEEN AT ANY TIME AT THE OTHER END

I. Species that recurred at Kona ¹	Most northwestward sighting
1. <u>Cephalopholis argus</u>	Niihau
2. <u>Aphareus furcatus</u>	French Frigate Shoals
3. <u>Monotaxis grandoculis</u>	" " "
4. <u>Parupeneus bifasciatus</u>	Niihau
5. <u>Chaetodon ephippium</u>	Nihoa
6. <u>C. reticulatus</u>	Kona
7. <u>C. lineolatus</u>	"
8. <u>Plectroglyphidodon sindonis</u>	French Frigate Shoals
9. <u>Coris gaimard</u>	" " "
10. <u>Thalassoma fuscus</u>	" " "
11. <u>T. quinquevittata</u>	" " "
12. <u>Scarus rubroviolaceus</u>	" " "2
13. <u>Ctenochaetus hawaiiensis</u>	" " "
14. <u>Naso lituratus</u>	" " "
15. <u>N. brevirostris</u>	" " "
16. <u>Plagiotremus goslinei</u>	Necker
17. <u>Rhinecanthus rectangulus</u>	"
18. <u>Cantherines sandwichiensis</u>	French Frigate Shoals
19. <u>Pervagor melanocephalus</u>	Kona
20. <u>Ostracion solorensis</u>	"
21. <u>Canthigaster amboinensis</u>	French Frigate Shoals

II. Species that recurred at Midway-Kure	Most southeastward sighting
1. <u>Carcharhinus amblyrhynchos</u>	Nihoa
2. <u>Ostichthys pilwaxii</u>	Midway
3. <u>Epinephelus quernus</u>	"
4. <u>Oplegnathus fasciatus</u>	"
5. <u>O. punctatus</u>	"
6. <u>Goniistius vittatus</u>	French Frigate Shoals
7. <u>Caranx ignobilis</u>	Necker
8. <u>C. cheilio</u>	Midway
9. <u>Carangoides ferdau</u>	"
10. <u>Epibulus insidiator</u>	French Frigate Shoals
11. <u>Cheilinus bimaculatus</u>	Oahu
12. <u>Cheilio inermis</u>	"

¹Other than species listed in Table 4.

²William Walsh, University of Hawaii, personal communication, November 1978.

prominent in the northwest (such as those at Kure-Midway, Tables 5 and 6, part II). Fishing pressure, too, would be expected to have an impact. But because, historically, fishing by humans has been concentrated in the southeastern part of the archipelago, a measurably impact would be expected only in the southeastward distributions of certain species more prominent in the northwest.

Environmental factors that limit distribution northwestward

All of the species more prominent at Kona (Tables 4 and 6, part I) demonstrate a close relationship with fishes in more southerly waters of the tropical western Pacific. Even the one Hawaiian endemic among the major forms--Chaetodon multicinctus--has a close Indo-West-Pacific analog, C. punctatofasciatus (Gosline, 1956). From this evidence alone one might expect these species to be limited northward by lower water temperatures, and undoubtedly many are. But at least over the southeastern half of the archipelago--from the island of Hawaii to French Frigate Shoals--it seems that other environmental factors are more powerful than water temperature in determining the distribution patterns of at least some species.

Consider, for example, Acanthurus nigrofuscus, which Randall (1960, p. 248) reported to be "...probably second in abundance among surgeonfishes in Hawaii only to the manini" (A. triostegus). Based on its occurrences in a variety of habitats during this study, A. nigrofuscus is dominant only where much of the seafloor is exposed basalt--a widespread feature of high-island reefs. Its dependence on some factor related to exposed basalt seems evident through the Northwestern Hawaiian Islands as far as French Frigate Shoals, where its prominence is confined to La Perouse Pinnacle, the only location there with exposed basalt. A. nigrofuscus was not seen at Midway or Kure, where exposed basalt is absent.¹ A similar dependence on some factor associated with exposed basalt, but with an added feature associated with surge-swept shallows, is suggested in the distribution patterns of the pomacentrids Plectroglyphidodon imparipennis and P. sindonis.

It would also appear that forces other than those associated with water temperatures limit the distribution of Zebrasoma flavescens into the Northwestern Hawaiian Islands. In this case, the limiting factor seems related to the absence there of well-developed lee shores. On the high islands--at least Oahu and Hawaii--this species is prominent only in certain leeward habitats (Brock, 1954).

Despite the low water temperature during the winter at French Frigate Shoals, the reef habitats are more favorable to at least some Indo-West-Pacific forms than are reef habitats in the high islands, such as corals of the genus Acropora and the co-occurring butterflyfish Chaetodon trifascialis. These species, common throughout most of the tropical Indo-Pacific

¹The apparent relation of Acanthurus nigrofuscus to exposed basalt in Hawaii is questioned by the widespread prominence of A. elongatus--considered synonymous with A. nigrofuscus by Randall (1956)--on basalt-less coral reefs of the Marshall Islands (Schultz and Woods, 1953).

region, are rare or absent from most of the Hawaiian Archipelago, in the south as well as in the north.

The butterflyfish Chaetodon citrinellus is another species widespread in the Indo-Pacific region and common at French Frigate Shoals, but was unseen elsewhere during this study. Gosline and Brock (1960) considered it to be rare in Hawaii.

The element favorable to certain Indo-West-Pacific species in reef habitats at French Frigate Shoals, but not around the high islands, is unknown. Perhaps barrier reefs that enclose expansive shallows--a prominent setting here and in the western Pacific, but limited around the high islands--establish some required element. Barrier reefs are widespread northwestward from French Frigate Shoals to Midway and Kure. I am anxious to sample the intervening islands--Gardner Pinnacles, Maro Reef, Laysan, Lisianski, and Pearl and Hermes--to determine where the various Indo-West-Pacific forms prominent at French Frigate Shoals, but absent at Midway-Kure, drop out. Because Midway and Kure are coral atolls, they must satisfy many of the environmental requirements of these species. But water temperatures on shallow reefs there drop below 18°C (Mauck, 1975), which probably are intolerably for many. However, low water temperatures have not limited Epibulus insidiator. This Indo-West-Pacific labrid apparently finds some needed environmental feature on reefs from French Frigate Shoals to Kure Atoll that is lacking on the volcanic islands to the southeast.

Environmental factors that limit distribution southeastward

The major species at Midway-Kure (Table 5), like the major species at Kona, discussed above, are closely related to fishes on the tropical western Pacific. But considered together, they probably are more representative of the Hawaiian fauna than is the Kona group. More evenly distributed over the archipelago, the Midway-Kure group includes four Hawaiian endemics (Chromis ovalis, Dascyllus albisella, Thalassoma duperreyi, and T. ballieui), compared to only one (Chaetodon multicinctus) in the other groups. Hence, the Midway-Kure group would seem generally more attuned to the Hawaiian environment.

A new element enters the discussion, however, when we consider those species less numerous than the above which nevertheless occurred in Midway-Kure transect counts, but absent at Kona (Table 6, part II). Among these are species that demonstrate close ties with more temperate regions of the western Pacific. Both Oplegnathus fasciatus and O. punctatus are prominent in coastal waters of Japan, where they are popular game fishes (Masuda et al., 1975). Despite their common occurrences at Kure and Midway they are rare southeastward in the Hawaiian chain. Oplegnathus punctatus has not been recorded in Hawaii until now and O. fasciatus has been recognized from just one specimen taken almost a century ago. Gosline and Brock (1960) considered it a dubious record.

Similar ties to warm temperate western Pacific habitats are suggested by the frequent occurrences on shallow (10 to 20 m) reefs of Ostichthys pilwaxii and Goniistius vittatus, as well as Histioporus typus (which

were not counted on transect lines but were seen repeatedly elsewhere). Both O. pilwaxii and H. typus occur in Japanese waters, as do close relatives of G. vittatus (Masuda et al., 1975), but here still another dimension enters the discussion: variations in depth of occurrence with latitude. Although H. typus appears to be genuinely rare to the southeast [Gosline and Brock (1960) were aware of just two specimens], the populations of O. pilwaxii and G. vittatus seem limited to deeper water. Based on experience centered in the high islands, Gosline and Brock (1960) made no mention of O. pilwaxii (as O. japonicus) being uncommon, but noted (p. 143) that it "...is probably the deepest water species of all the holocentrids." And they reported (p. 203) that G. vittatus (as Cheilodactylus vittata) is "...not uncommon in water about 100 feet deep."

It is a well recognized principle of zoogeography that fishes widely distributed over latitude occur in deeper water toward the equator (e.g., Hubbs, 1948). Furthermore, studies along the North American west coast, where the pattern is reversed with local upwelling, have shown that the phenomenon is based on water temperatures (Hubbs, 1948). So we should expect a straightforward relation between depth and water temperature to account for the distributions of at least some of the species that inhabit shallow reefs in the northwest, but only deeper reefs further south. This may account for the distribution of the angelfish Genicanthus personatus, for example, which is relatively common on reefs 20 to 30 m deep at Midway and Kure, but which has been reported only from deep water around the high islands (Randall, 1975). And it may explain why the large terminal male phase of the labrid Bodianus bilunulatus lives on reefs as shallow as 1 to 2 m at Midway and Kure, but at Kona rarely occurs in shallower depths than 20 m. It may even account for the similar distribution of the grouper Epinephelus quernus, which I found to be numerous in water as shallow as 5 m at Kure and Midway, but which frequents fairly deep water southeastward (Gosline and Brock, 1960). In this last case, however, the situation is clouded by yet another consideration--fishing pressures.

The impact of fishing pressures on distribution

The absence of fishes like Epinephelus quernus in shallow water to the southeast might reflect increased fishing pressures. Certainly E. quernus is an easy mark for spear fishermen, who without doubt have taken a heavy toll of shallow-water reef fishes around the high islands. Similar uncertainty surrounds the southeastward occurrences of Caranx cheilio. This species was represented on transect lines at Midway that were in depths of 5 m (Table 6, part II), but it was not seen at French Frigate Shoals or southward. Does this reflect fishing pressures or restriction to deeper water in the south?

The marked decrease in numbers of some species southeastward cannot be attributed to population shifts into deeper water, however, because they inhabit shallow reefs throughout the archipelago. Certainly the distribution patterns of some, like the shark Carcharhinus amblyrhynchos, may find some environmental feature of high-island reefs unfavorable, as they seem generally sparse there. Others, however, are known to thrive on reefs of the high islands, and their current low numbers in the study areas likely reflect fishing pressures. Considering just those listed in

Tables 5 and 6, part II, we can point to Myripristis kuntee and Caranx ignobilis. Myripristis kuntee is well known to be a prime target of spear fishermen, and C. ignobilis is coveted by spear fishermen and shore fishermen alike. A similar appraisal of the species more prominent in the south (Tables 4 and 6, part I) fails to suggest species likely to be subjected to strong fishing pressures. Of the species listed, only the grouper Cephalopholis argus and the snapper Aphareus furcatus would seem likely possibilities. Cephalopholis argus, however, has in fact been expanding its range northward since it was introduced into the high islands from Tahiti several decades ago, and A. furcatus, a relatively small, generally solitary species, is not particularly sought after.

ACKNOWLEDGMENTS

I thank Richard Shomura and his staff--especially Richard Uchida and Robert Skillman--at the Southwest Fisheries Center Honolulu Laboratory, NMFS, as well as Robert Iverson and John Naughton, Southwest Region, NMFS, for their cooperation and logistic support. I also thank Skip Naftel and his crew on RV Easy Rider for their capable support. For arranging our stay at Kure Atoll, I am grateful to Captain H. Holmgren, Chief of Operations, 14th Coast Guard District, and for their help in facilitating our stay on Midway, I thank Commander K.R. Miller and LTJG S. Loesch, US Naval Station, Midway, and various members of the Koral Kings Diving Club. Many individuals in Honolulu have helped in various ways, especially Richard Grigg, Steven Dollar, Michael Palmgren, and William Walsh, University of Hawaii; Leighton Taylor, Director of the Waikiki Aquarium; Richard Coleman, U.S. FWS, Honolulu; and James Parrish, Cooperative Fishery Unit, U.S. FWS. Finally, James R. Chess, Southwest Fisheries Center, Tiburon Laboratory, whose concurrent work with benthic invertebrates complements my study of fish communities, was a capable diving partner during many of the observations.

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