Proc. Res. Inv. NWHI
UNIHI-SEAGRANT-MR-84-01

THE STRUCTURE OF REEF FISH COMMUNITIES IN THE HAWAIIAN ARCHIPELAGO

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ABSTRACT

The great variety of reef habitats in the Hawaiian Archipelago has a profound influence on how the species of reef fishes are distributed. For some species, however, the pattern has been strongly modified by fishing pressures. The fauna is basically derived from the tropical western Pacific, a relationship that is generally most evident in communities at the southeastern end of the archipelago, but is also particularly evident at French Frigate Shoals which is located at the center of the archipelago. Although communities at the northwestern end of the archipelago similarly show close ties to the tropical Pacific, they also include species from more temperate regions of the western Pacific. These more temperate derivatives decrease in numbers and/or occur in deeper water southeastward. Conversely, some deep-water tropical forms that exist only on deeper reefs in the southeast occur on shallow reefs in the northwest. The predominant members of the northwestern communities, as a group, are better tuned 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. The southeastward distributions of species in the northwestern communities are limited by both environmental and fishing pressures, but the northwestward distributions of species in the southeastern communities are limited only by environmental factors.

fishes
Hawaii
fish communities
zoogeography

INTRODUCTION

The distribution of reef fish species in Hawaii is strongly influenced by the great diversity of reef habitats over the archipelago. Because each species' occurrence is defined by a combination of characteristics adapted to specific environmental conditions, its greatest numbers should occur where these conditions are best approximated. But patterns of occurrence no doubt have been distorted by fishing pressures, which have been species and area specific. These opinions remain largely conjectural because the actual patterns of distribution for the various species remain poorly known. This study was undertaken to improve and expand our knowledge of these relationships for the purpose of developing more effective management guidelines.

REEF HABITATS

Reef habitats in the Hawaiian Archipelago range from those that fringe the massive volcanic island of Hawaii, to those located more than 1,500 km northwestward that are the major structure of Kure Atoll. Each of the major high islands offers many distinct habitats, but it is a mix that tends to recur because these islands have similar topographies. Being in essence one or more large volcanic peaks that block the prevailing wind and seas, the high islands support distinctive windward and leeward reefs. Furthermore, so abrupt is their rise from great ocean depths that room for nearshore reefs is limited.

In contrast, highly dissimilar underwater settings exist 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 of the high islands. Probably more important, however, is the fact that 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, a 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.

METHODS

Between 1977 and 1982, reef fish communities between shore and depths of 20 to 35 m were assessed throughout the archipelago (Table 1). Because the various stations were sampled at different times during different seasons, often 1 or more years apart, it was important to know how much the species composition of the fish communities could be expected to vary over time. For this reason, assessments were repeated over 2 or more years in selected locations at each end of the archipelago. A site off the island of Hawaii was sampled throughout the 5 years of the study, including all seasons, and a site off Midway was sampled over 2 years, including two seasons. Repeated counts and observations also were made at several other sites during the study, but because the results relevant to this question were the same as for the stations off Hawaii and Midway, they are not presented in this paper. In general, however, the limited number of opportunities available to sample this vast area, with so many habitats, precluded replicate assessments at specific stations.

TABLE 1. ASSESSMENT OF REEF FISH COMMUNITIES AT VARIOUS STATIONS IN THE HAWAIIAN ARCHIPELAGO, JULY 1977 TO OCTOBER 1982

Station	No. of Habitats	No. of Transects	Transect Depths (m)
Hawaii	6	54	2-12
Oahu	6	17	5-12
Niihau	2	4	7-10
Nihoa	2	5	8-10
Necker Island	2	3	10-15
French Frigate Shoals	8	11	9-15
Gardner Pinnacles	3	3	10-12
Maro Reef	3	4	2-12
Laysan Island	4	4	3-16
Lisianski Island[1]	5	5	7-10
Pearl and Hermes Atoll	2	2	7-12
Midway Islands	8	16	2-12
Kure Atoll	8	14	2-12

[1]Including Neva Shoal

A standard procedure was used at all the islands in order to obtain comparable data. First, a general reconnaissance was made to obtain provide familiarity with the area and fauna, identify

representative habitats, and provide a list of the species present. Then in each representative habitat the community was characterized upon conducting two consecutive visual counts of the fishes in 4 m x 25 m transects. The intent was to determine which species frequented the sampled habitat and not to measure the existing biomass. Forty minutes were spent tabulating species on each transect. The final tally included many more individuals than were present in the sampled area at any one moment. Other details of the procedures used in making the counts are reported in Hobson (1980).

Counts were limited to individuals that appeared and behaved as adults because the occurrences of many juveniles varied greatly with season and from year to year for reasons unrelated to conditions on the reef. Inclusion of juveniles would have, in fact, obscured rather than clarified the zoogeographic questions considered in this paper.

Owing to limitations in the visual sampling method, highly cryptic forms such as muraenid eels are greatly underrepresented. Also, in some habitats the same is true of certain nocturnal species, such as holocentrids, that spend the daytime under cover. However, because this bias was constant throughout the study, the counts should illustrate any major differences in numbers of individuals of these species between sites.

Non-reef species that occurred near the reefs were excluded from the counts. These include certain small forms, such as atherinids and engraulids, that occurred just under the water's surface and also small benthic forms, such as gobiids, that often were abundant on the sand adjacent to the reef.

Following each count the surrounding area was inspected for other species, noting their relative numbers and any indications that the transect counts might have produced a misleading assessment of the community. These supplemental observations contributed to the interpretations drawn from the transect data and are especially important as added support when a species was noted as absent. The comparisons are limited to observations made during this study in order to reduce the bias that otherwise would stem from including the many observations made during other studies in previous years in the high islands, especially around Oahu and Hawaii.

RESULTS

Temporal Patterns

The major components of the reef fish communities remained relatively unchanged at the sites on Hawaii and Midway (Table 2). The 10 most numerous species at the time of the first counts at each site continued (with a few exceptions among the lower-ranked forms) to maintain similar proportions in the same communities in later years.

TABLE 2. TEMPORAL VARIATIONS IN FISH COMMUNITIES ON TWO HAWAIIAN REEFS

LEEWARD HAWAII	Jul 1977	Oct 1978	Sep 1979	Apr 1980	Oct 1982
Number of Transects	4	4	4	2	2
$\bar{x}$ Species	34	33	35	31	34
$\bar{x}$ Individuals	185	159	191	158	188
1977 Species Ranking	Relative Abundance Index[1]				
Chromis agilis	19.1	18.0	18.5	18.0	13.9
Ctenochaetus strigosus	12.7	15.8	15.4	13.2	17.6
Zebrasoma flavescens	12.1	16.6	13.8	17.2	23.2
Chaetodon multicinctus	8.4	10.1	8.3	9.4	6.4
Chromis vanderbilti	6.3	0.9	4.7	4.1	0
Thalassoma duperrey	6.1	4.4	3.4	4.1	1.9
Acanthurus nigrofuscus	4.4	1.7	1.0	0	0.8
Plectroglyphidodon johnstonianus	3.3	3.0	1.8	2.5	2.5
Centropyge potteri	3.1	3.3	3.8	3.5	3.5
Chromis hanui	2.4	2.8	1.8	1.9	0.8

WINDWARD MIDWAY	Aug 1977	Sep 1979
Number of Transects	2	2
$\bar{x}$ Species	33	35
$\bar{x}$ Individuals	316	223
1977 Species Ranking	Relative Abundance Index[1]	
Acanthurus triostegus	16.3	11.7
Chromis ovalis	14.2	13.9
Acanthurus leucopareius	12.3	12.8
Myripristis amaenus	7.0	6.1
Stegastes fasciolatus	6.3	8.5
Kyphosus bigibbus	5.4	4.9
Thalassoma duperrey	4.9	8.5
Acanthurus nigroris	4.7	0.4
Abudefduf abdominalis	2.7	7.6
Thalassoma ballieui	1.9	2.9

[1]Relative Abundance Index is the percentage of all individuals counted that were of this species.

Spatial Patterns

The species constituting the reef fish communities varied greatly from one reef habitat to another, but there were broad similarities in certain basic features. Although there were 30 to 40 species in most of the communities, just three or four of them included over 50 percent of the individuals present. Typically, one species included 15 to 20 percent of all individuals, whereas the other two or three species included 10 to 15 percent each. These major species, which differed from one habitat to another, presumably are those best attuned to the prevailing environment and thus probably can be considered characteristic of that particular habitat. It is instructive, therefore, to consider the distribution throughout the archipelago of species that were major forms in any one of the many distinctive communities examined (Table 3). Species included in this list are those that comprised at least 10 percent of the individuals counted in two or more transects in any one habitat.

These major species generally were most prominent at one or the other end of the archipelago. Significantly, those that predominated in the northwestern communities tended to be more evenly distributed over the archipelago than those that predominated in the southeastern communities. Thus, although the northern dominants -- Myripristis amaenus, Kyphosus bigibbus, Chromis ovalis, Stegastes fasciolatus, Thalassoma duperrey, T. ballieui, Acanthurus leucopareius, A. nigroris, and A. triostegus -- declined somewhat in numbers southeastward, the trend was uneven, and all were relatively numerous, if not dominant, throughout the archipelago. In comparison, the southern dominants -- Chaetodon multicinctus, Chromis agilis, C. vanderbilti, Acanthurus nigrofuscus, Ctenochaetus strigosus, and Zebrasoma flavescens -- lost dominance at some point northwestward and hence were few or absent at Midway and Kure.

The numbers of some prominent members of the northwestern communities declined sharply southeastward until at some point they were absent from the shallow reefs. Consider those species that occurred in two or more transects in any one habitat at Kure or Midway, but which were not seen off the island of Hawaii (Table 4). Three -- Pristilepis oligolepis, Epinephelus quernus (Figure 1), and Oplegnathus fasciatus -- were seen nowhere else, while two others -- Oplegnathus punctuatus and Carangoides othogrammus -- occurred southward only in sharply reduced numbers -- the former to Maro Reef, the latter to Nihoa. Two -- Cheilodactylus vittatus and Epibulus insidiator -- were relatively numerous at French Frigate Shoals, but were not seen farther south, and the other two -- Carcharhinus amblyrhynchos, and Caranx ignobilis (Figure 2) -- were numerous all the way to Nihoa, but were not seen in the major high islands during this study period. Two other species seen repeatedly on reefs as shallow as 20 m at Midway and Kure, but not in the transects,

TABLE 3. DISTRIBUTION OF MAJOR REEF FISHES THROUGHOUT THE HAWAIIAN ARCHIPELAGO

Species	Location[1]													
	Hl	Hw	Ol	Ow	NI	NE	FFS	GP	MR	LA	LI	PH	MKl	MKo
Myripristis amaenus	<0.1	•[2]	0[2]	0	•	0	0.1	0.2	0.1	<0.1	0	0.3	0	2.3
Kyphosus bigibbus	<0.1	•	•	0.1	4.4	0.2	0.6	6.0	0.8	4.6	0.2	3.1	2.2	5.9
Chaetodon multicinctus	4.7	3.2	5.0	0.2	0.8	0.6	0.8	0	0	1.3	0	0.1	0	<0.1
Stegastes fasciolatus	1.2	5.9	4.6	6.5	3.1	4.5	2.2	9.4	13.8	4.2	5.0	1.5	18.0	7.2
Plectroglyphidodon imparipennis	0.8	<0.1	•	1.7	1.7	0.7	0.4	1.0	0	0	0	0	0	0
Dascyllus albisella	•	0	•	•	0	•	2.8	0	<0.1	0	0.4	•	0.3	0
Chromis agilis	3.8	0.2	0.1	0	0	0	<0.1	0	0	0	0	0	0	0
C. ovalis	•	0.2	7.1	4.2	2.4	7.5	6.8	3.4	16.2	26.2	•	39.7	0.1	18.3
C. vanderbilti	5.7	4.0	<0.1	6.8	23.6	6.6	3.7	22.3	0	0.6	0	2.4	0	0.1
Thalassoma ballieui	<0.1	<0.1	0.4	0.2	<0.1	1.6	1.5	2.0	2.1	2.5	2.4	1.0	6.3	2.3
T. duperrey	4.8	4.0	6.0	10.6	4.8	13.9	7.0	6.2	8.8	4.8	9.9	1.2	18.9	10.4
Acanthurus leucopareius	0.3	<0.1	0	0.6	0.6	0.3	<0.1	•	•	0.4	•	0.1	0	5.4
A. nigrofuscus	8.6	9.3	11.2	9.8	5.6	0.7	1.4[3]	0.7	•	<0.1	0	0	0	0
A. nigroris	0.4	0.8	0.4	0	2.3	2.0	1.8	5.5	6.0	4.3	9.1	0.9	0.7	8.6
A. triostegus	0.2	0.1	0.6	0.5	0.1	2.0	0.5	4.7	7.4	<0.1	4.9	0.5	2.0	4.7
Ctenochaetus strigosus	13.1	13.5	9.3	1.7	3.4	0	7.0	0.2	2.2	1.4	7.5	1.2	1.4	0.4
Zebrasoma flavescens	16.6	0.7	1.5	0	<0.1	0	0.8	0	•	<0.1	<0.1	0.4	•	0
Melichthys niger	0.1	0.1	<0.1	0	0.2	0.3	8.1	3.0	<0.1	3.0	•	5.8	0	0.9
Pervagor spilosoma	<0.1	0	1.3	1.0	0	0.2	0.4	<0.1	0	1.1	8.8	0.1	<0.1	0

Note: Values given are occurrence indices, which are the product of the mean relative abundance index and frequency of occurrence for all transects at each location.

[1]Hl = Hawaii: leeward; Hw = Hawaii: windward; Ol = Oahu: leeward; Ow = Oahu: windward; NI = Nihoa; NE = Necker Island; FFS = French Frigate Shoals; GP = Gardner Pinnacles; MR = Maro Reef; LA = Laysan Island; LI = Lisianski Island; PH = Pearl and Hermes Atoll; MKl = Midway Islands - Kure Atoll: lagoons; MKo = Midway Islands - Kure Atoll: outside barrier reefs

[2]• = seen but not on transect; 0 = not seen

[3]Virtually all A. nigrofuscus at La Perouse Pinnacle; occurrence index there: 8.0 (4 transects)

TABLE 4. OCCURRENCES OF SPECIES COUNTED IN TWO OR MORE TRANSECTS IN ANY ONE HABITAT MOVING SOUTHEASTWARD IN THE HAWAIIAN ARCHIPELAGO

Species	Location[1]												
	KA	MI	PH	LI	LA	MR	GP	FFS	NE	NI	NU	OA	HI
Carcharhinus amblyrhynchos	*	*	*	*	●	●	●	*	*	x			
Pristilepis oligolepis	*	●											
Epinephelus quernus	*	*											
Oplegnathus fasciatus	●	*											
O. punctatus	x	*			●	●							
Cheilodactylus vittatus	*	*	●			●	x	x					
Caranx ignobilis	*	*	*	*	x	*	*	*	●	●			
Pseudocarnx dentex	●	*											
Carangoides othogrammus	●							*		●			
Epibulus insidiator	*	*	*	x		x		*					

Note: * = occurring in two or more transects; x = occurring in one transect; ● = seen. None were seen off Niihau, Oahu, and Hawaii.

[1]KA = Kure Atoll; MI = Midway Islands; PH = Pearl and Hermes Atoll; LI = Lisianski Island; LA = Laysan Island; MR = Maro Reef; GP = Gardner Pinnacles; FFS = French Frigate Shoals; NE = Necker Island; NI = Nihoa; NU = Niihau; OA = Oahu; HI = Hawaii

Figure 1. Epinephelus quernus on a reef 10 m deep at Midway

Figure 2. Caranx ignobilis at Maro Reef

were the pentacerotid Hystiopterus acutirostris and the pomacanthid Genicanthus personatus, neither of which were seen elsewhere during this study period.

In comparison, consider the many more species that occurred in two or more transects in any one habitat in the lee of the island of Hawaii, but were not seen at Kure or Midway (Table 5). Three -- Chromis agilis, Plectroglyphidodon imparipennis, and Acanthurus nigrofuscus -- were among the major species noted above. Five -- Chaetodon reticuluatus, C. lineolatus, Hemitaurichthys thompsoni, Forcipiger longirostris, and Ostracion whitelyi -- were seen nowhere else, while four -- Epinephelus argus, Chaetodon ephippium, Plectroglyphidodon sindonis, and Pervagor melanocephalus -- occurred northward only in sharply reduced numbers. Two -- Thalassoma quinquevittata and Cteno-chaetus hawaiiensis -- occurred only in the lee of Hawaii and at French Frigate Shoals. The remaining 11 species in this group -- Aphareus furcatus, Monotaxis grandoculis, Coris gaimard, Thalassoma fuscus, Scarus rubroviolaceus, Naso lituratus, N. breviorstris, Plagiotremus goslinei, Rhinecanthus rectangulus, Cantherines sandwichiensis, and Canthigaster amboinensis -- were relatively numerous as far as French Frigate Shoals, or Gardner Pinnacles, but declined sharply in numbers northward from there.

Perhaps the most striking departure from the general patterns of distribution outlined above was the almost total absence of small planktivorous fishes at Lisianski and adjoining Neva Shoal (data from the two locations are combined in Table 3). Not only were there no planktivores in the transects at these locations, but the only ones seen in all the widespread observations there were just a few scattered Chromis ovalis. At these same locations, on the other hand, the monacanthid Pervagor spilosoma was unusually abundant. It may be significant that most of the P. spilosoma were found above the reefs in small aggregations, much like those formed by the planktivorous Chromis spp. elsewhere, rather than scattered close to the reef as members of this species usually are. These same circumstances were paired at Kahe, on leeward Oahu, where in two transects conducted 4 months apart planktivores were absent, and P. spilosoma represented 4.6 and 5.6 percent of the fishes counted (compared with a mean of 0.5 percent; range 0 to 0.9 percent in transects elsewhere off leeward Oahu). Interestingly, the transects at Lisianski (and Neva Shoal) and at Kahe were the only ones during the entire study (in water more than 2 m deep) in which planktivores were absent (where in fact at least one planktivorous species was not a major form) and in which P. spilosoma represented more than 1 percent of the fishes present.

In all of the widespread locations visited during this study, only three species were seen that did not also occur either off the island of Hawaii or at Midway-Kure. Two of these -- the chaetodontids Chaetodon trifasciatus and C. citrinellus -- occurred only at French Frigate Shoals, whereas the monacanthid Cantherines verecundes occurred only at Laysan and Lisianski.

TABLE 5. OCCURRENCES OF SPECIES COUNTED IN TWO OR MORE TRANSECTS IN ANY ONE HABITAT MOVING NORTHWESTWARD IN THE HAWAIIAN ARCHIPELAGO

Species	Location[1]														
	Hl	Hw	Ol	Ow	NU	NI	NE	FFS	GP	MR	LA	LI	PH	MI	KA
Epinephelus argus	*				*										
Aphareus furcatus	*	*	*		*	●		x	●	x					
Monotaxis grandoculis	*	x	●		x	x	●	x			●				
Chaetodon ephippium	*				●	x									
C. reticulatus	*														
C. lineolatus	*														
Forcipiger longirostris	*														
Hemitaurichthys thompsoni	*														
Chromis agilis	*	x	x					x							
Plectroglyphidodon imparipennis	*	x	●	*	●	*	x	*	*						
P. sindonis	*	●						●	x						
Coris gaimard	*	x	x	●		●	*	x							
Thalassoma fuscus[2]	*	●	●	●	●	●	●	x	●	●					
T. quinquevittata	*							x							
Scarus rubroviolaceus	*	*	x	●	x	●	●	x							
Acanthurus nigrofuscus	*	*	*	*	*	*	x	*	x	x	●				
Ctenochaetus hawaiiensis	*							●							
Naso lituratus	*	*	*	*		*	x	*	x	●		●	●		
N. brevirostris	*				●		x	*	●						
Plagiotremus goslinei	*	*		x	x	x	x		x						
Rhinecanthus rectangulus	*	●	*	x		*	●	●	●		●				
Cantherines sandwichiensis	*	x	*	*	x	*	●	x	x						
Pervagor melanocephalus	*		*	x											
Ostracion whitelyi	*														
Canthigaster amboinensis	*	*	*	*		x		●							

Note: * = occurring in two or more transects; x = occurring in one transect; ● = seen.

[1]Hl = Hawaii: leeward; Hw - Hawaii: windward; Ol = Oahu: leeward; Ow = Ohau: windward; NU = Niihau; NI = Nihoa; NE = Necker Island; FFS = French Frigate Shoals; GP = Gardner Pinnacles; MR = Maro Reef; LA = Laysan Island; LI = Lisianski Island; PH = Pearl and Hermes Atoll; MI = Midway Islands; KA = Kure Atoll

[2]The nominal T. umbrostigma, which is considered the female of this species based on observations of spawning (Hobson, 1974), was numerous throughout the archipelago.

Chaetodon trifasciatus invariably occurred with coral of the genus Acropora, which dominated some reefs at French Frigate Shoals, but was not abundant elsewhere (see paper in this proceedings by Grigg). It was present on all four transect reefs rich in Acropora, where it represented a mean of 2.1 percent (range of 1.6 to 3.4 percent) of the fishes counted. Chaetodon cintrinellus was relatively abundant in the shallow waters behind the windward reef flat, but no transects were established in that habitat. Cantherines verecundes was seen in just one transect at Laysan that was set on a large patch reef at a depth of 20 m, but it represented 3.1 percent of the individuals there. At Lisianski, C. verecundes was in all the habitats sampled and represented a mean of 2.7 percent (range of 2.3 to 3.6 percent) of the fishes in the five transects conducted there.

An additional feature of fish communities in the Northwestern Hawaiian Islands was the relatively high incidence in shallow water of the large terminal male phase of many labrid species. Most prominent were: Bodianus bilunulatus, Coris flavovittata, Anampses cuvier, Thalassoma purpureum, and T. ballieui. These were especially numerous at Midway and Kure.

DISCUSSION

Temporal Stability

The question of whether reef fish communities are stable or unstable over time has evoked much interest in recent years (e.g., Sale, 1980b). Probably it is significant that proponents of the instability concept have based most of their arguments on short-term studies of small isolated reefs. Most have been experimental colonizations of isolated coral heads (e.g., Sale and Dybdahl, 1975) or artificial reefs (e.g., Talbot et al., 1978; Bohnsack and Talbot, 1980) over periods of less than 3 years. The proponents of the stability concept, on the other hand, have drawn most of their evidence from long-term studies of larger reefs. These have included studies of both natural (Brock et al., 1979) and artificial (Ogden and Ebersole, 1981) reefs that were examined more than 10 years after being defaunated and recolonized. A persistent uncertainty in these studies stems from not knowing how long it takes reef communities to fully recover from defaunation. The uncertainty is increased when artificial reefs are involved because no one knows whether these will in fact ever support truly natural communities. Significantly, however, Sale (1980a) found that the structure of fish communities on undisturbed natural, but small (20 m x 1 m x 1 m), patch reefs (which were controls for his defaunation experiments) changed continuously over time.

The major components of the Hawaiian fish communities described in this paper were stable over the duration of the study, and probably it is significant that these communities were established on extensive, natural reefs that had not been disturbed. Based on these circumstances and the variable results

noted above, the stability-instability controversy may stem from (1) differences in the size and complexity of the reef systems studied by the various investigators; (2) time passed since the communities had been disturbed; and (3) the extent to which the physical conditions of the reefs approximate those of natural, undisturbed reefs in the area. Also, it is important that the stability reported here refers to the adult populations. As mentioned in the "Methods" section, the numbers of juveniles varied with season and from year-to-year for reasons that seemed unrelated to circumstances on the reef, but this variability had no observable impact on the established adults during this study.

Spatial Distribution: General

Most Hawaiian reef fishes are widely distributed on the islands of the Pacific plate, which occupies most of the Pacific basin, and has been defined by Springer (1982) as a distinct biogeographic unit. Apparently these species are adapted to certain features held in common by the variety of high islands, low islands, atolls, and submerged sea mounts, that characterize this, the largest of the earth's lithospheric plates. It is not surprising, therefore, that so many of them occur in diverse habitats throughout the Hawaiian Archipelago. Despite these widespread occurrences, however, the major species differ greatly in their relative numbers from one habitat to another.

Because most of these major forms were most numerous at one end of the archipelago or the other, it is convenient to focus on the northwestward distribution of the southeastern dominants and the southeastward distribution of the northwestern dominants. Significantly, those species which dominated in the southeast were more restricted in their distribution over the archipelago than were those which dominated in the northwest. Apparently the southeastern dominants -- Chaetodon multicinctus, Plectroglyphidodon imparipennis, Chromis agilis, C. vanderbilti, Acanthurus nigrofuscus, Chaetodon strigosus, and Zebrasoma flavescens -- are less attuned to the overall Hawaiian environment than are their northwestern counterparts -- Myripristis amaenus, Kyphosus bigibbus, Chromis ovalis, Dascyllus albisella, Stegastes fasciolatus, Thalassoma duperrey, T. ballieui, Acanthurus leucopareius, A. nigroris, and A. triostegus (Table 3). Not only are the southeastern dominants less numerous in more places throughout the archipelago, but they also include fewer endemics -- just one (C. multicinctus) compared with four (C. ovalis, D. albisella, T. duperrey, and T. ballieui) among the northern groups. It is recognized that some of the most abundant Hawaiian species are endemics (Gosline and Brock, 1960), but not all of the endemics are abundant (e.g., the pomacentrid Plectroglyphidodon sindonis, Table 5).

Patterns of distribution northwestward are basically different from patterns of distribution southeastward presumably because of different selection pressures. In the discussion below several of these selection pressures are distinguished.

Environmental Selection Pressures That Influence Distribution Northwestward

The species in nearshore communities at the southeastern end of the archipelago show close relationships with the fishes of the more tropical regions of the Pacific. Even the one endemic species among the major forms -- Chaetodon multicinctus -- has a western Pacific analog in C. punctatofasciatus, and a South Pacific analog in C. pelewensis (Burgess, 1978). The several species that occurred in transects in the lee of the island of Hawaii, but were not seen elsewhere (Table 5) -- Chaetodon reticulatus, C. lineolatus, Hemitaurichthys thompsoni, Forcipiger longirostris, and Ostracion whitelyi -- are widespread Pacific species that apparently find conditions more suitable here than elsewhere in Hawaii. Gosline and Brock (1960) reported that C. reticulatus has been "reported only twice in Hawaii," that C. lineolatus inhabits "relatively deep water," and that H. thompsoni is "quite rare." They included O. whitelyi (as O. solorensis) in their account of the Hawaiian fauna based only on a small specimen from Johnston Island, but Randall (1972) subsequently noted its occurrence in the lee of Hawaii. F. longirostris was long confused with the common F. flavissimus, but now is recognized as a distinct species rare in the Hawaiian Archipelago except on the leeward reefs of the island of Hawaii (Randall and Caldwell, 1970). Chromis agilis is common and widespread in the tropical western Pacific (Allen, 1975) but has a limited distribution in Hawaii. Although it is the major species on certain reefs in the lee of Hawaii where the coral Porites compressa is abundant, its occurrence northwestward is limited to small aggregations off windward Hawaii and leeward Oahu (on a reef in Hanauma Bay which is rich in Porites compressa). One individual was seen at French Frigate Shoals.

One might assume that distribution of tropical Pacific fishes northwestward in the Hawaiian Archipelago would be limited by lower water temperature. This is probably true for some species, but certain other forces are more limiting for other species.

Reduced protection from prevailing wind and seas northwestward probably limits distribution for some species. Zebrasoma flavescens, for example, seemed to require some feature associated with leeward reefs. This species is the major component of communities on various reefs in the lee of Hawaii, the largest island, but is much less prominent in the lee of the smaller island of Oahu. On the windward side of Hawaii, adults were seen in numbers only south of Cape Kumukahi, where there is in essence a lee shore. North of the cape along the Hamakua Coast just one adult occurred in the transects, whereas juveniles were the most numerous fish on a reef rich in the coral Porites compressa in a sheltered bay near Hilo. Conditions suitable for adults were clearly lacking along the Hamakua Coast, however, as only a few were seen.

Zebrasoma flavescens was found to be sparse off windward Oahu, except in Kaneohe Bay. This pattern is consistent with the work of Brock (1954), who found this fish to be prominent only in certain leeward habitats around Oahu and Hawaii. Zebrasoma flavescens was sparsely distributed in the Northwestern Hawaiian Islands during this study, generally as a few individuals on the more protected reefs. The only sightings at Midway, for example, were a few scattered individuals on patch reefs in the lagoon where the coral Porites compressa also was most abundant. Apparently this coral, which grows as closely spaced finger-like branchings, is important to the juveniles of Z. flavescens, just as it appears to be for adult Chromis agilis.

The decreased occurrence of exposed basalt northwestward appeared to influence the distribution of several species, most notably Acanthurus nigrofuscus, which Randall (1960) described as "...probably second only to the manini (Acanthurus triostegus) in abundance among surgeonfishes in Hawaii." This species was numerous only where the reefs were largely exposed basalt, a widespread habitat in the high islands. The dependence of A. nigrofuscus on some factor related to exposed basalt was especially evident at French Frigate Shoals, where its prominence was confined to La Perouse Pinnacle, the only basaltic structure there. At Gardner Pinnacles, the last exposed basalt occurrence northwestward, A. nigrofuscus was numerous on the basaltic face of the pinnacles, but was not seen elsewhere. Only one individual was seen at Maro Reef and another at Laysan, the latter in a transect. None were seen northwestward from there. Despite the apparent dependence of Hawaiian A. nigrofuscus on habitats that include exposed basalt, the occurrences of this species, on Pacific atolls (Randall, 1956), which lack such habitats, indicates that conspecifics elsewhere may have different requirements. The same is true of the pomacentrid Plectroglyphidodon imparipennis, which was found only among surge-swept basaltic reefs during this study (it was not seen northwest of Gardner Pinnacles), but is widespread elsewhere in the Pacific on reefs that lack exposed basalt (Allen, 1975). Three other species with distributions that coincided with exposed basalt were Hawaiian endemics: the pomacentrid Plectroglyphidodon sindonis (which frequented surge-swept boulders), the blenniid Plagiotremus goslinei, and the monacanthid Cantherines sandwichiensis.

Certain species which are widespread in the central Pacific seem to find conditions more suitable at French Frigate Shoals than elsewhere in the Hawaiian Archipelago. Probably the most striking example is the common occurrence of the chaetodontid Chaetodon trifasciatus, a species that lives in close association with corals of the genus Acropora (Burgess, 1978). Both the fish and corals are common throughout most of the tropical Indo-Pacific, but are rare or absent in the Hawaiian Archipelago except at French Frigate Shoals. In noting the abundance of Acropora at French Frigate Shoals and its sharp decline both southward (to Kauai) and northward (to Laysan), Grigg et al. (1981) suggested that French Frigate Shoals is the site of active

colonization of some Indo-Pacific forms from the west (by way of the subtropical countercurrent), and that this location is the center of distribution of such forms to the other islands. This pattern is consistent with the distribution of some Indo-Pacific fishes in Hawaii. Another widespread Indo-Pacific species that was abundant at French Frigate Shoals, but which went unseen elsewhere during this study, was the chaetodontid Chaetodon citrinellus. This species, considered rare in Hawaii by Gosline and Brock (1960), was among the species that colonized a newly created harbor on the lee shore of Hawaii (Brock, 1981).

These two widely separated and very different settings -- French Frigate Shoals and leeward Hawaii -- may have characteristics that make them more suitable than other Hawaiian habitats for certain Indo-Pacific species. Leeward Hawaii is noted for its warm, sediment-free water and rich coral growth -- all of which are likely to be associated with environments favored by fishes adapted to more tropical Pacific habitats. French Frigate Shoals may be favorable to some because it is in essence a barrier reef that encloses expansive shallows -- a setting which is widespread in the more tropical areas of the central and western Pacific, but limited in those islands to the southeast of French Frigate Shoals.

Barrier reefs that enclose expansive shallows are prominent to the northwest of French Frigate Shoals, especially at Pearl and Hermes, Midway, and Kure -- which are atolls. But during the winter water temperatures fall below 18 C at these locations (Mauck, 1975) which presumably would be a problem for many Indo-Pacific species. Water temperature, however, has not limited Epibulus insidiator, a widespread Indo-Pacific labrid that is common from French Frigate Shoals northwestward to Kure, but which has not been reported southeastward to Hawaii.

Environmental Selection Pressures that Influence Distribution Southeastward

Although the major species in the northwestern communities are more distinctively Hawaiian than their southeastern counterparts, they too are closely related to fishes of the tropical western Pacific. But some of the less prominent species in the northwest are closely related to, or conspecific with, fishes of the more temperate regions in the western Pacific. Furthermore, in contrast with the major species in these communities, which are widely distributed in shallow water, these more temperate species have limited distributions on shallow reefs southeastward. Both Opelgnathus fasciatus and O. punctatus are prominent in coastal waters of Japan, where they are popular game fishes (Masuda et al., 1975). But despite the common occurrences of both species at Kure and Midway, they are uncommon elsewhere in the Hawaiian Archipelago. O. punctatus had not been recorded from Hawaii prior to this study (Hobson, 1980), and O. fasciatus was recognized from just one specimen taken almost a century ago (Gosline and Brock, 1960).

Similar relationships to fishes of more temperate regions in the western Pacific exist for Pristolepis oligolepis, Pseudocaranx dentex, Cheilodactylus vittatus, and Histiopterus acutirostris, all of which also occur in Japanese waters (Masuda et al., 1975; Springer 1982). But here another dimension of distribution must be considered -- variations in depth of occurrence with latitude. All four species are common inhabitants of shallow reefs at Kure and Midway, but occur at greater depths southeastward. Gosline and Brock (1960) noted that although H. acutirostris appears to be rare there, P. oligolepis and C. vittatus are not uncommon in deeper water. P. dentex (as Caranx cheilio), according to Gosline and Brock, is "not now common around the high islands, but is abundant from French Frigate Shoals to Midway," and Moffitt (1980) reported it to be a major target of offshore bottom fishermen in the Northwestern Hawaiian Islands.

Many fishes which have wide latitude distribution inhabit deeper water toward the equator (Hubbs, 1948). The distribution of such fishes often relates to water temperatures, as shown by studies along the western coast of North America where the pattern reverses at points of local upwelling (Hubbs 1948). Thus, at least some of the fishes that inhabit progressively deeper habitats southeastward in Hawaii may be responding to features related to water temperature. In addition to the species mentioned above, an affinity to lower water temperatures may account for the distribution of Genicanthus personatus, which is relatively common on reefs 20 to 30 m deep at Midway and Kure, but which has been reported only from deeper water around the high islands (Randall, 1975). The same pattern may hold true for the grouper Epinephelus quernus, which is common on shallow reefs at Midway and Kure, but is only found in deeper water southeastward. This species constitutes a large part of the catch of the offshore hand-line fishery at depths below 60 m around the high islands (Ralston, 1980). The same pattern may hold true for the large terminal male phase of the labrid Bodianus bilunulatus, which is another form that commonly frequents reefs as shallow as 1 m at the northwestern end of the archipelago, but rarely occurs shallower than 20 m at the southeastern end.

Pristolepis oligolepis, P. dentex, C. vittatus, and H. acutirostris, as well as certain congeners of G. personatus, B. bilunulatus, and the two oplegnathids, have antitropical distributions that are thought to have been established when surface waters were cooler than at present (Randall, 1981). Springer (1982), however, cited evidence that equatorial sea-surface temperatures have been relatively stable since these antitropical distributions are thought to have been established. He suggested that these distributions have an ecological basis related to the antitropical distribution of the high islands, but this possibility is inconsistent with the fact that most of the species involved are more numerous around the Hawaiian atolls than around the high islands.

The Planktivore-*Pervagor spilosoma* Anomaly

The possibility of a connection between an absence of planktivores and an abundance of *Pervagor spilosoma*, is strengthened by the fact that at the only locations where either circumstance occurred -- Lisianski (and Neva Shoal) and Kahe, Oahu -- they occurred together. The basis for the apparent relationship between these species, or between these species and the two locations, remains unclear. Perhaps it is significant that the water at Lisianski was noted to have a milky quality and that a fine sediment coated much of the seafloor, especially at Neva Shoal. This condition can mean that the water is not circulating, which would in turn mean a reduced supply of zooplankton. On the other hand, it is conceivable that certain materials in suspension could adversely affect small planktivores. There is no measure of the zooplankton at these locations, but it was striking that in the absence of planktivores at Lisianski, the normally bottom-dwelling *P. spilosoma* aggregated above the reef, just as the planktivores did elsewhere. These *S. spilosoma* were not seen feeding, however, and a diet of zooplankters certainly would have been a radical departure from the usual diet of this species. Under more typical circumstances at the island of Hawaii, *P. spilosoma* fed primarily on scleractinian coral polyps (Hobson, 1974). On the other hand, it is conceivable that under appropriate circumstances, features adapted to pluck coral polyps could also be effective in feeding on zooplankters.

Fishing Pressures

Because fishing pressures have been concentrated on just certain places, they seem likely to have distorted patterns of distribution for at least some species. Fishing pressures seem to account for the reduced numbers in the southeast of certain of the species prominent in the northwest (Tables 3 and 4). Perhaps this was predictable, because fishing pressures should have been expected to increase toward the fishing ports on the major high islands. Nevertheless, it is difficult to hold fishing pressures accountable for the southeastward decline of some species. Although *Epinephelus quernus* and *Pseudocaranx dentex* are major targets of fishermen in the area southeast of Midway, the fishing effort is in deeper water offshore. There has been virtually no fishing on the shallow reefs of the Northwestern Hawaiian Islands from Pearl and Hermes Atoll southeastward; hence, the absence of *E. quernes* and *P. dentex* from these reefs cannot be attributed to fishing pressures. Probably both species are simply better adapted to deeper water in southeastern areas.

Population shifts into deeper water cannot account for the southeastward decline in numbers of some shallow-water potential target species. This is because they inhabit shallow reef areas throughout the archipelago. Some of those which are abundant throughout the Northwestern Hawaiian Islands, but generally sparse throughout the major high islands, such as the shark

Carcharhinus amblyrhynchos, may find certain environmental features of major high island reefs unfavorable. On the other hand, shark populations are known to be particularly vulnerable to fishing pressures, and there have been concerted and apparently successful efforts to reduce the populations of these fishes around the high islands.

The most likely victims of fishing pressures are those species known to be well adapted to shallow-water reef areas in the high islands, but which were found only in low numbers during this study. Examples among the species listed in the tables are the holocentrid Myripristis amaenus and the carangid Caranx ignobilis. M. amaenus and its congeners M. murdjan and M. kuntee, are prime targets of fishermen and are especially vulnerable owing to their habit of concentrating in reef caves during the day. [M. kuntee was considered a major species in the preliminary report on this study (Hobson, 1980) based on its numbers in one transect in the lagoon at Kure atoll.] C. ignobilis is coveted by both spearfishermen and shore fishermen and is especially vulnerable to the former owing to its boldness. Fishing would seem to have had a major influence on the observed distribution of C. ignobilis. In contrast to its extreme prominence from Nihoa northwestward to Kure, it was never observed in the major high islands during this study. On other occasions in the high islands, sightings have been infrequent and usually involved solitary individuals.

ACKNOWLEDGMENTS

I thank Richard Shomura and his staff -- especially Richard Uchida, Robert Skillman, and Alan Everson -- 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, Waikiki Aquarium; Richard Coleman, U.S. FWS, Honolulu; and James Parrish, Cooperative Fishery Unit, U.S. FWS. Finally, James R. Chess and Dan Howard, Southwest Fisheries Center Tiburon Laboratory, were capable diving partners during many of the observations.

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