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MAINTENANCE OF HIGH DIVERSITY IN CORAL REEF
FISH COMMUNITIES

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The high diversity typical of tropical communities has been of interest for some time (Fischer 1960; Connell and Orias 1964; MacArthur 1965, 1969; Paine 1966; Pianka 1966; Whittaker 1969). Colwell (1973), remarking on the causes of this high diversity, pointed to “rather general agreement on theoretical grounds that tropical species should be more specialized ecologically than species at higher latitudes.” He may have overstated the degree of consensus, since a number of alternative hypotheses have been proposed and not all of them predict greater specialization in the tropics (see summaries in Krebs 1972; MacArthur 1972; McNaughton and Wolf 1973; Pianka 1974). Pianka (1974) provides a table of 10 hypothetical mechanisms for increasing diversity. Of the 10, five act by reducing niche breadth, and two others act by allowing greater resource overlap and competition among coexisting species. A fair statement of the current consensus is that the tropical community is a mature equilibrium community of numerous species whose coexistence is satisfactorily explained in the theory based on Lotka-Volterra competition and predation equations. This “equilibrium view” takes no account of environmental change or patch structure and emphasizes ways of efficiently partitioning resources.

This view of the tropical community has developed through theoretical considerations of resource partitioning (e.g., MacArthur and Levins 1967; Roughgarden 1974; Roughgarden and Feldman 1975) and through field investigations, primarily of terrestrial biota, particularly birds (Diamond 1973; MacArthur 1969), but including insects (Janzen 1973) and forest trees (Janzen 1970; Whittaker 1969). This emphasis on terrestrial groups might be expected to make it a view which most accurately describes the tropical rain forest. However, not all scientists working in rain forest communities accept it (e.g., Connell 1971).

While we know little about rain forests, we know still less about coral reef communities. Until recently, Kohn's (1959, 1968, 1971) data represented practically the only thorough study of resource partitioning in an assemblage of coral reef species. They showed a high degree of specialization and little overlap in food requirements of coexisting species of *Conus*, an important genus of reef gastropod. These results are consistent with the view that tropical communities are comprised of numerous specialist species effectively dividing

the resources available, and in the absence of information to the contrary it has seemed best to assume that coral reef communities are organized in this way.

In fact, the limited data now available on reef fishes appear not to support the equilibrium view. Inasmuch as reef fishes may be representative of other reef fauna, these data must force us to reconsider the maintenance of high within-habitat diversity in the coral reef community. Current data indicate that many reef fishes do not finely partition resources of food or living space, that they are often, if not usually, limited by the supply of suitable living space, and that they live in an environment which, with respect to the supply of living space, is unpredictable in time and space. This paper is an attempt to bring together and evaluate these data and to reexamine in their light the maintenance of high within-habitat diversity in reef fish communities. The conclusions reached here can only be tentative, but my hope is that they will stimulate a search for more data and experimental tests of the proposed hypotheses.

REEF FISHES—HIGH DIVERSITY AND HIGH NICHE OVERLAP

That reef fish communities are diverse is well known (Bakus 1966; Smith and Tyler 1972; Talbot and Goldman 1972). For example, the numbers of species on the Great Barrier Reef range from 1500 in the north to 900 at One Tree Reef close to the southern limit of reef development.

Part of this high diversity is of a between-habitat type, since reef fishes tend to be sedentary and, to a limited extent, habitat specialists. Nevertheless there remains a high diversity within habitats. For example, Smith and Tyler (1972) reported 53 resident species and a total of 75 species ($H'_{[\text{base E}]} = 3.3$) on a single patch reef approximately 3 m in diameter and 1.6 m high. Smith (1973) collected up to 67 species in single small rotenone samples in the Bahamas. Goldman and Talbot (1976) cite collections from single rotenone stations which contained 150 (One Tree Reef) and 200 (Palau) species of fish. Coexistence of such large numbers of species of fish on a small area of reef demands explanation. An attempt at explanation might begin with an examination of the degree of specialization and pattern of resource partitioning among coexisting species of reef fish.

If reef fishes are predominantly specialists which finely partition the resources available to them, it follows that an examination of their use of the major resources of food and habitat should disclose two things. Most species will be relatively narrow niched (i.e., specialized) with respect to one or both of these resource categories. More important, they will be specialized upon different resources, exhibiting low overlap in their use of food or habitat space. Some species may be more generalized, but these would be expected to be in the minority. As will be shown below, however, the degree to which reef fishes are narrow niched and nonoverlapping in requirements is not great. It appears insufficient to account completely for their high diversity within habitats.

General feeding habits of reef fishes have been examined by Hiatt and Strasburgh (1960) and Randall (1967). Bakus (1969) has reviewed feeding

processes in shallow marine waters. Herbivorous fishes, uncommon outside coral reef communities, comprise roughly 22% by weight and a similar percentage of species of reef fishes (Bakus 1966). They are notably generalists in their feeding habits. Choat (1969) could find no differences in foods taken by Scaridae on Heron Reef, Great Barrier Reef; Jones (1968), although emphasizing those differences which did exist, found few differences in foods taken by Acanthuridae in Hawaii. In both of these major families of herbivores, individuals feeding in the same place take the same foods, and multispecies feeding schools are commonly seen.

Predatory and omnivorous species are somewhat more specialized in diet. Roughgarden (1974) used Randall's (1967) data to demonstrate partitioning by food particle size in the Serranidae, and Vivien and Peyrot-Clausade (1974) have demonstrated a partitioning of prey by taxonomic category among three species of Holocentridae. Nevertheless it remains true that differences between the foods of coexisting, related species are usually minor (see Hiatt and Strasburg 1960; Vivien 1973), and the degree of partitioning of food resources demonstrated in *Comus* (Kohn 1959) has not been approached in any study of an assemblage of reef fishes.

Bakus (1969) compared several species of Labridae and claimed that tropical species were more specialized in diet than closely related temperate ones. His measure of niche breadth yields low values (high specialization) when small proportions of the sample of fishes examined contain each type of food, even if many different types of food are taken. Considering this bias, the small number of species examined, and the relatively slight difference in niche breadth demonstrated between tropical and temperate forms, his data can only be taken as suggestive. They urgently require substantiation.

There are a few pronounced food specialists among reef fishes, just as there are fish which feed upon items not available to fish in the temperate zone. Their existence should not be permitted to detract from the fact that the majority of reef fishes are generalist feeders. Even among the food specialists it is common for two or three sympatric species to show nearly identical specialization, thus overlapping greatly in the foods they consume (table 1). This would not be expected if the specializations had evolved as a means of partitioning the food resources available and suggests instead that those food sources specialized upon are in abundant supply.

A fine partitioning of living space appears, at first, a more likely characteristic of reef fishes. They are predominantly sedentary animals. Bardach (1958), Reese (1973), and Springer and McErlean (1962) have provided data on the range of movements of many species. Smith and Tyler (1972) provided estimates of the area used (none greater than 7 m radius) by individuals of 63 species, although individuals of 12 other species ranged more widely. Russell et al. (1974) have listed 58 of 85 species which colonized their artificial reefs as residents. Resident fish restricted their movements to the immediate vicinity of a single reef, $1.6 \times 0.6 \times 0.6$ m in size. Ogden and Buckman (1973) demonstrated that the apparently wide-ranging feeding schools of *Scarus croicensis* restricted their movements to about $\frac{1}{2}$ hectare of a reef and that their membership included

TABLE 1
 SOME REPRESENTATIVE EXAMPLES OF GROUPS OF SYMPATRIC REEF FISHES WHICH ARE FOOD SPECIALISTS WITH
 SIMILAR DIETARY SPECIALIZATIONS

Species in Group	Comments	Source
<i>Holacanthus ciliaris</i> , <i>H. tricolor</i> , <i>Pomacanthus arcuatus</i> , <i>P. paru</i> , <i>Cantherines macrocerus</i>	Sponges comprise at least 70% of diet of all species; all consume a wide range of species of sponge.	Randall and Hartman 1968
<i>Chaetodon citrinellus</i> , <i>C. lunula</i> , <i>C. trianguulum</i> , <i>C. trifasciatus</i> , <i>Megaprotodon strigangulum</i>	All feed principally upon polyps of <i>Acropora</i> spp. <i>M. strigangulum</i> and <i>C. trianguulum</i> defend feeding territories where they coexist with <i>C. trifasciatus</i> at Heron Reef <i>M. strigangulum</i> , <i>C. lunula</i> and <i>C. citrinellus</i> occur together at Eniwetok Atoll	Reese 1973 Hiatt and Strasburg 1960
<i>Epibulus insidiator</i> , <i>Gomphosus varius</i>	Both adapted (though in different ways) to feed upon crustacea found within ramose coral heads	Hiatt and Strasburg 1960
<i>Labroides bicolor</i> , <i>L. dimidiatus</i> , <i>L. rubrolabiatus</i>	All are exclusively "cleaner" species which coexist in the Society and Tuamotu Islands, where they were seen occupying the same cleaning station <i>L. bicolor</i> and <i>L. dimidiatus</i> were observed with contiguous cleaning areas at Heron Reef	Randall 1958 Robertson 1974

individuals that successively joined and then departed from the school, remaining members only while the school traversed their own home sites of up to 50 m².

Such sedentary habits are conducive to the development of narrow habitat requirements by reef fishes, especially when one considers the diverse array of habitats provided on a coral reef. As habitat specialists, reef fishes could finely partition the living space available to them as long as each species used a slightly different type of space.

Habitat partitioning does occur, to the extent that few species of reef fish occur over all regions of a reef. Thus it is profitable, as has long been recognized, to list the species likely to occur in broadly defined habitats such as "surge channel" and "reef flat" (see Choat 1969; Fishelson et al. 1974; Hiatt and Strasburg 1960; Jones 1968; Talbot and Goldman 1972). The resulting lists are lengthy, and little further separation of species is attained by a finer resolution of habitats. Clarke has recently quantified habitat overlap for pomacentrid and chaetodontid fishes near Bimini. Despite clear partitioning of space by fish, five of the eight habitats examined each contained 17 of the 22 species recorded, leading him to conclude that coexistence must largely be explained by factors which operate within habitats (Clarke, in press).

When we examine the space requirements of fish which coexist within these broadly defined habitats, we do not find, as a general rule, a high degree of specialization on microhabitats and a resulting fine partitioning of living space. A small minority of primarily inquiline forms are highly specialized and are discussed below, but the species listed in table 2 are representative of the majority of species for which data exist. Consider, for example, *Dascyllus aruanus* with a home range of only 1 m radius. It requires living branched coral adjacent to a patch of sand, yet on Heron Reef it uses 12 species from four genera of coral and sand patches from at least a 15-m depth on the reef slope, to the reef flat, and lagoonal patch reefs (Sale 1970, 1971a). It is easy to visualize many ways in which this sedentary species might have developed more specialized requirements. Yet it has not and coexists with several other species with similar habitat needs.

An alternative approach to the question of how specialized the space requirements of reef fishes are is to compare them with fishes of temperate rocky shores. Adopting this approach entails an obvious danger in trying to compare the degree of specialization of species from different places (the koala-opossum paradox of Colwell and Futuyma 1971), and furthermore, quantitative data are sparse. The data in table 3 are representative of what is available for temperate species. I suggest that the reef fishes in table 2 are not notably more specialized in requirements for space than the temperate shore fishes in table 3, but a definitive statement must await a comparative study of reef and temperate communities.

As noted above, there are a minority of species on reefs with highly specialized habitat needs, especially among fish with inquiline habits. Yet, just as feeding habits of sympatric food specialists may coincide, the habitat requirements of coexisting habitat specialists often overlap greatly (table 4). The partitioning

TABLE 2
SOME RECENT ATTEMPTS TO CHARACTERIZE THE HABITAT REQUIREMENTS OF PARTICULAR REEF FISHES (Compare with Table 3)

Species	Known Requirements	Source
<i>Acanthuridae</i> (20 spp).....	Assigned to midwater, surge zone, sand patch, and submerge reef habitats	Jones 1968
<i>Acanthurus triostegus</i>	Juvenile requires shallow water, cover within 1 m, and algal food on the substratum	Sale 1969
<i>Dascyllus aruanus</i>	Requires living, branched coral (12 spp. at Heron Reef) adjacent to sand patch, and 0-15 m depth of water	Sale 1970, 1971 ^a
<i>D. trimaculatus</i>	Shelters among large coral boulders of many species, in shallow water; juveniles also use anemone, <i>Gyrostoma</i> , and sea urchin, <i>Diadema</i>	Fricke 1973
<i>Pomacentrus flavicauda</i>	Require dead coral rubble interspersed with sand; occurrence is correlated with amount of rubble-sand interface	Low 1971
<i>Opistognathus aurifrons</i>	Build burrows in substratum which must contain rubble mixed with sand; within 1 m of rock outcrops, 2-50 m depth	Colin 1973

TABLE 3
 EXAMPLES OF HABITAT REQUIREMENTS HELD BY TEMPERATE MARINE FISHES

Species	Known Requirements	Source
<i>Chromis dispilus</i>	Aggregate above rocky outcrops or cliffs in 10-30 m depth; nest sites on smooth even rocky surfaces	Russell 1971
<i>Hyppypops rubicunda</i>	Favor high-relief rocky substrata in 0-20 m depth, use large holes or crevices for shelter	Clarke 1970
<i>Crenilabrus melanocercus</i>	Occurred in 15-18 m depth at foot of cliff where <i>Posidonia</i> covered slope commenced	Potts 1968
<i>Hyppoblenius gilberti</i> , <i>H. jenkinsi</i> , <i>H. gentilis</i>	<i>Gilberti</i> occurs from intertidal to 5 m depth over any hard substratum; <i>jenkinsi</i> occurs subtidally to 10 m, using holes or small crevices; esp. pholadid burrows, <i>Serpulorbis</i> masses and fouling masses; <i>gentilis</i> at intermediate depths, usually subtidal, most common in <i>Mytilus</i> beds	Stephens et al. 1970
<i>Paralabrax clathratus</i>	Requires some bottom relief whether provided by rock, kelp, or debris; ranges 0-30 m depth	Quast 1968
<i>Chasmodes bosquianus</i>	Shelter enclosures must have a somewhat restricted opening and firm walls, dead oyster shells the most common shelter	Phillips 1971

TABLE 4
 EXAMPLES AMONG REEF FISHES OF COEXISTING HABITAT SPECIALISTS

Species	Comments	Source
<i>Evermannichthys metzelaari</i> ,	Obligate sponge-dwelling gobies collected from same 5 specimens of <i>Sphaecio-spongia vesparia</i> ; <i>E. metzelaari</i> occurred only in that species	Tyler and Bohlke 1972
<i>Pariah scotius</i>		
<i>Gobiosoma chancei</i> , <i>G. horsti</i> ,	All are obligate sponge dwellers; <i>G. horsti</i> and <i>P. xenus</i> were collected from the same chimneys of specimens of 2 species of sponge; <i>G. chancei</i> occurred in the same specimens of a third species of sponge as <i>P. xenus</i> and as <i>R. ruber</i> but not in the same chimneys	Tyler and Bohlke 1972
<i>Risor ruber</i> , <i>Phaeoptyx xenus</i>		
<i>Amphiprion chrysopterus</i> ,	Obligate commensals of anemones, all occur at Eniwetok Atoll where <i>A. tricinctus</i> occupies both species used by <i>A. melanopus</i> , and 2 of 3 used by <i>A. chrysopterus</i>	Allen 1972
<i>A. melanopus</i> , <i>A. tricinctus</i>		
<i>Gobiodon ceramensis</i> , <i>G. erythrospilus</i> ,	Obligate commensals of living branched corals, all were collected from <i>Acropora corymbosa</i> more often than from other species, and overlapped extensively in the other species in which they occurred	Tyler 1971
<i>G. histrio</i> , <i>G. quinquestrigatus</i>		

of living space is not achieved by the coexistence of specialists that are specialized on the same types of space.

It is surprising that reef fishes have failed to partition their habitats more finely than their foods, because there is considerable evidence that reef fishes are far more likely to compete for suitable space than for food (Smith and Tyler 1972). For example, sea grasses away from the shelter of reef outcrops in Puerto Rico are not grazed by reef fishes (Randall 1965), and fish are rapidly recruited to artificial reefs established in reef lagoons (Russell et al. 1974). The refilling of space when territorial (Low 1971; Sale 1974, 1975), or nonterritorial (Sale and Dybdahl 1975) fish are experimentally removed, and the existence, in at least one species, of behavioral mechanisms which achieve an efficient dispersion of individuals over the available habitat (Sale 1972*a*, 1972*b*) all suggest that suitable space is important and frequently limiting. Species vary in the degree to which the individual maintains exclusive occupancy of a living site. Many fish require only a suitable shelter site within which they sleep, while some carry on all activities within a territory from which their own or many species may be excluded.

Because of the high overlap in habitat and food requirements among many reef fishes, the concept of a guild (Root 1967) is useful. A guild is a group of species which use the same environmental resources in similar ways. The members of a guild of reef fishes may be spatially separated to some extent, but the high diversity of fish within reef habitats derives from the simultaneous presence of two or three species of each of a number of guilds sharing their common space and food resources. Examples of guilds where habitat overlap is known to occur are listed in table 5.

The guild of territorial Pomacentridae present on Heron Reef (Sale 1974) can serve as an example. Some spatial separation exists among its eight members, but at least three species are potentially resident on any site suitable for this guild, and six species can come into contact on the reef crest. Most information is available for the three species which occur on the upper reef slope. These are *Eupomacentrus* (= *Pomacentrus*) *apicalis*, *Pomacentrus wardi*, and *Plectroglyphidodon* (= *Abudefduf*) *lacrymatus*. Within rubble patches on the upper slope, all available space is occupied by a series of contiguous and usually nonoverlapping territories held by individuals of these three species. All individuals hold territories throughout juvenile and adult life. When fishes die the vacated space is rapidly refilled by residents and by new colonists. A site within a rubble patch can be used by any of these three species, and I have found no tendency for space initially held by one species to be taken up, following mortality, by the same species. There is no evidence of a successional sequence of ownership of a site by the three species in turn (Sale 1975), nor have I yet detected any differences between *E. apicalis* and *P. lacrymatus* in abilities to capture space and to hold onto space once gained. *Pomacentrus wardi* shows higher rates of recruitment and mortality in rubble patches and uses a refuge in nonpreferred space off rubble patches to maintain its occupancy of space inside rubble patches in the face of competition with the other two species (Sale 1974, 1975). Even the differences in competitive ability between *P. wardi* and

TABLE 5
 EXAMPLES OF GUILDS OF REEF FISHES WITHIN WHICH SOME DEGREE OF HABITAT OVERLAP IS KNOWN TO OCCUR

Species in Group	Comments	Source
<i>Acanthurus</i> (12 spp), <i>Ctenochaetus</i> (2 spp), <i>Naso</i> (4 spp), <i>Zebrasoma</i> (2 spp)	20 species of Acanthuridae from Hawaii and Johnston Islands fall into 3 guilds based on foraging methods; there is extensive habitat overlap in all guilds; heterotypic feeding schools common	Jones 1968 (see also Barlow 1974)
<i>Scarus</i> (15 spp)	All species forage on the reef slope at Heron Reef; at least 5 species forage in each of the other habitats recognized; heterotypic schools are common and may include Acanthuridae and Siganidae	Choat 1969
<i>Glyphidodontops</i> (<i>Abudefduf</i>) <i>biocellatus</i> , <i>Plectroglyphidodon</i> (<i>A.</i>) <i>lacrymans</i> , <i>Eupomacentrus</i> (<i>Pomacentrus</i>) <i>apicalis</i> , <i>E. (P.) fasciatus</i> (<i>jenkinsi</i>), <i>E. gascoynei</i> , <i>Pomacentrus bankanensis</i> (<i>dorsalis</i>), <i>P. flavicauda</i> , <i>P. wardi</i>	All are territorial herbivores on coral rubble substrata at Heron Reef; territories are defended interspecifically; <i>P. wardi</i> occurs wherever any member of the guild might occur; the other 7 species are partially spatially separated but at least 3 species may occur at any rubble patch	Sale 1974
<i>Chromis atripectoralis</i> , <i>C. caeruleus</i> , <i>C. dimidiatus</i> , <i>C. lepidolepis</i> , <i>C. leucurus</i> , <i>C. ternatensis</i>	All are midwater planktivores which hover 1-2 m above the substratum while feeding; heterotypic feeding schools of at least 3 species occur at Eniwetok Atoll; <i>C. atripectoralis</i> and <i>C. caeruleus</i> are nearly identical in ecology, as are <i>C. dimidiatus</i> and <i>C. leucurus</i>	Swerdlhoff 1970
<i>Chaetodon triangulum</i> , <i>C. trifasciatus</i> , <i>Megaprotodon strigangulum</i>	All feed on coral polyps and maintain feeding territories or home ranges on the Heron Reef slope	Reese 1973
<i>Holocentrus diadema</i> , <i>H. lacteoquittatus</i> , <i>H. scythrops</i> , <i>H. spinifer</i> , <i>H. xantherythrus</i> , <i>H. tere</i> , <i>Holotrachys lima</i> , <i>Myripristis argyromus</i> , <i>M. berndti</i> , <i>M. multiradiatus</i>	All are nocturnal predators feeding upon a wide range of invertebrates; some species are morphologically very similar; all were taken in one or both collections made in 8-12 and 10-25 m water in Hawaii; heterotypic schools occur	Gosline 1965

NOTE.—That these guilds each contain species from a single family may indicate the approach of the investigator rather than the true extent of the guild. Roughgarden (1974) has discussed a scarid-acanthurid guild.

the other two species are minimal, and I have observed newly settled juveniles of all three species maturing while surrounded by adults of the other species (Sale 1974). Coexistence of the three species on rubble patches is thus maintained despite virtually identical space requirements and, for two of them, nearly identical ability to acquire and hold space.

To summarize, all of the data presented above suggest that reef fishes are habitat specialists to the extent that broadly defined habitats on a reef contain different assemblages of species. Within habitats, however, reef fishes, with few exceptions, do not show extreme specialization with respect either to food or to space requirements. Furthermore, those few species with highly specialized requirements often coexist with other species showing the same specializations. Characteristically, several members of each guild of fishes coexist in the same habitat, often foraging in the same places at the same time. There is evidence that living space, in particular, may be limiting to reef fish populations, yet competition for space has not resulted in a fine degree of partitioning of space among the species present.

It is not a necessary requirement of the equilibrium view that reef species finely partition the resources available. Theoretical studies indicate that more overlap in resource requirements may be tolerated in tropical communities if coexisting species have leptokurtic resource utilization curves (Roughgarden 1974) or if predation is more intense (Roughgarden and Feldman 1975). No field data exist to indicate that either of these possibilities applies in reef communities, and other theoretical work rules out the possibility that overlap can be greater in the tropics simply because environmental conditions are less variable there (May and MacArthur 1972). The data considered in the remainder of this paper provide strong support for an alternative view.

THE REEF ENVIRONMENT—BENIGN BUT UNPREDICTABLE

Conditions in an environment vary. Environments can be severe, showing large variations in conditions, or they can be benign, showing only slight variations. The changes in conditions will be patterned in a predictable environment and without pattern in an unpredictable one. While severity and predictability may be correlated (Slobodkin and Sanders 1969), it is best to consider them as separate attributes.

Variations in environmental conditions may occur temporally or spatially and on a larger or a smaller scale. Reef fishes, because they are sedentary and have life spans of 1 to several years, will be most influenced by small-scale spatial (over meters rather than kilometers) and temporal (over months or years rather than decades) changes. There is evidence that, on this scale, the reef environment is both spatially and temporally unpredictable in topography, despite being a generally benign environment.

A considerable small-scale spatial patchiness is evident on reefs primarily because of the differing growth forms of various species of coral. In addition, living coral is interspersed with a variety of other substrata. Superimposed upon this small-scale patchiness is a larger-scale pattern: the topographic

zonation to which considerable attention has been given in the past (see Stoddart 1969*a*). This zoned pattern is quite coarse. For example Loya and Slobodkin (1971) recognized only six zones to a depth of 30 m at Eilat, Red Sea. To date a zoned pattern has not been demonstrated on the small scale where topographic variation is due principally to the presence of corals of differing form. It is this unzoned small-scale variation which influences reef fishes.

A variety of temporal changes occur on reefs which have a direct effect on the availability of particular types of living space for fishes. Many of these changes are unpredictable in time of occurrence and affect only a small area of reef. Growth processes of the corals themselves change the relative availability of particular kinds of living space. These changes are predictable, but they are frequently and unpredictably interrupted by events causing destruction of coral. Small-scale changes due directly or indirectly to wave action include the breaking off or turning over of colonies or parts of colonies, silting, and the shifting of sand or unconsolidated rubble. In addition, competition with other corals (Lang 1970), and the action of borers and other coral predators have an important effect. Connell (1973) has documented such small-scale changes for corals at Heron Reef.

Changes on a larger spatial scale, which remain unpredictable temporally, are produced by cyclonic storms. The varied effects of storms have been documented by Stoddart (1969*b*), Glynn et al. (1964), and Connell (1973). Physical abrasion of coral cover, rolling and tossing of coral boulders, and extensive movements of sand and rubble all cause pronounced changes to the small-scale topography over large portions of an affected reef.

The changes considered so far affect the availability of living space by directly creating or destroying habitat. Those brought about by storms and wave action must have their most pronounced effects on the shallower parts of a reef. Those due to biotic factors will be most important in the deeper, less physically disturbed regions. However, another type of change may be more important in all habitats than any of these. Predators of reef fishes affect the availability of living space by releasing space for reoccupancy. Predators may hunt in particular habitats and at particular times of day, but as far as the prey fishes are concerned the time and place of capture of each food item is unlikely to be predictable. And the removal of one prey fish creates a vacant living space of a particular type.

ADAPTATIONS TO AN UNPREDICTABLE SUPPLY OF SPACE

Observations on the life cycles of reef fishes provide evidence compatible with the claim that the unpredictability of the supply of living space is important to them. In a situation in which the supply of living space is limiting and vacant living space is generated unpredictably in space and time, the production of numerous offspring scattered widely in space and time appears to be the only satisfactory way of getting some offspring successfully to living sites. Similarly, successful offspring should stay put. (Selection for offspring with the ability to oust prior residents from suitable space might be an alternative possibility, but

since this has not occurred among reef fishes, discussion of this point is deferred until later).

In fact, with very few exceptions, reef fishes are sedentary animals which breed often, producing numerous clutches of dispersive eggs or larvae. Breeding seasons are long, if not year round, and individuals breed frequently during the season. Munro et al. (1973) have documented the times of occurrence of reproductive ripe fish for 83 species off Jamaica. In many of these there is a pronounced peak of activity in February and March, but extended seasons are usual, and in some cases (e.g., Pomadasyidae, Lutjanidae, *Abudefduf saxatilis*) ripe fish are present throughout the year. Their data do not permit determining the frequency of spawning by individuals, but I would expect multiple spawning to occur in most cases. *Labroides dimidiatus*, whose adults breed every day just after high tide for 7 months at Heron Reef (Robertson 1974) represents an extreme, but data on a number of other species are listed in table 6. The extended seasons and the frequent clutches by each individual are the strongest evidence that these life cycles are in response to the unpredictability of the supply of living space in the reef environment. There could be other reasons for producing dispersive larvae.

The larvae of reef fishes are presumably dispersed by means of currents. To this extent, dispersal is not unpredictable. It remains, however, beyond the control of the adult population. Larval life may last as long as 2½ months (*Acanthurus triostegus*, Randall 1961) and usually for at least a week, so that offspring can be dispersed widely.

As noted earlier, reef fishes do not often have highly specialized habitat requirements. Perhaps the necessity of finding living space provided so unpredictably precludes narrowing of the choice by development of stringent space requirements. Thus, despite a shortage of space, reef fishes are seldom extreme space specialists, and the result is that guilds exist with similar requirements for space.

MAINTENANCE OF HIGH DIVERSITY WITHIN HABITATS

The data summarized in the preceding pages demonstrate that most reef fishes are closely tied to the substratum and require living sites on a reef and that the supply of living space is often short and is in any event unpredictable. The fish succeed in obtaining this unpredictably supplied resource by (1) dispersing numerous pelagic larvae widely, both in space and time, so as to maximize chances of getting some offspring to suitable space; (2) having requirements for space that remain general enough for there to be some chance of finding a suitable site; and (3) remaining in a site, once found, for extended periods or throughout adult life. But as a result, guilds of reef fish exist with similar requirements for space. Competition within guilds for space can be expected to occur and is well documented in one case (Sale 1974, 1975). It is not immediately clear how diversity within reef habitats is maintained under these circumstances.

TABLE 6
 PATTERNS OF REPRODUCTION IN SOME REPRESENTATIVE REEF FISHES

SPECIES	DURATION OF SEASON (Months)*	FREQUENCY OF SPAWNING BY INDIVIDUAL	PELAGIC LIFE†		SOURCE
			Eggs	Larvae	
Pomacentridae:					
<i>Amphiprion chrysopterus</i>	9 ^a	Monthly	No	Yes	Allen 1972
<i>Acanthochromis polyacanthus</i>	4 ^b	?	No	No	Robertson 1973
<i>Chromis caeruleus</i>	8 ^b	Up to twice per week	No	Yes	Sale 1971 ^b
<i>Glyphidodontops biocellatus</i>	2 ^b	Each 2 weeks	No	Yes	Keenleyside 1972
<i>A. saxatilis</i>	5 ^c	Multiple	No	Yes	Fishelson 1970
<i>Eupomacentrus partitus</i>	12 ^d	Multiple	No	Yes	Myrberg 1972 ^a
Labridae:					
<i>Crenilabrus</i> (8 spp)	? ^e	Weekly	No	Yes	Fiedler 1964
<i>Thalassoma bifasciatum</i>	12 ^d	Many times during year	Yes	Yes	Feddern 1965
24 species in family	(most spp) ^b	Multiple	Yes	Yes	Choat 1969
Labroides dimidiatus					
	7 ^b	Daily	Yes	Yes	Robertson 1974
Scaridae:					
<i>Scarus</i> (15 spp)	6 ^b	Multiple	Yes	Yes	Choat 1969
<i>Sparisoma rubripinne</i>	12 ^f	?	Yes	Yes	Randall and Randall 1963
<i>Acanthurus triostegus</i>	8 ^g , 12 ^a	Multiple	Yes	Yes	Randall 1961
Gobiidae:					
<i>Gobiosoma oceanops</i>	5 ^d	2-3 times per month	No	Yes	Valenti 1972

NOTE.—Species selected are from five of the most important families in numbers of species on reefs. Except for the Acanthuridae, there is considerably more information available on species of these families than is listed. However, I know of no species other than *Acanthochromis polyacanthus* without pelagic larvae. Pomacentridae have been particularly well studied (see Fishelson et al. 1974; Reese 1964; Russell 1971), but they are one of few families (others are Apogonidae, Gobiidae, Blenniidae) with demersal eggs. Breder and Rosen (1966) indicate that extended seasons and pelagic eggs are usual among reef fishes, but little further information exists for most families. Observation sites are shown as follows: a = Eniwetok, b = Heron Reef, c = Eilat, d = Florida, e = Naples, f = Virgin Islands, g = Hawaii.

* Duration of season varies with latitude.
 † Duration of larval life has been determined as 2½ months in *Acanthurus triostegus* (Randall 1961). Morphology of newly hatched larvae in many forms indicates a minimum of ½ to 1 month larval life.

I believe the maintenance of the high diversity of reef fish communities is a direct result of the unpredictability of the supply of living space. This unpredictability has forced fish to adopt the strategy of producing numerous, highly dispersive larvae, and therefore the recruitment of young to any place on a reef is largely independent of the composition of the population of adult fishes already there. Because of the requirement that they be numerous and dispersive, the young recruited are small, frail organisms unlikely to be very good at ousting other residents from spaces they hold. It is a measure of the unpredictability of the reef environment that no fish has evolved the production of a clutch of one or two nondispersive, but competitively superior, space-grabbing larvae. When colonists of two species of a guild compete for space it is probably a competition in which no particular species is favored. Instead, each interaction that occurs is likely to be decided in favor of the prior resident—the individual which is already at home has a psychological advantage (Braddock 1949; Frey and Miller 1972; Greenberg 1947; Myrberg 1972*b*; Phillips 1971), and frequently a size advantage, in any struggle. Thus, the species of a guild are competing in a lottery for living space in which larvae are tickets and the first arrival at a vacant site wins that site. The lottery operates within habitats and at the level of the individual fish. Single vacant sites are unpredictably generated and are filled by individual colonists, to be held until these fish also disappear and are replaced by new colonists of their own or of other species. In this lottery, there is no reason to expect that the number of chances at winning—that is, the number of larvae seeking to settle—will be closely correlated with the size of the population of adults of a species present in an area. Fisheries biologists find either no correlation or a very weak one between numbers of recruits to a fishery and the size of the adult population (Beverton and Holt 1957; Cushing 1973). Thus, chance successes by one species need not lead to that species progressively usurping all living spaces within habitats of that type from other species in the lottery.

That chance processes are important in allocating space among species coexisting within habitats does not imply that there is no pattern to the distribution of fishes over the reef. As discussed above, reef fishes are habitat specialists on a broad scale, and we can expect that newly settling larvae of each species will show appropriate habitat preferences. Each species competes in only some of the many lotteries operating for different kinds of living sites in different habitats on a reef.

A different sort of competition may develop between residents if, as they grow in size, they require larger living spaces. Fish which maintain exclusive use only of a shelter site may have to move to larger quarters, and territorial forms might have to increase the size of the area defended. In both circumstances, certain species may consistently win over others of their guild, but several factors act to prevent this competition from becoming very lopsided. For example, all residents will have the psychological advantage of being at home when neighbors attempt to encroach upon them, and smaller individuals may use the topography of their home sites by seeking shelter in places inaccessible to larger neighbors rather than fleeing from the area. In any event, this com-

petition is for space for an individual—space that will become vacant again as soon as that individual dies.

In those guilds whose member species are morphologically quite similar, it is likely that the advantage of being at home will be sufficient to ensure that residents of any species usually outcompete invading individuals. However, even in guilds in which considerable morphological or behavioral differences exist between member species, the competitively inferior species may be able to survive by adopting a fugitive strategy. *Pomacentrus wardi* makes use of a fugitive strategy to coexist with the competitively superior members of its guild (Sale 1974, 1975). So long as all species of a guild win some of the time and in some places, they will continue to put larvae into the plankton and hence into the lottery for new sites.

As intimated above, data concerning the coexistence of *P. wardi* and other members of its guild (Sale 1974, 1975) are fully compatible with this lottery hypothesis. In addition, recent study of another guild provides further support for the concept. A wide range of species of fish on Heron Reef makes use of the interstices in living or dead coral as shelter. Isolated coral colonies are occupied by small groups of resident fishes belonging to several species. A study of the patterns by which species of fish were distributed among colonies of coral (Sale and Dybdahl 1975) indicated that chance was the principle determinant of species composition within single colonies of coral. These results indicate that the lottery hypothesis has validity for species that are not strictly territorial.

There are many similarities between the lottery hypothesis presented here, and the theory of island biogeography (MacArthur and Wilson 1967). In both systems the species composition of a single patch of habitat is a function largely of chance colonization and chance extinction, while the diversity within patches depends, in addition, on the species richness of the region that serves as a source of colonists—the mainland source area in island theory, and the totality of patches of similar type in the lottery system. However, one major difference exists between these systems. In the lottery system there is no provision for population growth within patches of habitat other than through colonization of the patch by additional individuals of the same species. All reproduction by residents is exported to other patches, and the analogues of immigration and extinction of species in island theory are the colonization and loss of individuals in the lottery hypothesis. In addition, the patches considered are smaller and more ephemeral than those considered in island theory.

This system of lotteries for space has many points in common with those mechanisms believed to explain the maintenance of diversity in other potentially space-limited communities. Considerable information now exists concerning the sessile fauna of the rocky intertidal zone (Connell 1961*a, b*; Dayton 1971). Much importance had been placed on predation by starfishes in maintaining the diversity of this community (Paine 1966, 1971), but this predation is only one of several ways in which vacant living space is generated here. Dayton (1971) has pointed to the importance of drifting logs in creating living space on some coasts, and it appears that the important characteristic is that, as on the coral reef, the production of new living space is unpredictable. Fager (1971) has

emphasized the importance of chance patterns of settlement in determining the diversity and structure of communities on fouling plates, and Porter (1972) has suggested that predation by *Acanthaster* and other unpredictably timed events maintain the diversity of corals on reefs on the Pacific coast of Panama by generating vacant space.

Levins and Culver (1971), Horn and MacArthur (1972), Levin (1974), and Slatkin (1974) have all recently examined the theory of interactions of competing species in a patchy environment. While there are important differences in the assumptions of their various models, all are agreed that in some cases in which it would not be possible in a homogeneous environment, the coexistence of quite similar species is permitted in patchy environments because of migration between patches. Levins and Culver (1971) and Horn and MacArthur (1972) considered the survival of a competitively inferior, fugitive species in the presence of a superior competitor. For the fugitive to survive, its rate of successful migration between patches must be greater than the rate of extinction of its populations within patches. Rate of extinction is higher in those patches occupied by the superior species. Horn and MacArthur (1972) point to the interesting case in which two different sorts of patch existed. Here, coexistence is sometimes possible even when the fugitive is inferior to its competitor in both types of patch. Horn and MacArthur (1972) state that it is possible to build up a community of fugitives so long as each species has a rate of migration between patches that is greater than that of any species competitively superior to it. Their assumption of random migration between patches seems likely to be applicable to the reef environment. For communities of fugitive species, the limit on the number of species is reached when migration rates become great enough that the environment ceases to be treated as patchy. The limit is higher in environments in which rates of extinction of local populations are greater. Slatkin (1974) modified the model of Levins and Culver (1971) to remove the assumption that species were independently distributed among habitat patches. His model predicts that similar species can never exclude each other from a region made up of patches between which migration occurs. If the species differ sufficiently for one to exclude the other from the region, the system is determinate in the sense that there is no possibility of a priority effect whereby the first species to invade the region can always exclude the other.

Levin (1974) considered the survival of species similar enough that, once established in a patch, either could prevent the colonization of that patch by the other species. Again, migration between patches did not prevent coexistence, although his model tolerates less migration than that of Slatkin (1974). Levin points out that it is the patchy quality of the environment, rather than the number of kinds of patch, that permits coexistence.

The results of Horn and MacArthur (1972) and Slatkin (1974) in particular seem applicable to the coral reef environment and may provide a basis for a numerical treatment of the lottery hypothesis. The life histories of reef fishes are such that migration between patches occurs at each generation, and the variety of small-scale disturbances on reefs makes extinction rates of local

populations (i.e., within patches) high. These important facets of the ecology of reef fishes are ignored in the more classical theories supporting the equilibrium view.

CONCLUSIONS

If the system I advocate is correct, we can make two predictions about reef fish communities. The first is that at the level of the species, rather than the guild, reef fish communities have an unstable structure (that is, the species composition of the fish at a site will not tend to recover following disturbance caused by the addition or removal of fish). The relative abundance of the species of a guild at any site is largely a result of the chance recruitment of young to that site and will change from time to time. Neighboring sites may show different patterns of change. The selective experimental removal of individuals of one species of a guild should not be followed rapidly by recovery of the original species composition of that site.

Changes in abundance of species of reef fishes have not been noted, partly because appropriate data have not been collected and partly because the reef environment is benign. It is unlikely that naturally occurring changes in abundance will be pronounced or occur over an extensive area of reef. But this is constancy (Lewontin 1969), not stability.

The second prediction is that the diversity of reef fish communities is directly correlated with the rate of small-scale, unpredictable disturbances (including predation) to the supply of living space. This can be tested by measuring the diversity of fishes in similar habitats in sheltered and in exposed reef areas. Diversity should be higher in the exposed sites, since rates of small-scale disturbances will be higher there. It can also be tested experimentally by manipulating the rate of disturbance, perhaps by increasing the rate of predation through a program of spearing randomly selected resident fishes.

SUMMARY

Data have been drawn together to demonstrate that reef fishes by and large are food and habitat generalists with a large amount of overlap in requirements among coexisting species. Suitable living space is the resource most likely to be in short supply for them, and their environment, although benign, is one in which the supply of living space is both spatially and temporally unpredictable. The argument is developed that reef fishes are adapted to this unpredictable supply of space in ways which make interspecific competition for space a lottery in which no species can consistently win. Thus, the high diversity of reef fish communities may be maintained because the unpredictable environment prevents development of an equilibrium community.

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