

# AMERICAN MUSEUM *Novitates*

PUBLISHED BY  
THE AMERICAN MUSEUM  
OF NATURAL HISTORY

CENTRAL PARK WEST AT 79TH STREET  
NEW YORK, N.Y. 10024 U.S.A.

NUMBER 2572

APRIL 9, 1975

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Number 2572, pp. 1-18, figs. 1-6, tables 1-7

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## Succession and Stability in Fish Communities of Dome-shaped Patch Reefs in the West Indies

C. LAVETT SMITH<sup>1</sup> AND JAMES C. TYLER<sup>2</sup>

### ABSTRACT

The scleractinian coral *Montastrea annularis* often forms dome-shaped heads that may reach a diameter of 5 m. Eventually these heads become too large to support their own weight and they collapse, leaving a base on which other corals can grow and ultimately form complex patch reefs. We have studied the fishes associated with reefs in the solid colony stage, small, middle-sized, and large domes, and partially collapsed domes. One reef was censused in 1970 and again in 1973. Between visits part of the reef had collapsed reducing the amount of large shelters available

for cardinalfishes (Apogonidae), squirrelfishes (Holocentridae), and grunts (Pomadasyidae). Concomitantly there was a dramatic increase in the population of gobies (Gobiidae) and blennies (Clinidae). Nevertheless, there was little change in the total number of species and individuals inhabiting the reef. An analysis of the sizes of the infaunal residents can provide a measure of niche utilization and equilibrium. A model is presented to show how size of the individual fish functions in the regulation of species composition and population structure within reef fish communities.

### INTRODUCTION

Safe and efficient diving equipment has enabled ecologists to direct more attention to the structure of coral-reef communities (Loya and Slobodkin, 1971; Loya, 1972; Risk, 1972; Porter, 1972). These attractive, shallow-water assemblages are ideal subjects for studies of species composition and diversity. Rich in number of species and confined to clear, warm waters, they lend themselves to direct observation and visual censusing (Smith and Tyler, 1973a), readily yielding the kinds of data that are critically needed by

the theoretical ecologists whose ultimate goal is understanding the function and evolution of biological communities.

Implicit in all community studies is the assumption that the assemblage under consideration is stable for some period of time, which can be a matter of hours, days, or generations. At the same time it is recognized that communities change with time as the physical environment changes and as the populations of species themselves evolve.

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The present paper summarizes fish census data from a series of five reefs that we believe represent stages in the development of a distinctive type of West Indian patch reef. Two of these reefs have been studied twice, one after three years' time and the other after seven months. In each case the fishes were removed after the first study period, and the pattern of repopulation provided a measure of the specificity of the community composition.

Only common names of fishes are given in the text but scientific names may be found in the tables.

### STRUCTURE AND DEVELOPMENT OF MONTASTREA DOME PATCH REEFS

Montastrea dome patch reefs are dominated by very large single colonies of the helmet form of the scleractinian coral, *Montastrea annularis*. This abundant West Indian hermatypic coral commonly assumes one of two alternate growth forms, the ramose or the helmet. The ramose form exhibits a globose mass of thick branches and tends to be most abundant in shallow, well-lighted situations where individual masses may attain diameters of 2 or 3 m. (Smith, 1973, fig. 1). The helmet form, which is more abundant in deeper waters with low-light intensity, is unbranched and assumes a hemispherical shape, sometimes flaring at its base. Single colonies can reach a diameter of as much as 4 or 5 m. and a height of 2 or 3 m. Diagrammatic cross sections

of developing Montastrea domes are shown in figure 1. At first the edge of the colony grows beyond the base to form an overhanging lip. As the colony continues to grow, the undersurface erodes leaving numerous chambers. By the time the colony has attained a diameter of about 1 m., it will typically consist of a hollow, domelike structure with multiple openings into its central cavity. By this time other sessile organisms will have invaded the base and other dead areas so that the structure can be considered a patch reef rather than a single colony. Eventually the colony becomes too large to support its own weight and to withstand the hydraulic pressures of storm waves. It then partially or completely collapses becoming a limestone platform ringed with the coral colonies that were attached to the old base. These will eventually spread over its entire surface and continue to grow into a more complex patch reef. Some of these changes have been documented by Storr (1964).

Because of their hollow form, Montastrea domes provide an excellent habitat for shelter-loving fishes. As the original colony grows, it provides more space and more diverse microhabitats so that the associated fish communities can increase in complexity. Assuming an average growth of 10 mm. in diameter per year, it appears that the largest Montastrea domes may be four or five hundred years old or more. Obviously it is not possible to follow succession in a single such structure, but these reefs are common enough so that it is relatively easy to find examples of all stages in their development.



FIG. 1. Hypothetical stages in the development of a Montastrea dome reef. The scale line indicates 1 meter; the time scale is unknown.

Fish census and sample data were obtained from five reefs as follows:

Bimini dome reef 2. A single colony of *Montastrea annularis* off the west side of Turtle Rocks, south of Bimini, Bahamas, in water 10 m. deep. The colony had a maximum diameter of 35 cm. and had overgrown its base leaving a space of undetermined depth along the periphery of the colony. It was sampled with rotenone on February 25, 1974, when three specimens, two rusty gobies, and one dusky cardinalfish, were collected. One bicolor damselfish was observed using the colony as a shelter site but escaped the rotenone.

Flare reef (fig. 3A). A small dome about 1.5 m. in diameter, in 10 m. of water, 3 km. south of The Elbow in the Florida Keys. It was studied by visual census methods during two days and one night of saturated diving during project FLARE (Florida Aquanaut Research Expedition). Forty-two species were recorded of which 14 were resident, represented by 69 individuals. We estimate that at least seven additional individuals of four additional cryptic resident species were present.

Bimini dome reef 1 (fig. 3B). A well-isolated mound about 60 m. west of Turtle Rocks, south of Bimini, Bahamas, at a depth of 11 m. It is a symmetrical, hollow mound about 2.5 m. in diameter. It was first sampled with two applications of rotenone in August, 1973, by George Dale in his studies on the ecology of cardinalfishes. Dale collected 39 species that were represented by 563 individuals. The reef was sampled again on February 25, 1974, when 147 individuals of 28 species were taken.

Tektite Study Reef B (fig. 3C). A large dome with a maximum diameter of about 4 m. about 20 m. east of the Tektite Study Reef A at a depth of 9 m. It was censused visually October 9 and 10, 1973. Although only 48 species were recorded, by analogy with the other reefs we estimate that at least eight cryptic species were also present. The size and complexity of this reef are exceptional for a dome reef due, no doubt, to its location in Beehive Cove, a protected area of Lameshur Bay, St. John, Virgin Islands.

Tektite Study Reef A (figs. 2, 3E, F). This reef is described in some detail by Smith and Tyler (1972). Situated in Beehive Cove, Lame-

shur Bay, St. John, Virgin Islands, at a depth of 11 m. it is roughly triangular, the east, south-west, and northwest sides being 5.5, 5.5, and 5.0 m., respectively. The reef consists of a coralline limestone base forming an irregular platform rising to approximately 1 m. above the surrounding sands. This platform is divided by a deep valley into a larger northern and smaller southern section. Large coral colonies are concentrated around the rim of the north section, leaving a flat central area to which smaller corals are attached. The southern section is dominated by *Montastrea annularis*, which forms a high pinnacle near the southern apex and a roof over the east end of the transverse valley.

In 1970 as part of project TEKTITE II, we made a careful census of the fishes inhabiting a small patch reef in Lameshur Bay (fig. 2; also see Smith and Tyler, 1972). From September 25 to October 10, we made repeated visual counts until we obtained consistent estimates of the numbers of fishes utilizing the reef and the contiguous sand flats. During these observations, we made a particular effort to discover the preferred microhabitats of the resident species and in many cases we were able to recognize individuals that occupied the same spots day after day. At the end of the observation period, we sampled the reef twice with emulsified rotenone. The samples supplemented our visual observations and added several cryptic species which we had not been able to observe. Together the two methods gave a reasonably complete picture of the fishes utilizing the microhabitats of the reef.

Three years later, in October, 1973, we repeated the census using the same techniques except that the observation period was shorter and did not include night dives. Furthermore, we used standard open-circuit scuba rather than the bubble-free rebreather units that were used exclusively in 1970. These disadvantages, however, were compensated for by our previous experience and familiarity with the reef. Except for a few special cases we believe that the 1970 and 1973 data are comparable. Smith (1973) found that similar patch reefs had become completely repopulated less than one year after rotenone sampling; we therefore do not attribute the observed changes to the effects of the initial sampling.

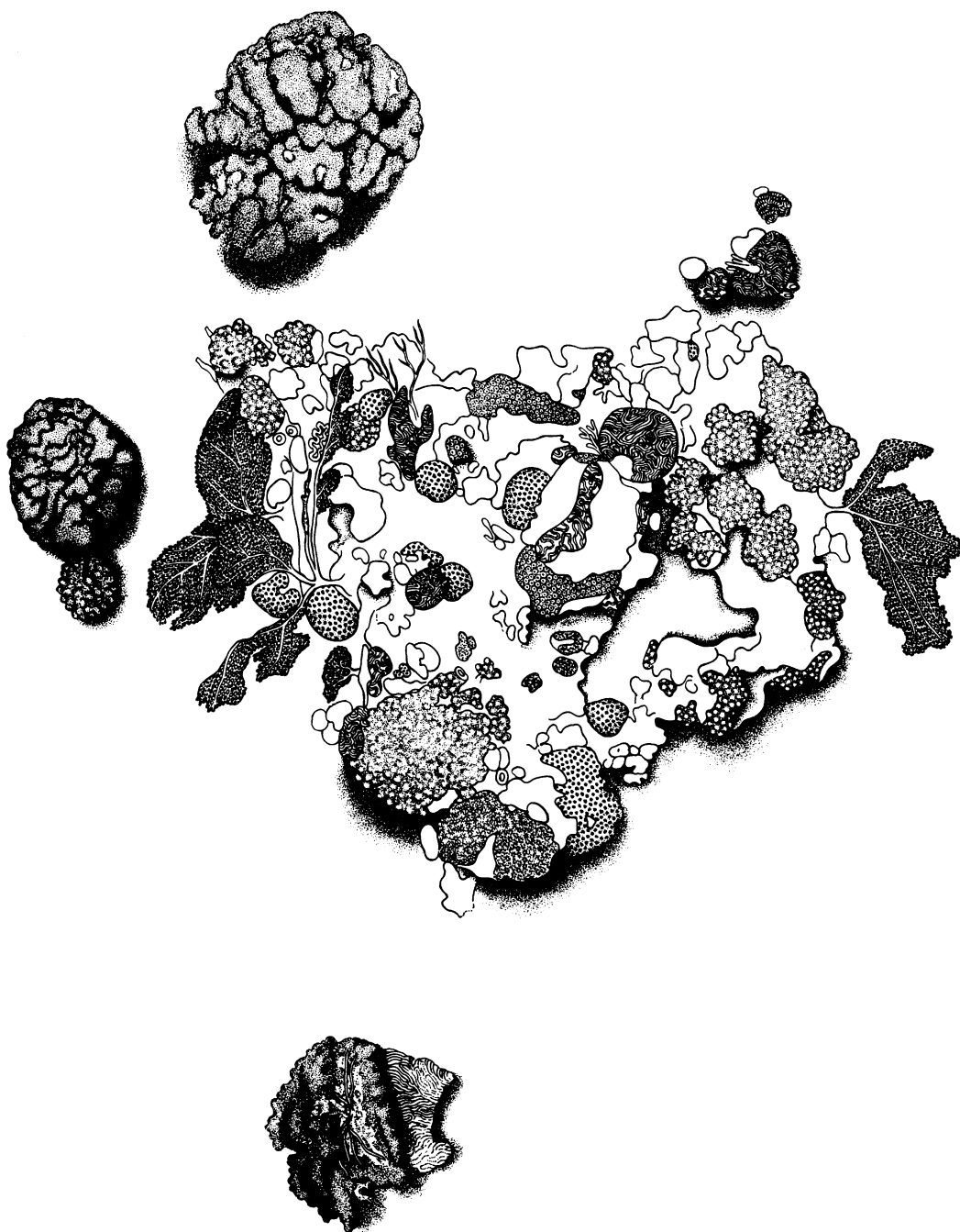


FIG. 2. Drawing of Tektite reef A as it appeared in 1973.



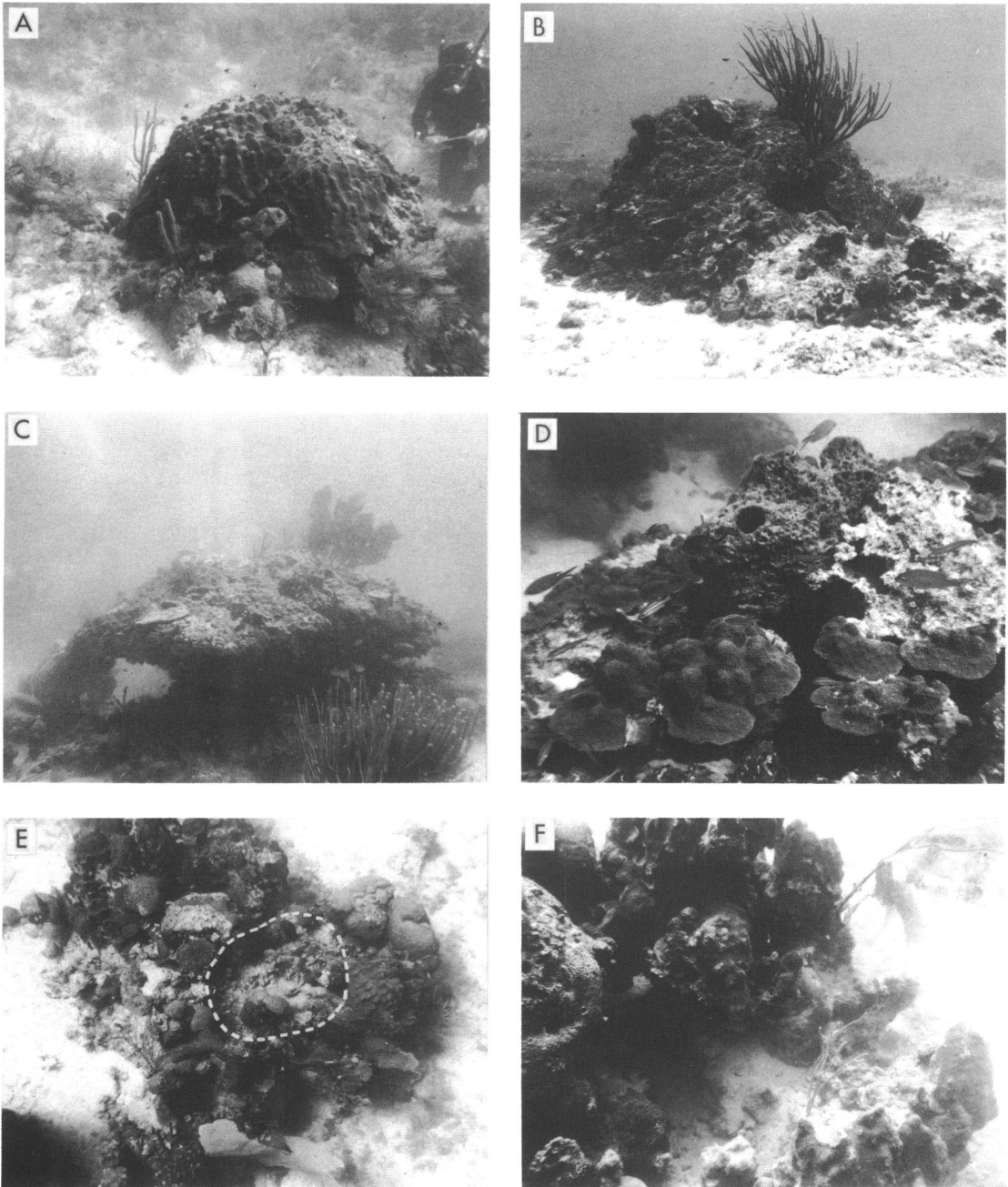


FIG. 3. Stages in the development of *Montastrea* dome reefs. A. Flare reef, a small *Montastrea* dome. B. Bimini dome reef 1, a moderate-sized dome that is completely penetrated by a large cave. C. Tektite B, a very large *Montastrea* dome with a pronounced overhang and many large caves. D. Tektite B, showing dead areas of *Montastrea annularis* and a large sponge. E. Tektite A. White dashed line indicates probable outline of a *Montastrea* dome that collapsed many years ago. F. Close-up of the south end of Tektite A showing where a section of *Montastrea annularis* collapsed and disappeared between 1970 and 1973.

### Changes in Tektite Reef A 1970-1973

Careful study of more than 240 35 mm. color transparencies (62 from 1970, 178 from 1973) of the reef has revealed a number of changes in its physical structure from 1970 to 1973. The overall effect of these changes is that in 1973 the reef had a more open, barren look, giving the impression of being less "diverse."

Three large sea fans, two at the north and one at the south, are conspicuous features of the reef. Between 1970 and 1973 the two more southern fans showed some destruction but the northernmost one remained in excellent condition. Two smaller sea fans had increased from approximately 0.1 to 0.3 m. in diameter (estimates from photographs). Several sea whip colonies in the southern part had disappeared, and this made the reef look more "barren." Anastomosing rod-shaped sponges were conspicuous on the east side near the valley area in 1970 but were not present in 1973. Upright rod-shaped sponges at the northern apex were still present but were heavily infested with small sea anemones and had an unhealthy appearance.

The most conspicuous change in stony corals was the collapse and disappearance of a large section of *Montastrea annularis* in the western side of the southern part of the reef. A smaller, mushroom-shaped pillar of *Montastrea* and other corals (about 0.3 m. in diameter) had disappeared from the northwest part of the reef as well. A colony of *Eusmilia* in the northwest could not be found, but a colony of *Mussa angulosa* in the north apex was still thriving.

Some corals appeared in better health in 1973 than in 1970; others did not appear to be prospering. Immediately north of the cave area at the east end of the cross valley, there is a large head of *Diploria* sp. Part of the colony is dead and eroded and part covered with an encrusting red sponge with sea anemones. (Unlike the situation of the rod-shaped sponges infested with sea anemones, the red sponge appeared to be in excellent condition suggesting that it is a normal host for these anemones.) A central strip of the *Diploria* was still alive but worn and discolored in 1970. By 1973 it had recovered entirely and was uniformly of a healthy yellowish green color.

During our 1970 study, part of a *Montastrea*

*annularis* colony at the south apex of the reef suffered some mechanical damage and exhibited areas of white spots where the living tissue had been abraded. These scars had healed completely by 1973 with no indication that the coral had ever been damaged.

At least two colonies of *Siderastrea* sp. in the north-central part of the reef had dark irregular splotches over their surface. These appeared pathological in contrast to the usual uniform and clean tawny appearance of this species.

A large clump of *Porites porites* had disappeared from the north-central part of the reef but other masses in the east and near the north had changed very little during the three years. One colony of this species on the east side had grown from a low mound into a forked rod about 0.1 m. long. A new *Porites* colony had appeared near the west point on eroded parts of a large *Siderastrea* head.

A large sector of the *Colpophyllia* (wrongly called *Diploria* sp. in our 1972 paper) colony of the northwest satellite was dead in 1973 but the remainder appeared healthy enough. The northeast satellite, which consists of a single clump of the ramose form of *Montastrea annularis* about 1 by 1.5 m., had some abraded whitish patches. Moreover, there was much more sediment in the spaces between the branches than there had been in 1970.

Apparently there has been some accumulation of sand around the base of the reef. A string, placed as a guideline in 1970, had been attached a few cm. above the sand. It was still in place in 1973 but its attachment was buried, indicating that at least 50 to 100 mm. of sediment had accumulated around the reef.

With the destruction of its *Montastrea* roof, the southwestern part of the reef now resembled the northern section (fig. 3F). Both consisted of low limestone platforms with rounded coral colonies along their margins and smaller colonies at their centers. We therefore conclude that the study reef began as a dome of *Montastrea annularis* that reached a diameter of about 3 m. before it collapsed. While it was growing, a second *Montastrea* dome evidently formed a meter or so south of it. Eventually the two domes fused, nevertheless leaving the transverse valley, which ultimately became covered over at



its eastern end. Fortuitous timing of our two censuses, before and after the partial destruction of the shelter, provided an opportunity to document some of the changes in fish fauna associated with changes in reef structure.

Changes in the Fish Community of Tektite A  
1970-1973

The results of the two censuses are compared in table 1. In 1970 the total was 675 individuals representing 53 resident species. The 1973 count

was 688 individuals representing 47 resident species. Nevertheless, the biomass was probably somewhat less in 1973. For present purposes we define resident species as those that had a definite home within the study reef or whose home range included the study reef so that the same individuals returned repeatedly to the reef. Under the limitations of this definition, we may have failed to recognize some individuals with large home ranges and designated these species visitors when they were in fact residents. It is less likely, however, that we erred in the other direction and designated visitors as residents.

TABLE 1  
Transient and Visitor Species at Tektite A Reef 1970-1973

Species	1970 Status	1973 Status
<i>Gymnothorax moringa</i> (Cuvier)	Visitor	Absent
Spotted moray		
<i>Synodus intermedius</i> (Agassiz)	Visitor	Visitor
Sand diver		
<i>Jenkinsia lamprotaenia</i> (Gosse)	Visitor	Absent
Dwarf herring		
<i>Allanetta harringtonensis</i> (Goode)	Absent	Transient
Reef silverside		
<i>Holocentrus ascensionis</i> (Osbeck)	Absent	Transient
Squirrelfish		
<i>Holocentrus rufus</i> (Walbaum)	Visitor	Absent
Longspine squirrelfish		
<i>Aulostomus maculatus</i> (Valenciennes)	Absent	Visitor
Trumpetfish		
<i>Hypoplectrus puella</i> (Cuvier)	Resident	Transient
Barred hamlet		
<i>Serranus tigrinus</i> (Bloch)	Absent	Transient
Harlequin bass		
<i>Serranus tabacarius</i> (Cuvier)	Absent	Transient
Tobaccofish		
<i>Epinephelus guttatus</i> (Linnaeus)	Absent	Visitor
Red hind		
<i>Priacanthus cruentatus</i> (Lacépède)	Absent	Transient
Glasseye snapper		
<i>Chloroscombrus chrysurus</i> (Linnaeus)	Visitor	Absent
Atlantic bumper		
<i>Caranx ruber</i> (Bloch)	Visitor and transient	Visitor and transient
Bar jack		
<i>Caranx latus</i> Agassiz	Transient	Absent
Horse-eye jack		
<i>Ocyurus chrysurus</i> (Bloch)	Visitor and transient	Visitor and transient
Yellowtail snapper		
<i>Lutjanus cyanopterus</i> (Cuvier)	Transient	Absent
Cubera snapper		

TABLE 1—(Continued)

Species	1970 Status	1973 Status
<i>Calamus pennatula</i> Guichenot	Transient	Absent
Pluma		
<i>Gerres cinereus</i> (Walbaum)	Absent	Transient
Yellowfin mojarra		
<i>Pseudupeneus maculatus</i> (Bloch)	Visitor	Visitor
Spotted goatfish		
<i>Pomacanthus arcuatus</i> (Linnaeus)	Transient	Visitor
Gray angelfish		
<i>Holacanthus tricolor</i> (Bloch)	Absent	Visitor
Rock beauty		
<i>Chaetodon capistratus</i> Linnaeus	Absent	Visitor
Foureye butterflyfish		
<i>Scarus croicensis</i> Bloch	Visitor	Visitor
Striped parrotfish		
<i>Scarus taeniopterus</i> Desmarest	Transient	Visitor
Princess parrotfish		
<i>Sparisoma aurofrenatum</i> (Valenciennes)	Visitor	Visitor
Redband parrotfish		
<i>Sparisoma viride</i> (Bonnaterre)	Visitor	Visitor
Spotlight parrotfish		
<i>Cryptotomus roseus</i> Cope	Absent	Transient
Bluelip parrotfish		
<i>Halichoeres bivittatus</i> (Bloch)	Visitor	Absent
Slippery dick		
<i>Halichoeres garnoti</i> (Valenciennes)	Visitor	Visitor
Yellowhead wrasse		
<i>Halichoeres maculipinna</i> (Muller and Troschel)	Transient	Absent
Clown wrasse		
<i>Clepticus parrai</i> (Bloch and Schneider)	Absent	Transient
Creole wrasse		
<i>Chaenopsis limbaughi</i> Robins and Randall	Absent	Transient
Yellowface pikeblenny		
<i>Acanthurus bahianus</i> Castelnau	Visitor	Visitor
Ocean surgeon		
<i>Acanthurus coeruleus</i> Bloch and Schneider	Visitor	Visitor
Blue tang (adult)		
<i>Scomberomorus regalis</i> (Bloch)	Transient	Transient
Cero		
<i>Bothus lunatus</i> (Linnaeus)	Absent	Visitor
Peacock flounder		
<i>Monacanthus tockeri</i> Bean	Visitor	Visitor
Slender filefish		
<i>Balistes vetula</i> Linnaeus	Absent	Visitor
Queen triggerfish		

During both observation periods, 37 species were resident in the study reef and 16 of these were present in approximately the same numbers (table 2). These species appear to share the

characteristic of being strongly territorial or at least having a well-defined home range. The graysby, Nassau grouper, and smooth trunkfish are large and conspicuous and relatively free

TABLE 2  
Comparative Abundance of Resident Species at Tektite  
A Whose Numbers Were Stable 1970-1973

Species	Numbers Present	
	1970	1973
<i>Epinephelus cruentatus</i> (Lacépède)	2	2
Graysby		
<i>Epinephelus striatus</i> (Bloch)	1	1
Nassau grouper		
<i>Phaeoptyx xenus</i> (Böhlke and Randall)	3	5
Sponge cardinalfish		
<i>Pomacentrus planifrons</i> Cuvier	10	8
Threespot damselfish		
<i>Pomacentrus variabilis</i> (Castelnau)	9	8
Cocoa damselfish		
<i>Pomacentrus partitus</i> Poey	6	5
Bicolor damselfish		
<i>Thalassoma bifasciatum</i> (Bloch)	16	12
Bluehead		
<i>Labrisomus haitiensis</i> Beebe and Tee-Van	10	10
Longfin blenny		
<i>Starksia Lepicoelia</i> Böhlke and Springer	4	6
Blackcheek blenny		
<i>Starksia hassi</i> Klausewitz	2	1
Thinline blenny		
<i>Enneanectes altivelis</i> Rosenblatt	2	3
Lofty triplefin		
<i>Hypoleurochilus</i> sp.	2	1
Combtooth blenny		
<i>Coryphopterus dicrus</i> Böhlke and Robins	6	6
Colon goby		
<i>Risor ruber</i> (Rosen)	3	4
Tusked goby		
<i>Acanthurus coeruleus</i> Bloch and Schneider	3	4
Blue tang (juveniles)		
<i>Lactophrys triqueter</i> (Linnaeus)	1	1
Smooth trunkfish		

from predation. The threespot damselfish and cocoa damselfish vigorously defend their territories. The bicolor damselfish, bluehead wrasse, blue tang, and colon goby are less vigorous in defending territories but nevertheless have well-defined territories. The sponge cardinalfish and tusked goby are sponge dwellers. The remaining species, the blackcheek blenny, thinline blenny, longfin blenny, combtooth blenny, and lofty

triplefin, are secretive species whose habits are not known, although we suspect that they, too, have rigorously defined home ranges.

Twelve species were definitely more abundant in 1973 than in 1970 (table 3). The flagfin blenny and the figure-eight goby live on the surface of globose corals where their color or transparency serves as camouflage. The bridled goby, pallid goby, bartail goby, and goldspot goby are sand dwellers and are also camouflaged by their hyaline appearance. The rusty goby spends the daylight hours resting on the undersides of overhanging ledges; it is also camouflaged by its orange color which is surprisingly inconspicuous

TABLE 3  
Comparative Abundance of Resident Species at Tektite  
A That Were More Abundant in 1973

Species	Numbers Present	
	1970	1973
<i>Phaeoptyx pigmentaria</i> (Poey)	3	9
Dusky cardinalfish		
<i>Emblemariopsis signifera</i> (Ginsburg)	6	10
Flagfin blenny		
<i>Acanthemblemaria spinosa</i> Metzelaar	1	4
Spinyhead blenny		
<i>Coryphopterus thrix</i> Böhlke and Robins	4	25
Bartail goby		
<i>Coryphopterus eidolon</i> Böhlke and Robins	25	33
Pallid goby		
<i>Coryphopterus glaucofraenum</i> Gill	27	92
Bridled goby		
<i>Coryphopterus personatus</i> (Jordan and Thompson)	23	258
Masked goby		
<i>Gnatholepis thompsoni</i> Jordan	6	11
Goldspot goby		
<i>Lythrypnus nesiotes</i> Böhlke and Robins	23	44
Island goby		
<i>Lythrypnus elasson</i> Böhlke and Robins	3	7
Dwarf goby		
<i>Quisquilius hipoliti</i> (Metzelaar)	4	39
Rusty goby		
<i>Gobiosoma saucrum</i> (Robins)	7	11
Figure-eight goby		



in the shadows. The spinyhead blenny lives in abandoned worm tubes. Its increase seems due to the addition of suitable shelter sites in a clump of sponge and oysters on one of two large sea fans in the north part of the reef. The dusky cardinalfish is often associated with sea urchins and hovers with them in cave areas during the day. The island goby and dwarf goby have not been observed alive. The masked goby spends daylight hours hovering just above the bottom. In 1970 it was represented by 23 individuals that seldom ventured more than a few centimeters from one of three large sea fans. In 1973 we collected 250 specimens, and they were dispersed all over the reef—top, sides, and in caves. Thus its habits changed as it became more abundant.

We judge all of these species (except the spinyhead blenny) to have been predator limited in 1970 and less so in 1973 because fewer resident predators were present in 1973.

Ten species were present in 1973 only (table 4). Without more detailed knowledge of their habits it is perhaps best to regard them as ecological opportunists. There is also the possibility that they are ecological replacements that have

been favored by the changes in the physical structure of the reef. For example, the sand-dwelling eels, the key worm eel and the juvenile snake eel are possible replacements for the rock-dwelling golden tail moray. The indigo hamlet is structurally similar to the barred hamlet and apparently has similar habits. The juvenile rainbow wrasse hovers over the reef cropping plankton in the same way as the boga. The reef scorpion fish is about the same size and as secretive as the spotted soapfish but may be able to survive better in the reduced shelter of the reef as it was in 1973. The papillose blenny is generally similar in size and form to the smallflap blenny. Finally the diamond blenny and the red-spotted hawkfish spend daylight hours on the surface of the reef although the hawkfish tends to be in more open and higher parts of the reef and the diamond blenny tends to keep to the shaded areas. These observations should be checked in future studies and tested under laboratory conditions for they are of critical importance in understanding community structure. Moreover they cast doubt on the common assumption that the nearest relative of a species is its closest competitor.

Nine species were considerably less abundant in 1973 (table 5). In 1970 French grunts were present as subadults and juveniles but only one juvenile was reported in 1973. Sub-adults of this species hover around the bases of corals during the day and move off the reef to feed at night. The belted cardinalfish, flame-fish, barred cardinalfish, and freckled cardinalfish are nocturnal species that hover in caves during the day. Their reduced numbers are surely the result of the reduction in available shelter sites. The blue chromis and brown chromis are diurnal species that sleep in small holes in the reef, often between the branches of the ramose form of *Montastrea annularis*. Because some of the spaces in the northeast satellite were choked with sand by 1973, it appears that these species, too, have been limited by a lack of hiding places.

The sharknose cleaning goby is a cleaner species. Its reduction may be due either to a loss of available sites or to a reduction in number of larger fishes to be cleaned.

Sixteen species were present only in 1970 (table 6). Some of these clearly are associated

TABLE 4  
Relative Abundance of Species That Were Present at  
Tekite A only in 1973

Species	1973
<i>Ahlia egmontis</i> (Jordan)	1
Key worm eel	
<i>Myrichthys</i> sp.	1
Juvenile snake eel	
<i>Scorpaenodes caribbaeus</i> Meek and Hildebrand	1
Reef scorpionfish	
<i>Hypoplectrus indigo</i> (Poey)	1
Indigo hamlet	
<i>Halichoeres pictus</i> (Poey)	5
Rainbow wrasse	
<i>Acanthemblemaria chaplini</i> Böhlke	7
Papillose blenny	
<i>Blennius marmoreus</i> Poey	1
Seaweed blenny	
<i>Emblemaria pandionis</i> Evermann and Marsh	2
Sailfin blenny	
<i>Malacoctenus boehlkei</i> Springer	3
Diamond blenny	
<i>Coryphopterus</i> sp.	1

TABLE 5  
Comparative Abundance of Species at Tektite A  
Whose Numbers Declined 1970-1973

Species	1970	1973
<i>Apogon townsendi</i> (Breder)	118	13
Belted cardinalfish		
<i>Apogon maculatus</i> (Poey)	10	2
Flamefish		
<i>Apogon binotatus</i> (Poey)	70	22
Barred cardinalfish		
<i>Phaeoptyx conklini</i> (Silvester)	11	4
Freckled cardinalfish		
<i>Haemulon flavolineatum</i> (Desmarest)	40	10
French grunt (juveniles)		
<i>Chromis multilineatus</i> (Guichenot)	18	1
Brown chromis		
<i>Chromis cyaneus</i> (Poey)	35	5
Blue chromis		
<i>Gobiosoma evelynae</i> Böhlke and Robins	10	4
Sharknose cleaning goby		
<i>Canthigaster rostrata</i> (Bloch)	8	4
Sharpnose puffer		

with particular features of the reef structure. The tomtate sub-adults require shelter during the daylight hours as do the longjaw squirrelfish, reef squirrelfish, blackbar soldierfish, and sawcheek cardinalfish. Their absence in 1973 appears to be correlated with reduction of cover. The short-stripe goby (erroneously listed as the yellowline goby in Smith and Tyler, 1972) is an obligate sponge-dwelling species whose absence may be attributable to a lack of suitable habitat. The queen parrotfish is a night resident whose shelter site had disappeared. The redspotted hawkfish lives on live and dead coral; we have no idea as to why it was not present in 1973 as the habitat seemed suitable for it. The queen angelfish juveniles are cleaners but they are not so restricted to particular sites as are the cleaning gobies, and we see no obvious reason for their disappearance. The sawcheek cardinalfish lives in holes at the base of the reef and underneath rocks; the additional sand around the base of the reef may have obliterated some of its hiding places. The boga and the juveniles of the French grunt and tomtate are suprabenthic hoverers. Their decline and disappearance is also unexplained. The barred hamlet may have been re-

TABLE 6  
Relative Abundance of Species that Were Present at  
Tektite A only in 1970

Species	1970
<i>Muraena miliaris</i> (Kaup)	2
Goldentail moray	
<i>Syngnathus</i> sp.	1
Pipefish	
<i>Holocentrus marianus</i> (Cuvier)	30
Longjaw squirrelfish	
<i>Holocentrus coruscus</i> (Poey)	8
Reef squirrelfish	
<i>Myripristis jacobus</i> Cuvier	10
Blackbar soldierfish	
<i>Hypoplectrus puella</i> (Cuvier)	4
Barred hamlet	
<i>Rypticus subbifrenatus</i> (Gill)	1
Spotted soapfish	
<i>Apogon quadrisquamatus</i> Longley	12
Sawcheek cardinalfish	
<i>Haemulon aurolineatum</i> Cuvier	40
Tomtate (juveniles)	
<i>Haemulon aurolineatum</i> Cuvier	15
Tomtate (sub-adults)	
<i>Haemulon flavolineatum</i> (Desmarest)	20
French grunt (sub-adults)	
<i>Inermia vittata</i> Poey	10
Boga	
<i>Holacanthus ciliaris</i> (Linnaeus)	2
Queen angelfish	
<i>Amblycirrhitis pinos</i> (Mowbray)	2
Redspotted hawkfish	
<i>Scarus vetula</i> Bloch and Schneider	1
Queen parrotfish	
<i>Emblemariopsis leptocirris</i> Stephens	1
Smallflap blenny	
<i>Gobiosoma chancei</i> Beebe and Hollister	1
Shortstripe goby	
<i>Lythrypnus</i> sp.	2

placed by the indigo hamlet and the goldentail moray may have been replaced by other eels. The island goby, dwarf goby, smallflap blenny, and spotted soapfish were never observed.

#### SUCCESSION IN THE FISH COMMUNITIES OF MONTASTREA DOME REEFS

Pertinent statistics on these study reefs are summarized in table 7, and in figure 4 the six reef stages are compared. Although we do not

TABLE 7  
Comparative Data on Patch Reefs Representing Six Stages in the Life Cycle of *Montastrea* Domes

Stage	Bimini 2	Flare	Bimini 1		Tektite B	Tektite A	
			August	February		1970	1973
	Solid colony	Small dome	Large dome	Large dome	Very large dome	Partly collapsed dome	More collapsed dome
Diameter in meters	.35	1.5	2.5	2.5	5	5	5
Height in meters	.35	1.5	2	2	2	1.5	1.5
Volume in <sup>a</sup> cubic meters	.0336	2.65	9.82	9.82	39.27	29.45	29.45
Resident <sup>b</sup> species	3	18 (14)	39	28	56 (45)	53	47
Resident <sup>c</sup> individuals	4	76 (69)	563	147	748 (680)	675	688
H' (base e) <sup>d</sup>	1.0396	(1.9459)	2.4739	2.5538	(2.9314)	3.2250	2.5913

<sup>a</sup>The volume is calculated as a cylinder.

<sup>b</sup>For Flare and Tektite B the total number of resident species has been estimated by adding 25 percent to the number of obvious species. The actual numbers of species observed are given in parentheses.

<sup>c</sup>For Flare and Tektite B the total number of resident individuals has been estimated by adding 10 percent to the number of obvious individuals. The actual numbers observed are given in parentheses.

<sup>d</sup>Calculations of the Shannon Index of diversity (H') for Flare and Tektite B are based on the numbers of individuals actually observed.

have a reliable measure of the amount of shelter present in a patch reef, it is apparent that larger patches have more fish. For our present discussion we have calculated the volume of the cylinder that would enclose the reef, i.e., with the same diameter as the base of the reef and the same height as the highest part of the reef. Obviously this is only a crude indication of the volume of the reef and does not indicate how many shelter sites are available; nevertheless, there is a close correspondence between volume and number of individuals present, particularly for larger reefs (Bimini 1, Tektite B, Tektite A). Bimini 2, FLARE, Bimini 1, and Tektite B represent stages in the development of *Montastrea* domes from solid colonies to maturity; the two observations at Tektite A represent more advanced stages. Corresponding stages in the development of the fish community can be summarized as follows.

1. As the colony of *Montastrea* coral develops an overhanging margin, it provides shelter for

some small fishes—gobies, cardinalfishes, and pomacentrids at first. Between the solid colony stage (Bimini 2) and the small dome stage (FLARE) the number of species and the Shannon Index of diversity increase more rapidly than the number of individuals, apparently because new shelter sites that are qualitatively different become available as the reef becomes hollow. This appears to represent a distinct phase of colonization.

2. A second phase of colonization, during which the reef increases greatly in size but changes little in form, is represented by Bimini 1 and Tektite B. As larger cavities develop in the head, more cardinalfishes, groupers, and holocentrids become established. At this stage the reef is still overwhelmingly dominated by *Montastrea annularis*. The number of species and diversity of the fishes continue to increase but more slowly than the number of individuals, and the lines cross (fig. 4).

3. As the reef attains its maximum size (Tek-



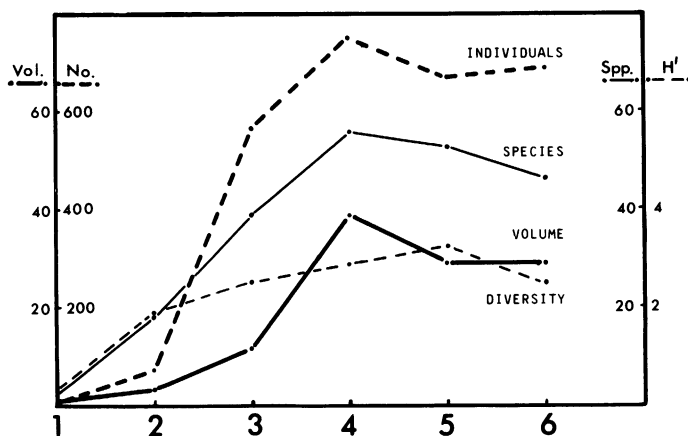


FIG. 4. Graphs summarizing the development of the fish communities associated with *Montastrea* dome reefs. Stages on the abscissa correspond to reefs mentioned in the text as follows: 1. Bimini dome reef 2. Flare reef. 3. Bimini dome reef 1. 4. Tektite study reef B. 5. Tektite study reef A 1970. 6. Tektite study reef A 1973.

tite B) and begins to collapse (Tektite A), there is close correspondence between the volume of the reef and the number of individuals present.

Partial collapse of the dome provides a substratum for other kinds of corals and algae and this permits a greater diversity of fish species in the community even though fewer individuals may be present. Paradoxically, full maturity of the fish community may not be attained until after the decline of the coral structure has begun. Further collapse of the *Montastrea* dome reduces the amount of shelter for predators, and this results in a decline in the number of species the reef can support. The diversity index is slightly reduced and the fish community becomes dominated by secretive, infaunal species rather than by conspicuous, cave-dwelling forms.

#### Stability and Consistency of Reef-Fish Communities

Previous studies have confirmed the casual impression that reef fish communities are stable for periods of many days and weeks (Allen, 1972; Smith and Tyler, 1973b; Dale, In press). Like other aspects of communities, this is un-

doubtedly a stochastic phenomenon; some individuals remain in the same reef for their entire adult life of two or three years or more, others remain for a few days and then move away leaving lebensraum for new individuals of the same or different species. In effect, mortality from various causes leaves vacant niches that are then available to other individuals.

It appears that juveniles usually occupy different niches than do adults. Sometimes this is obvious as in the case of *Haemulon* whose pre-juveniles hover over the reef and later move down into spaces between coral colonies. Other species may utilize the same microhabitats throughout their post-larval lives but change their feeding habits as they grow larger.

Community structure, i.e., the species present and their relative abundance, will be determined by what niches are available, what species are capable of occupying these niches, and the timing of the recruitment process.

A conservative estimate of the number of species of shore fishes that live in the vicinity of Lameshur Bay would be between 400 and 500 species. Of these, perhaps 250 or 300 are reef dwellers. Since the maximum number of species

that occurs in a small patch reef at any one time is about 70, it seems that for most niches there must be several species that could fill it more or less equally well. There are probably generalized niches, such as midwater plankton cropping, that could be occupied by many species and specialized niches that are available to only a few. Living in sponges may be an example of the latter. The fact that many fishes change their niche as they mature, usually from a generalized way of life to a more specialized one, imposes constraints on the structure of the community.

For the Bimini 1 and Tektite A reefs, depopulation by rotenone sampling provided a test of the community stability. The three-year period between sampling of the Tektite reef allowed ample time for complete recovery. Most of the smaller reef fishes have life spans no greater than two or three years, and so the individual fish would have been replaced one or more times even if the sample had not been taken in 1970. The catastrophic removal of nearly all the fishes may, however, have resulted in more variation in the community than would have occurred naturally. Comparison of the results of the two censuses, using the species similarity index:

$$C = \left( \frac{Ic1}{I1} + \frac{Ic2}{I2} \right) \times .5^1$$

yielded a value of 0.88 for Tektite A. The same index applied to the two samples from Bimini 1 gave the value of 0.92. Smith (1973) sampled 10 reefs from the Bahamas two or more times and obtained similarity values for samples from the same reef of 0.68 to 0.94.

At the Tektite A reef, 53 species in all were recorded as residents during the two census periods. More than half (59%) of these occurred in both samples. More than 70 percent of the resident species in both populations were held in common. At the Bimini 1 reef, 46 species were residents with 53 percent of the species in the first sample and 75 percent of the species in the

second sample occurring in both. Transient species are excluded here because they do not permanently occupy niches in the community and hence do not exert a consistent selective pressure on the residents. We do recognize, however, that particular hunting strategies of some species may lead to intense pressure on certain prey species and that transient predators may thus selectively affect community composition. Smith and Tyler (1973b) have suggested other ways in which transient predators play important roles in the community.

The most consistent species of the community occurred in approximately equal numbers during the two study periods. They appear to have very precise microhabitat requirements and definite territories or home ranges. Their feeding and food habits seem to be secondary because several trophic levels are represented. Most of the species that decreased or disappeared seem to have done so in response to the reduction in available shelter and those that increased seem to have responded to a decrease in shelter-dependent resident predators. (There is no evidence of a general decrease in wide-ranging predators in Lameshur Bay although we cannot rule this possibility out).

## DISCUSSION

Because coral-reef fishes have a great diversity in their ways of life, it is difficult to find a single parameter that reflects the niches well enough to serve as a basis of comparison. Recently, however, Smith (In press) has found that when the largest specimens of the resident species are graphed in order of increasing size, the result is an exponential curve of the form:

$$R_n = R_1 C^{n-1}$$

where  $R_n$  is the standard length of the largest specimen of the  $n$ th species,  $R_1$  is the length of the largest specimen of the smallest species and  $C$  is a constant whose value usually lies between 1.03 and 1.12. This relationship holds only for the infaunal resident species; a sharp inflection point separates this part of the curve from that for larger (>60-80 mm.) fishes that are transients or are otherwise using the habitat in a different way. Some species represented only by juveniles lie below the curve.

<sup>1</sup>Ic1 is the number, in the first sample, of individuals belonging to species that are present in both samples. Ic2 is the number of individuals in the second sample belonging to species that are present in both samples. I1 is the total number of individuals in the first sample and I2 the total number of individuals in the second sample.

Apparently, the limits imposed by both space and food items available in the coral-reef biotope are sufficiently critical that size is of primary importance in determining what species can and cannot be assimilated by the community. Fishes have plastic growth patterns and adverse conditions can limit growth so that the realized size is somewhat less than the potential under ideal conditions. Smith postulated that each species has upper and lower, genetically determined growth limits. The upper limit is the asymptotic maximum size ( $L_{\infty}$ ) of the Von Bertalanffy growth curve, whereas the lower limit is the minimum size that must be achieved if the fish is to survive as an adult. Within this genetic size range, the size actually attained will be determined by competition with other species. [The social control of growth that has been demonstrated for anemone fishes by Allen (1972) is one of the suggested mechanisms by which this may be accomplished.] Intraspecific density-dependent competition may limit the size that individuals achieve in monospecies communities such as farm ponds, but we believe that in the complex community of the coral reef, the primary effect

of intraspecific competition will be to limit numbers of individuals rather than size. Conclusive evidence on this point is not available at this time but we believe that space is more often limiting than food, hence, members of the same species would vie for shelter sites and this would limit the numbers of individuals a given coral reef can sustain.

Size curves of the samples from Tektite A 1970 and 1973 and Bimini 1 August and February are shown in figures 5 and 6. Two curves are shown from each collection, one based on the actual size of individuals collected, the other based on average lengths of the largest individuals of the same species collected in a series of rotenone samples from the Bahamas. In each case the curve for the lengths of the actual specimens lies below the curve derived from averages. One explanation for this might be that both of these communities had a larger than average number of species so that the sizes of all the species were correspondingly more limited.

The size order of the species as determined from averages and from actual specimens is not the same, although the Kendall rank coeffi-

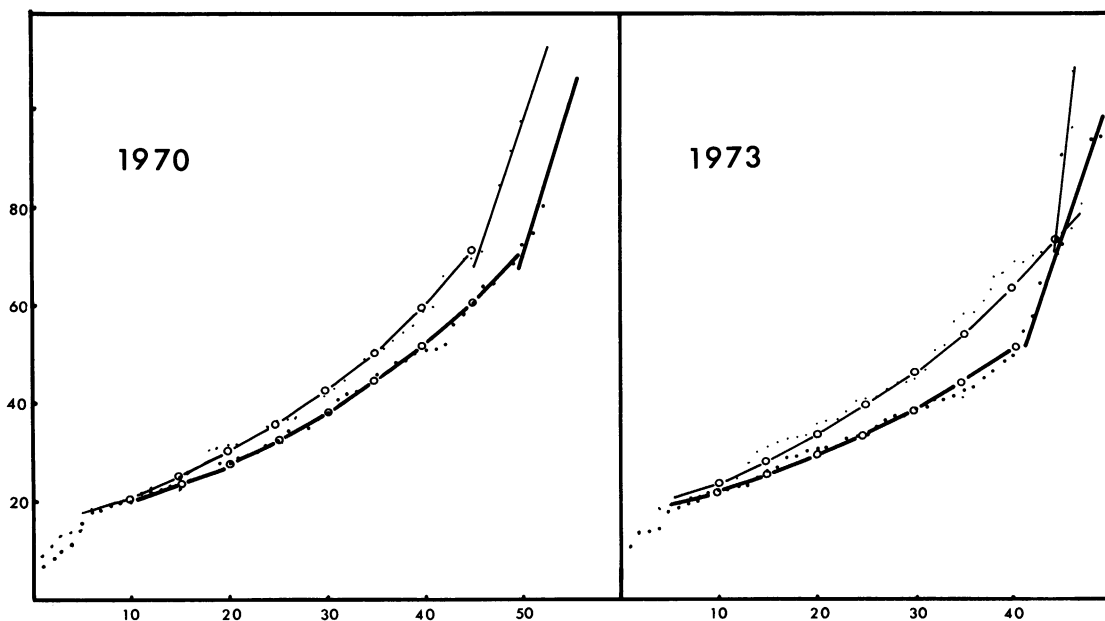


FIG. 5. Size-order curves for fishes of Tektite A. See text for explanation.



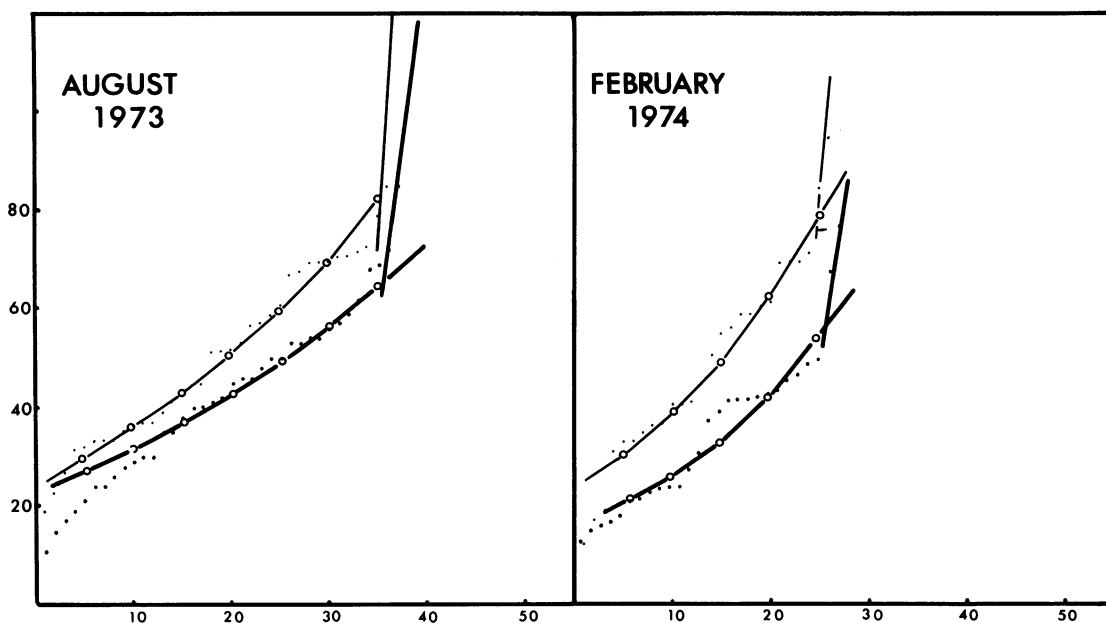


FIG. 6. Size-order curves for fishes of Bimini 1. See text for explanation.

cient is highly significant ( $P < .001$ ) for all but the February sample from Bimini 1 for which  $0.2 < p < 0.5$ . We believe that this also indicates limitation of length by competing species. One set of competitors may limit the realized size more than another. Laboratory experiments on growth in different competitive environments are sorely needed.

The curves from the Bimini 1 reef are more irregular and show less correspondence with the fitted curve than those from Tektite A. The February sample is the most erratic and we interpret this as evidence that the population had not recovered from the August sampling. Moreover, the February sample contained only 147 individuals, whereas the August sample had 563. In comparison with a reef from Nurse Cay in the southern Bahamas, repopulation of Bimini 1 reef seems to have been slow. The reef from Nurse Cay was sampled on March 21, 1965, and July 8, 1965, and the July sample contained more individuals (811 as compared with 229 in the March sample) and more species (61 vs. 43). Possibly this more rapid colonization was due to seasonal availability of recruits. Munro et al. (1973) have shown that while many West Indian fishes have

prolonged spawning seasons, there is a definite peak of reproductive activity in February and April. We would expect there to be a corresponding peak in abundance of late larval stages.

We visualize the reef-fish environment as consisting of a linear series of niches each of which can be filled only by fish of a certain size. These niches are defined by several factors such as size of shelter sites, size of food, size of hunting territory, etc., all of which directly or indirectly restrict the niche and allow it to be used only by fish of a certain size. We do not consider size to determine the niche but it is a feature by which the niche can be defined and quantified.

If a new reef were suddenly to appear, one that was complete in every way except that it had no fish, and if this reef were to be colonized by a single fish we would expect that that individual would enter the habitat as a newly transformed pre-juvenile and as it grew, it would progress through a more or less predetermined series of size-limited niches until it reached its own maximum size. In doing so, its microhabitat and diet might undergo several changes, but the critical limiting factors at each stage would be correlated with size.

If the next individual to arrive on the reef were of the same species, it would go through the same stages and eventually would reach the same terminal niche. When that niche was filled to its carrying capacity, no more individuals of that species could be accepted into the community.

When individuals of other species arrived on the reef, they would also progress through a series of niches except that they would not be able to enter a niche that was already fully occupied. Since competitive interactions are not instantaneous, however, a rapidly growing fish might be able to utilize an occupied niche long enough to pass through it in order to move into the niche for larger fish. Competitive interactions would only affect species that were nearly the same size, in which case the presence of a larger species would prevent the smaller one from attaining its maximum size.

In this way the community would eventually become fully saturated. It would not, however, become static because as individuals die or emigrate, their places could be filled by the same species or by different species that will eventually move into higher order niches (i.e., niches that are available to larger fish).

In addition to the generally recognized seasonal superabundance of recruits entering the reef, two mechanisms operate to ensure that the niches there are fully utilized most of the time. First, a reservoir of more species than can occupy any given reef at any one time assures that there will always be some recruits ready to move into the reef or into higher order niches from the lower niches that they occupy as juveniles.

Second, because the growth of the individual can be slowed by environmental factors, a particular fish can remain in a lower order niche for a prolonged time period until a higher order niche becomes available.

This model suggests that: (1) Within the community there is a linear series of size-determined niches. A community in equilibrium will have all the niches filled and the size-order curve will be nearly smooth. (2) In coral reef faunas there are many species whose genetic size ranges overlap, hence a given size range can be occupied by more than one species; this accounts for the observation that when the fishes are removed from a particular site the assemblage of species that re-

populates the area will be similar but not identical. (3) Within the community there will be rejection of species whose size range is already occupied. Moreover the availability of the niche is determined by next higher and lower order species as well as by the presence or absence of species of the same size range. Thus, competitive interaction as related to size of individual fishes regulates the composition of the community.

The relative abundance of the species that make up the community can be explained by the quantities of necessary resources, such as space and food, that are available for each species. However, attempts to explain species composition in terms of the availability of resources are not satisfactory except in crudest terms. Obviously if the habitat is unsatisfactory for a given species that species will not be present but this does not suggest why one of two species of similar requirements will exclude the other. The size limitation model presented here, we believe, forms a working hypothesis that accounts for many of the observations on species composition of coral reef fish communities and this model may equally apply to a wide variety of other aquatic and terrestrial communities.

#### ACKNOWLEDGMENTS

The original field work for the study of Tek-tite Reef A was carried out as a part of project TEKTITE II. Our 1973 visit to the TEKTITE II site was sponsored by a grant from The American Philosophical Society Penrose Fund, grant no. 6719. The Flare reef was studied as part of Project FLARE (Florida Aquanaut Research Expedition) in 1972. We thank the personnel of TEKTITE II and the FLARE program for courtesies that made our work not only profitable but also enjoyable. Dr. O. Marcus Buchanan and his staff at the Virgin Islands Ecological Research Station went out of their way to make our stay pleasant and profitable. Drs. James W. Atz and Donn E. Rosen read the manuscript and offered helpful suggestions. Mrs. Alice M. Lawson checked the common names of the fishes and Mrs. M. Norma Feinberg checked the identifications of all the fishes in the samples. All of these have our appreciation.

## LITERATURE CITED

- Allen, Gerald P.  
1972. The anemone fishes their classification and biology. Neptune City, N.J., T. F. H. Publications, Inc., 288 pp.
- Dale, George  
[In press.] Observations on the cardinalfish population of a patch reef in the Bahamas. *Hydrolab Jour.*
- Loya, Y.  
1972. Community structure and species diversity of hermatypic corals at Eilat, Red Sea. *Marine Biol.*, vol. 13, no. 2, pp. 100-123.
- Loya, Y., and L. B. Slobodkin  
1971. The coral reefs of Eilat (Gulf of Eilat, Red Sea). *Symp. Zool. Soc. London*, vol. 28, pp. 117-139.
- Munro, J. L., V. C. Grant, R. Thompson, and P. H. Reeson  
1973. The spawning seasons of Caribbean reef fishes. *Jour. Fish Biol.*, vol. 5, pp. 69-84.
- Porter, James W.  
1972. Patterns of species diversity in Caribbean reef corals. *Ecology*, vol. 53, no. 4, pp. 745-748.
- Risk, Michael J.  
1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Res. Bull.*, vol. 153, 5 pp.
- Smith, C. Lavett  
1973. Small rotenone stations: a tool for studying coral reef fish communities. *Amer. Mus. Novitates*, no. 2512, pp. 1-21.  
[In press.] Analysis of a coral-reef fish community: sizes and relative abundance. *Hydrolab Jour.*
- Smith, C. Lavett, and James C. Tyler  
1972. Space resource sharing in a coral reef fish community. In Collette, Bruce B., and Sylvia A. Earle (eds.), *Results of the Tektite program: ecology of coral reef fishes*. Los Angeles County Mus. Sci. Bull. 14, pp. 125-170, 1 chart.
- 1973a. Direct observations of resource sharing in coral reef fish. *Helgoländer Wiss. Meeresunters.*, vol. 24, pp. 264-275.
- 1973b. Population ecology of a Bahamian suprabenthic shore fish assemblage. *Amer. Mus. Novitates*, no. 2528, pp. 1-38.
- Storr, John  
1964. Ecology and oceanography of the coral-reef tract, Abaco Island, Bahamas. *Geol. Soc. Amer.*, special paper, no. 79, 98 pp.











