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## Population Ecology of a Bahamian Suprabenthic Shore Fish Assemblage

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### ABSTRACT

The fishes living within 6 meters of the bottom around natural and artificial reefs on the outer shelf of the Great Bahama Bank were censused repeatedly during six observation periods of three to seven days each between March, 1970, and June, 1971. Counts were made through a closed-circuit television system (UTV) with the camera permanently mounted on the sea floor in water 17 meters deep. The television caused no disturbance to the fishes and permitted relatively accurate counts of the fishes that hover in the water column and are too wary to be approached by divers.

Sixty-six species were observed in a cylinder of water approximately 20 meters in diameter and 6 meters high. Thirty-three of the observed species were truly suprabenthic nomadic species; the rest were either benthic forms that used the lower part of the water column or midwater species that occasionally fed near the bottom.

The suprabenthic species are classified according to feeding specializations and an attempt is made to examine the interactions and flow of energy and information within the community. Some mechanisms for maintaining the homeostasis of the community are postulated.

### INTRODUCTION

Theoretical approaches to the general question of the origin and maintenance of diversity in natural communities recently have emphasized systems modeling techniques in attempts to analyze community

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structure and interspecies relationships. Mathematical models serve not only to quantify the data already at hand but also to suggest the most promising avenues for future research. All mathematical models, however, are limited by the basic assumptions on which they are founded, as well as by the precision of the qualitative and quantitative data on which these assumptions are made. Modelers, for example, are often limited (or prone) to treating predation as a single phenomenon when it is obvious to field observers that there are many kinds of predation and that subtle adaptations of morphology and behavior can affect the relationship between the predator and its prey. It is equally obvious that modeling would become a sterile exercise unless the systems ecologists were provided with the right kinds of basic data that would enable them to construct models that are close approximations of nature.

There is now abundant evidence that fish communities are more than random assemblages of species whose general habitat requirements happen to be similar. These associations are stable, particularly in the more speciose communities of the tropical littoral environments. This suggests that these communities are maintained in dynamic equilibrium by coadaptations for resource sharing (Smith and Powell, 1971, pp. 28–29).

The purposes of the present paper are to: (1) examine the community structure of the fishes that utilize the suprabenthic zone of the outer shelf region of the Bahamian Banks; (2) describe and define a nomadic fish community; (3) postulate mechanisms that control the structure and functioning of the community.

This suprabenthic assemblage of fishes is of particular ecological interest because it includes most of the largest higher order predators of the food chain of tropical reefs. It is also of practical concern because many of the species are valued as either sport or commercial fishes.

## METHODS

Analysis of the community structure of tropical marine shore fish assemblages often has been hampered by the difficulty of censusing in irregular and often labyrinthine habitats where collecting is difficult because traps and hand lines are ineffectual for a majority of the species and conventional nets cannot be used. The use of fish toxicants (usually rotenone-based preparations) and self-contained underwater breathing apparatus (SCUBA) has made it possible to sample small cryptic species effectively in these environments, at least at times when there is not too much current. Midwater species, on the other hand, and those that react to the diver by fleeing, cannot be sampled effectively in this way. These

midwater species either escape the rotenone altogether or succumb at such a distance from the point of application of the chemical that they are difficult to find before they are consumed by other animals. Even this qualitative sampling of midwater fishes is difficult, requiring large amounts of the toxicant and often resulting in undesirably large kills of benthic species in the area. Furthermore, when large amounts of rotenone are used, the samples usually include specimens from more than one habitat and are thus of limited use for ecological studies. Talbot and Goldman (In press) have found a partial solution to this problem in the use of explosives. An explosive can be planted and left in an area until the fishes settle back into their routine spatial and behavior patterns before detonation of the charge from a distance. This method, however, also is selective because some species are more vulnerable to shock waves than others, and because other species, especially small secretive ones, tend to become inextricably buried in the rubble resulting from an explosion.

Fortunately, however, it is not necessary to collect and kill the population in order to make a census and, in fact, any such sampling immediately precludes all efforts to monitor the community over a period of time. Alternative approaches include live trapping with marking, release and recapture, or visual counts without collecting specimens. Although visual census techniques are widely used for birds and large mammals, they have seldom been applied to fishes. One reason is that many aquatic environments are too turbid to permit such observations, and another is that open-circuit self-contained underwater breathing apparatus (SCUBA) is severely time limited and disturbs some fishes but not others. Hence, it introduces a bias that is difficult to evaluate. A part of the latter problem, however, can be avoided by the use of an underwater "blind" or observation chamber that remains in place long enough to be accepted by the fishes as part of their environment. Underwater television is essentially an unmanned underwater blind that has no time limit and causes no disturbance to the fishes. However, the instrument used in this study has some limitations. It cannot be used with low light levels and its monochrome resolution is not adequate for observing fishes smaller than about 30–50 mm. in standard length if they are more than a meter away from the camera housing. Moreover, viewing from a fixed point limits observation to the individuals that move into the field of view, and many cryptic and secretive fishes are never seen.

Perhaps an ideal approach to *in situ* studies of fish communities would be the use of an underwater television (UTV) with two cameras: one a color unit for daytime, and the other with an image intensifier device for night observations. These observations would need to be supplemented

with direct observations by divers working from a habitat and using silent rebreather SCUBA gear.

The underwater television used in the present study is permanently mounted on the sea floor at 17 meters depth, approximately 1.6 kilometers west of the Lerner Marine Laboratory on the island of North Bimini, Bahamas, on the eastern edge of the Gulf Stream. This installation was designed and built as part of a long-range bioacoustics program under the aegis of the Lerner Marine Laboratory staff and personnel of the University of Miami Institute of Marine Sciences (now the Rosenstiel School of Marine and Atmospheric Sciences). It has also been used for behavioral studies on fishes (Myrberg, 1972; Colin, 1971) because it permitted long-term observations without disturbing the fishes.

The television camera is mounted in a cylindrical housing topped by a clear plastic dome. The camera is aimed vertically against a mirror that can be controlled from an observation room at the Lerner Marine Laboratory. The mirror and the camera can be tilted up and down and rotated to sweep a full circle. It can also be focused and adjusted for distance and amount of light from the observation room. The volume swept by the camera is shown in figure 1. There are no lights so observation is restricted to the daylight hours.

The base of the plastic dome has 12 fasteners that can be seen when the mirror is tilted downward. These fasteners are 30 degrees apart and serve as marks for locating fishes in the field of view. It is convenient to assign them numbers like the dial of a clock with the 30-degree radial number 1,

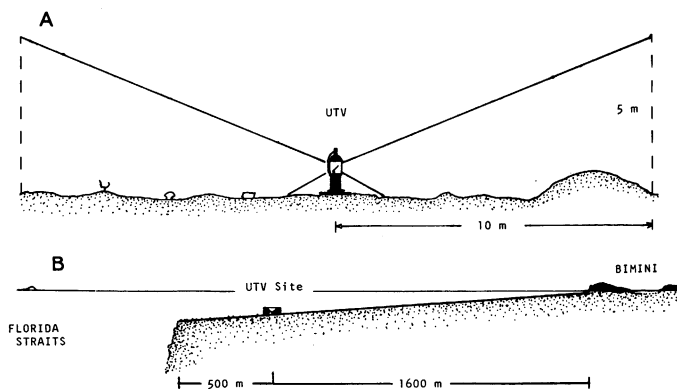


FIG. 1. A. Sketch showing volume scanned by Underwater Television Camera. B. Cross section of Great Bahama Bank west of Bimini indicating location of camera. Vertical scale greatly exaggerated.

the 180-degree radial number 6, and so on. The sectors between the radials are designated by the radial forming their right limit; thus, section 6 is the sector between the 150- and 180-degree radials.

For a standard sweep of the field of view the observer starts in sector 1 (the north sector, easily located because it is the limit of travel of the camera). The camera is moved until it is centered between radials one and two, then the mirror is tilted to scan the sector to the limit of the field of view and back, with the observer recording all the fishes present in that sector. The camera is then rotated to the next sector and the observer scans it in the same way. A full sweep, scanning all 12 sectors, takes about 10 to 20 minutes, varying according to the amount of activity and the numbers of fishes present at the time. The total number of sweeps plus additional UTV observations between sweeps represents about 70 hours of observations.

Observations were made at the following times:

March 1-7, 1970	38 sweeps
June 4-10, 1970	56 sweeps
December 7-13, 1970	52 sweeps
January 20-22, 1971	8 sweeps
May 5-7, 1971	10 sweeps
June 24-30, 1971	86 sweeps

During each of these observation periods we tried to make standard sweeps each hour during the daylight hours, although this was not always feasible. At times of low light levels or intense fish activity the sweeps were made more frequently.

Raw data from the individual sweeps were punched on paper or magnetic tape for use with specially written computer programs that permitted combining the data and calculating diversity indexes. These programs were designed for use with a shared time system.

Identification of fishes through the television requires some practice. Colors usually used for field identifications are not available when a monochrome camera system is used, and many important morphological details cannot be observed. Identifications from the UTV monitor screen must therefore be based on monochromatic color patterns, shape, and perhaps to a greater degree than usual, behavioral traits. These identifications were greatly aided by firsthand knowledge of the fishes in the vicinity of the UTV gained in part by SCUBA diving in that area before and during the course of UTV observations. After the first few days we had reasonable confidence in most of our identifications. Some individuals, however, did not remain in view on the UTV long enough for positive recognition. Length estimates of fishes are given as total length.

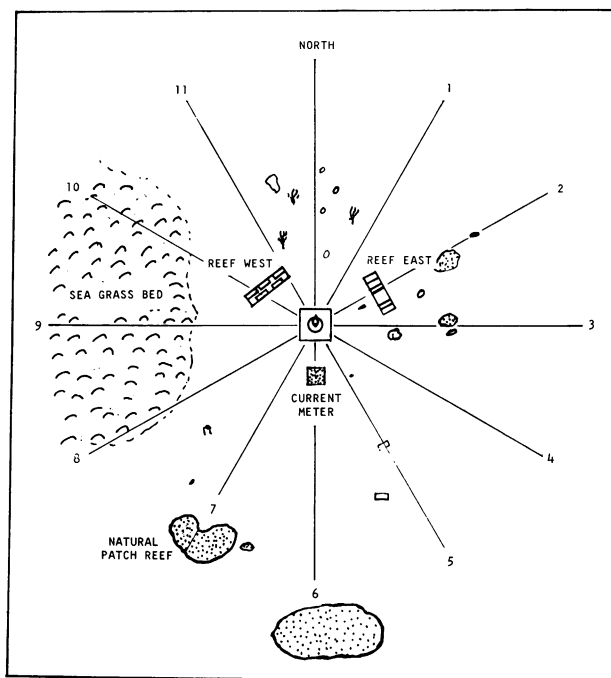


FIG. 2. Map of visible landmarks in range of Underwater Television Camera.

The television camera is situated near the center of a slight depression (about 25 meters diameter), on a bottom mostly composed of a marine limestone, with a layer of sand covering all but occasional outcrops. The depression is surrounded by low, rocky mounds 1 to 3 meters high, covered with dense stands of brown algae, with some corals and sponges. One of these natural mounds is close enough to be studied through the television but the others are too far away to consistently be seen clearly. Several man-made structures are in the camera field: the base and post supporting a current meter; a series of concrete blocks supporting Secchi disks, miscellaneous pieces of wire rope, chains, float lines, etc., and two concrete block artificial reefs designated Reef East and Reef West. The visible field is mapped in figure 2.

#### ACKNOWLEDGMENTS

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and made all phases of the work go smoothly. Joel Jay Sohn assisted with the diving and with the preliminary phases of data taking. Computer time and many incidental expenses were provided by the American Museum of Natural History.

FISHES OF THE SUPRABENTHIC ZONE

Observations through the television and by divers suggest that the greatest concentration of fishes occurs within 3 meters of the substratum. This layer, which we term the suprabenthic zone, is utilized by three groups of fishes: benthic residents that move up into the water column to feed; midwater fishes that spend most of the time more than 3 meters above the bottom but occasionally descend to feed; and wandering fishes that have large home ranges or are completely nomadic (fig. 3).

These categories can be identified subjectively on the basis of observations but they can also be recognized objectively on the basis of pattern of occurrence. In figure 4 the cumulative total number of species is graphed against the number of sweeps during the June, 1970, December, 1970, and June, 1971, observation periods. This is essentially the same as the familiar species-area curve used by ecologists with the quadrat sampling methods, except that in this case the observation point is fixed and the organisms move into the field of view.

For each observation period the pattern is the same. There is an initial period of rapid increase, then an inflection point followed by a less rapid increase. After a second inflection point the total continues to rise but slowly and more erratically. The first part of the curve includes most of the benthic residents with home ranges smaller than the area swept by the

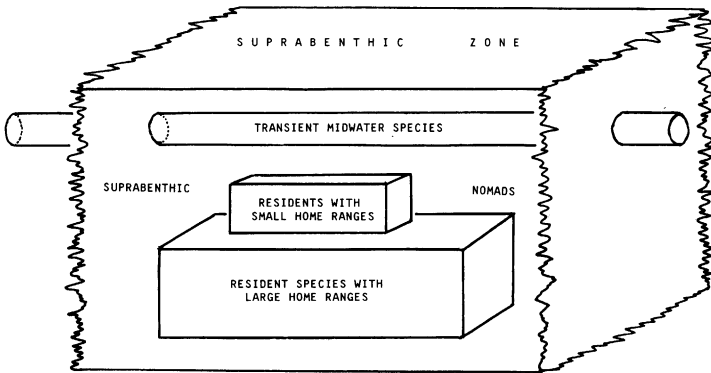


FIG. 3. Types of fishes of suprabenthic zone.

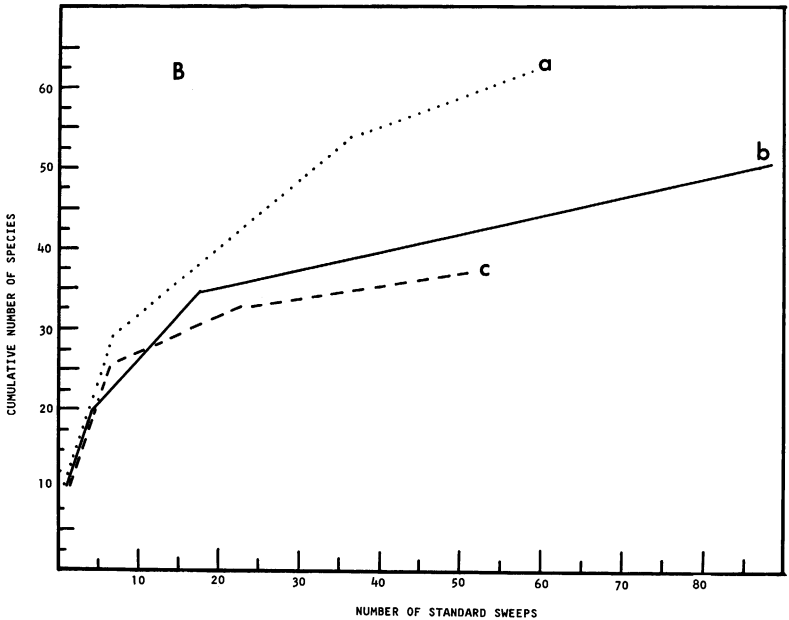
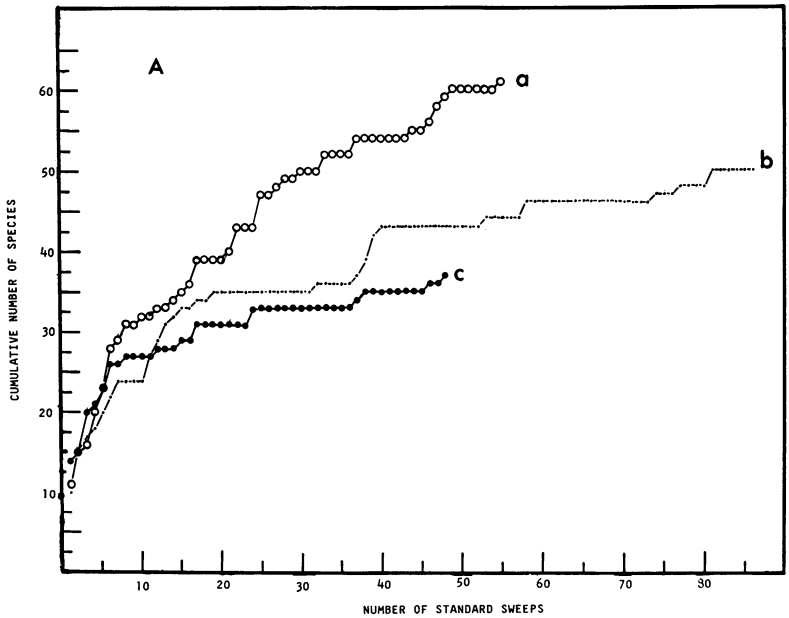


FIG. 4. "Species Area Curves." In A, cumulative number of species recorded are plotted against number of sweeps made in: (a) June, 1970, (b) June, 1971, and (c) December, 1970. In B, curves are shown without data to emphasize inflection points.



television, while the second part also includes the residents with large home ranges that spend a lesser fraction of their time within the viewing area. The last part of the curve encompasses the nomadic species, both the suprabenthic forms and the midwater visitors. Presumably the list would increase as long as the observations continued because in time every West Indian species large enough to be seen on the UTV would be recognized and this could ultimately include more than 300 species.

These curves also emphasize that, because of the low number of sweeps during the January and May, 1971, observation periods, little importance can be attached to the absence of any given species. The January observations especially were made under poor viewing conditions and during a severe storm that affected the behavior patterns of the fishes.

### ANNOTATED LISTS OF THE SPECIES OBSERVED

A. **BENTHIC RESIDENTS**—species with places of retirement or home ranges on or in the bottom within the effective visual range of the UTV, although they may feed well up in the water column.

1. *Holocentrus ascensionis* (Osbeck): A single, large longjaw squirrelfish was observed consistently hovering over the eastern part of the natural patch reef in sector 7 during the June, 1970, observation period. Another large individual was seen during the 1971 observation periods, but in a natural patch reef just at the limit of vision in sector 3 where it could only be seen when the light conditions were ideal. The latter individual was not included in our calculations as it was outside of the volume consistently censused effectively with the television. This species apparently is disturbed either by the sound or sight of divers, for its behavior as observed through the television is somewhat different from that seen by divers. Day after day it hovered about a meter above the substrate, remaining essentially motionless. At this time its color pattern was blotched with a dark hourglass-shaped blotch behind the head and a diamond-shaped blotch on the side below the soft dorsal fin with the head, tail, and interspace blanching white. At the approach of a diver it repairs to shelter spaces in caves and holes.

2. *Serranus tabacarius* (Cuvier): The tobacconfish is a very common species in the area and was present during all six observation periods. It was recorded in 58 percent of the sweeps made in June, 1970, in 88 percent of the sweeps during December, 1970, and in 59 percent of the sweeps during June, 1971. It was usually seen hovering or swimming slowly about 0.5 meters above the bottom. Its slow movements, conspicuous color pattern, and exposed position make it easy to census. Juveniles were rarely seen at the television site, although we observed small individuals of about 30 to 40 mm. length in the Virgin Islands during October, 1970. It is usually solitary, although as many as five or six individuals might be seen during a standard census sweep.

3. *Serranus tigrinus* (Bloch): The harlequin bass is a smaller but more conspicuously patterned species than *S. tabacarius*, and hovers closer to the substratum. It was recorded during all six observation periods but was less abundant than *S. tabacarius*; in June, 1970, it appeared in only 13 percent of the standard sweeps, in

June, 1971, it was present in 41 percent, and in December, 1970, it was recorded in 38 percent.

4. *Epinephelus fulvus* (Linnaeus): The coney is a small species of grouper that was observed while SCUBA diving in the natural patch reef in December, 1970. It was observed through the television near both of the artificial patch reefs in May and June, 1971, where it appeared, respectively, in 50 and 49 percent of the sweeps. It usually lurks near bottom structures, but occasionally it swims leisurely from one shelter to another. Collette and Talbot (1972) found that it was a primarily nocturnal forager, although it is often seen and caught during the daylight hours. Apparently its daily cycle is not clearly divided into periods of activity and inactivity.

5. *Epinephelus cruentatus* (Lacépède): The graysby was recorded during all six of the observation periods, in 33 to 75 percent of the sweeps. One individual moved into the artificial reefs within minutes after the reefs were first erected and others were seen around the reefs on numerous occasions. It spends most of its time resting on the bottom in reef caves or against outcroppings, occasionally venturing out and cruising slowly a few centimeters above the bottom.

6. *Epinephelus striatus* (Bloch): The Nassau grouper is one of the most conspicuous resident serranids. Its large size and distinctive color pattern make it unmistakable and yet the vertical banded color pattern apparently serves as camouflage when the fish is among dense gorgonians. Sometimes a large grouper would rest against the television dome and obstruct the view. More than one individual was involved for we occasionally saw two in the field at one time but usually it was our impression that a single individual returned again and again to the site. A measure of the area being patrolled by the individual can be made by comparing the time spent at the site with the time between consecutive visits. There is no reason to assume that the fish passes through the area swept by the television any more or less rapidly than it does through the rest of its hunting range. Therefore a simple proportion gives at least a crude approximation of its hunting range. Five such estimates on June 9 and 10, 1970, yielded estimates ranging from 1884 to 5652 square meters.

7. *Haemulon album* Cuvier: The margate was seen during all six observation periods in 21 to 60 percent of the sweeps. We consider it to be a suprabenthic resident, although it might also be a very abundant but nomadic species. Until individuals can be tagged it is impossible to be certain whether the same or different individuals are seen each time. This grunt seems to show definite periods of increased activity during early morning and late afternoon. During June, 1971, one individual settled on a concrete block in sector 10, posturing for a few seconds before swimming away. We visited the spot later and found that there was an anemone with several "cleaning" shrimp, *Periclemenes pedersoni*, around its tentacles, within the cavity of the concrete block. Apparently the grunt was being cleaned by the shrimp at the time of its visit. Through the television the grunt appears pale with a very dark tail and soft dorsal fins. Its general shape is quite similar to typical lutjanids.

8. *Malacanthus plumieri* (Bloch): The sand tilefish is well known for its habit of piling bits of coral debris into large mounds, beneath which it has a burrow. It was often observed transporting fragments in its mouth to a mound at the south end of the East Reef and also around the base of the current meter. It was recorded in all six of the observation periods in 50 to 94 percent of the sweeps. Two to four

individuals were usually present. On several occasions during the December, 1970, observation period it was seen digging channels in the sand using its anal fin in an undulating fashion.

9. *Pseudupeneus maculatus* (Bloch): The spotted goatfish is one of the species that was consistently present in a large proportion of the samples during all six observation periods. It occurs in polarized schools of as many as 25 individuals, but groups this large are apt to be composed of smaller individuals. Larger individuals seem to travel in loose schools of about two to five individuals. Although we frequently saw them feeding, more often they were merely cruising around the area close to the bottom. Through the television they appear light in color with a row of four dark spots along the side, the anteriormost of which is the eye.

10. *Equetus lanceolatus* (Linnaeus): The jack-knife fish was not seen in June, 1970. It spends most of the day under ledges and deep within the artificial reefs so it was often missed on the television. This is undoubtedly why it was recorded in only (an average of) 43 percent of the sweeps. At least two individuals were present during June, 1971, and five were seen in Reef West during December, 1971.

11. *Pomacentrus partitus* Poey: The bicolor damselfish was, during all six observation periods, the only species recorded during each and every standard sweep. There was a dense population in the area and during some sweeps as many as 55 to 60 individuals were observed. These demoiselles spend most of the day cropping plankton well up in the water column. Counts tend to be somewhat higher early in the morning and late in the afternoon but this may be biased by the fact that large individuals during most of the daylight hours tend to move high into the water column where they are difficult to see with the television. During SCUBA observation periods the populations were closer to the substrate and appeared more numerous, apparently because they moved closer to shelter in response to the divers. Myrberg (1972) has made an extensive study of the behavior and habits of this species from the same UTV installation.

12. *Chromis cyaneus* (Poey): The blue chromis was seen during all six observation periods in 35 to 90 percent of the sweeps. In the television the blue color shows as white. This species tends to feed high in the water column during the day and was usually present over the natural patch reef in sector 7. Its absence during some sweeps probably was a result of its being so high in the water column that it could not be seen when the sun was close to the meridian. Like *Pomacentrus partitus* it is a daytime plankton feeder.

13. *Chromis multilineatus* (Guichenot): The brown chromis has habits similar to the blue chromis and they often feed in the same area. Usually several could be seen above the natural patch reef in sector 7. In the television they appeared much darker than *C. cyaneus* and usually there was a conspicuous white saddle-shaped spot at the end of the dorsal base. It was present during all six observation periods in 29 to 88 percent of the sweeps.

Apparently these two species of *Chromis* in the Bahamas utilize the same food resources, but, because the abundance of the plankton on which they feed is independent of the abundance of the fishes, there is no food shortage and no competition. Certainly this is a case in which food is not a limiting factor. A study of the way in which these plankton feeders maintain their equilibrium is much needed. We suspect that shelter sites for the nocturnal inactive periods in nooks and crannies of reefs are the limiting factors to population densities.

14. *Thalassoma bifasciatum* (Bloch): The bluehead wrasse was one of the most

abundant and conspicuously present species, occurring during all six observation periods in 85 to 100 percent of the sweeps. Large supermales are readily recognized, but the juveniles and females (the *nitidum* color phase) resemble both *Halichoeres garnoti* and *maculipinna* in the UTV monitor, and at a distance they are easily confused or overlooked. We did not see evidence of reproductive activity at the television site, although it spawns throughout the year and we did see a large spawning aggregation near South Bimini in June, 1970.

15. *Halichoeres garnoti* (Valenciennes): All color phases (juvenile, female, low male, supermale) of the yellowhead wrasse were common around the television and it occurred during all six observation periods in 60 to 87 percent of the sweeps. Juveniles with the longitudinal blue stripe were difficult to recognize through the television and may have been missed during some sweeps. Like the other wrasses in the study area, it spends most of its time inspecting and picking at the substrate, presumably cropping small invertebrates. Both *H. garnoti* and *Thalassoma bifasciatum* often follow feeding goatfishes, themselves feeding on small organisms that escape or are unwanted by the goatfishes.

16. *Halichoeres maculipinna* (Müller and Troschel): The clown wrasse is distinguished through the television by its wide, lateral dark band with a narrower (bright yellow in life) band along the dorsal side of the body. It is less common than *H. garnoti* and its occurrence seems to be more erratic. It was present in 8 to 50 percent of the sweeps of five of the observation periods, but in December, 1970, it was recorded in 81 percent of the sweeps. However, not too much weight should be attached to these figures because of the possibility of misidentifications and the overlooking of small individuals. No supermales were seen.

17. *Halichoeres bivittatus* (Bloch): The slippery dick is easily recognized by its color pattern of two narrow longitudinal dark stripes on a light background. It was seen during all six observation periods in 40 to 92 percent of the sweeps. Most of the individuals were rather small. This species spends most of its time foraging over sand flats and around the base of the reef, singly or in groups of two or three.

18. *Bodianus rufus* (Linnaeus): The Spanish hogfish is a midwater species, small individuals of which occasionally came close to the camera housing and were frequently seen near the natural patch reefs. It was present in 29 percent of the sweeps in March, 1970, 12 percent in June, 1970, and only 6 percent in December, 1970. It was not seen in January or May, 1971, but was observed once in June, 1971. Its conspicuous shape and color pattern make it readily identifiable, and we suspect that these figures represent its true abundance. Small individuals sometimes remained near the dome for hours at a time.

19. *Opistognathus aurifrons* (Jordan and Thompson): The yellowhead jawfish was introduced at the UTV site during a behavioral study (Colin, 1971) in 1969. It is difficult to see with the television unless specifically sought, but once located it can be seen hovering over its home hole, occasionally rearranging the stone around the burrow entrance. Apparently this fish is reproducing in the area, for we have the distinct impression that the fish were smaller in June, 1971, than they had been in December, 1970, suggesting that the adults had been replaced by another generation. The fish spent most of its time hovering over the burrow, occasionally darting upward, presumably to crop a passing zooplankton. The approach of many fishes was ignored, but groups of wrasses and especially the approach of *Malacanthus plumieri* caused it to withdraw. Upon emerging it almost always spat out a

mouthful of sand. From time to time it made short forays to pick up a bit of coral rock to deposit near the opening of the burrow.

20. *Sparisoma aurofrenatum* (Valenciennes): Juveniles of the redband parrotfish appeared striped but almost always showed the conspicuous saddle-shaped white spot at the base of the dorsal fin (similar to that of *Chromis multilineatus*). It was present during all the observation periods in 50 to 94 percent of the sweeps, except for the first observation period when it was either not present or went unrecorded.

21. *Acanthurus bahianus* (Castelnau): The ocean surgeonfish appeared in so many sweeps (86 to 100%) during all six observation periods that we consider it to be a benthic resident, although there is the possibility that it is a very abundant nomad and the fish we saw were often different individuals. The other two species of acanthurids (*A. coeruleus* and *chirurgus*) are clearly wanderers. The shape and the white caudal peduncle of *A. bahianus* serve as recognition characters. The species forages, often in pairs, over hard bottom and was primarily day active. Generally more individuals were seen in the morning than at other times.

22. *Canthigaster rostrata* (Bloch): The sharpnose puffer was present during all six observation periods in 50 to 83 percent of the sweeps. It spends most of its time hovering close to the surface, sometimes cropping organisms off the rock or the television dome. During a dive to the camera, we observed two individuals of this species circling each other near one of the natural patch reefs.

**B. CRYPTIC BENTHIC RESIDENTS**—Species too small or well hidden to be seen on the UTV.

In addition to the 22 benthic resident species observed through the UTV, there were many other species of small fishes present in the vicinity of the television. On three separate occasions (June, 1970, December, 1971, and April, 1972) we attempted to make rotenone collections in order to census these species but none of these were satisfactory, owing to strong currents that carried the toxicant away before the fishes were affected. The following list is therefore only a partial tabulation of the infaunal fishes of the UTV site. The June, 1970, collection was taken approximately 100 yards north of the UTV. The June, 1971, collections were taken 50 yards east of the camera and at both of the artificial reefs (Reef East and Reef West [RE, RW]). The April, 1972, collection was from the natural patch reef in sector 8.

1. *Kaupichthys hyoprорoides* (Strömann)—June, 1970, June, 1971 (RE)
2. *Gymnothorax moringa* (Cuvier)—June, 1971 (RE)
3. *Moringua edwardsi* (Jordan and Bollman)—June, 1971 (RE)
4. *Antennarius multiocellatus*—June, 1970
5. *Holocentrus coruscus* (Poey)—December, 1971<sup>1</sup>
6. *Scorpaena plumieri* Bloch—June, 1970<sup>1</sup>

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<sup>1</sup> Species observed but not collected.

7. *Scorpaena* sp.—June, 1970
8. *Scorpaena albifimbria* (Evermann and Marsh)—April, 1972
9. *Pseudogramma bermudensis* (Kanazawa)—June, 1970, June, 1971 (RE)
10. *Epinephelus guttatus* (Linnaeus)—June, 1970<sup>1</sup>
11. *Apogon binotatus* (Poey)—June, 1970
12. *Apogon townsendi* (Breder)—June, 1971
13. *Apogon maculatus* (Poey)—June, 1970, April, 1972
14. *Astrapogon puncticulatus* (Poey)—June, 1970
15. *Centropyge argi* Woods and Kanazawa—June, 1971
16. *Pomacentrus variabilis* (Castelnau)—June, 1970, June, 1971
17. *Amblycirrhitus pinos* (Mowbray)—June, 1970
18. *Sparisoma radians* (Valenciennes)—June, 1970
19. *Sparisoma atomarium* (Poey)—April, 1972
20. *Starksia lepicoelia* Böhlke and Springer—June, 1970
21. *Starksia nanodes* Böhlke and Springer—June, 1971 (RE)
22. *Labrisomus haitiensis* Beebe and Tee-Van—June, 1970
23. *Gnatholepis thompsoni* Jordan—June, 1970, June, 1971 (RE, RW)
24. *Coryphopterus glaucofraenum* Gill—June, 1970, June, 1971 (RE, RW), April, 1972
25. *Coryphopterus dicrus* Böhlke and Robins—June, 1971 (RE)
26. *Coryphopterus eidolon* Böhlke and Robins—June, 1971 (RE), April, 1972
27. *Coryphopterus thrix* Böhlke and Robins—June, 1970, June, 1971 (RE)
28. *Quisquilius hipoliti* (Metzelaar)—June, 1970, June, 1971 (RE, RW), April, 1972
29. *Diodon holocanthus* Linnaeus—June, 1971 (RW)

C. MIDWATER VISITORS—Species that normally live high in the water column but occasionally descend to search for food.

1. *Carcharhinus* sp.: Sharks appeared only infrequently and usually swam past without pausing, apparently unaffected by the television. Sightings were in March and June, 1970, and June, 1971. Whether their absence in December and January was due to sampling error or to their scarcity is not known, but collectors from the Lerner Marine Laboratory report that sharks are generally less easily caught during the colder months.

2. *Sphyræna barracuda* (Walbaum): Although the great barracuda is common in the vicinity of the UTV, it was observed through the television only once, in December, 1970, when a single individual passed close to the television. This large predator normally hovers and patrols well above the bottom. Small individuals are common in nearby shallower waters in many cove areas. Its size and profile make it easily identifiable.

3. *Scomberomorus regalis* (Bloch): The cero apparently ranges throughout the water column more freely than does the great barracuda and we have often encountered it while diving. It often cruises singly or in pairs within a meter or two of the bottom. It was recorded through the television in June, 1970, May, 1971, and June, 1971, but not in December, 1970, or March, 1970. Again, however, this could be because of sampling error rather than any seasonal abundance. Its shape and color pattern are unmistakable.

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<sup>1</sup> Species observed but not collected.

4. *Canthidermis sufflamen* (Mitchill): Ocean triggerfish were seen through the television only in June, 1970, and June, 1971. Easily recognized by their size, shape, and distinctive way of swimming, they were often encountered while diving on the outer shelf area, usually well above the bottom, often in groups of two to five or many more.

5. *Aluterus scriptus* (Osbeck): The scrawled filefish was seen through the television only in June, 1970, and June, 1971. This large filefish is often seen at or near the surface around ships and piers or floating sargassum weed.

D. SUPRABENTHIC NOMADS—Species that move about constantly in search of food. These species either have no definite home range or home ranges so large that they are, in effect, wanderers. Some are bottom feeders; others feed well up in the water column.

1. *Dasyatis americana* Hildebrand and Schroeder: The southern stingray is a large species that passed the television infrequently. It was recorded in June, 1970 (2% of sweeps), December, 1970 (41%), and June, 1971 (4%). Occasionally one would bury itself and remain motionless in the sand for some time, but it was not likely to be seen unless it was in motion. No more than one was observed at a time. Their appearance did not seem to be confined to any particular time of day although there are so few sightings that cycles might not be noticed.

2. *Urolophus jamaicensis* (Cuvier): The yellow stingray is a small species that was a more frequent visitor, having been recorded during all six observation periods in 6 to 21 percent of the sweeps. Occasionally one would remain in the area for a short time, but usually they continued past without stopping. They seemed to be most active between 0700 and 0900 hours and between 1500 and 1900 hours.

3. *Synodus synodus* (Linnaeus): Lizard fishes believed to be this species (the red lizardfish) were recorded in March and June, 1970, and in June, 1971, but they were not common (1 to 6% of the sweeps). They rested motionless on the bottom near the camera and moved in only short spurts. The shape is characteristic but we are uncertain of the species as the detail through the camera is not adequate for specific identification.

4. *Dactylopterus volitans* (Linnaeus): A single individual believed to be a flying gurnard passed by the television camera during March, 1970. Its swimming motion strongly resembled that of a ray but its body profile appeared similar to a slender *Acanthostracion*. The light was too poor for a positive identification but we believe it was this species.

5. *Mycteroperca bonaci* (Poey): The black grouper was recorded only during March, 1970, December, 1970, and May, 1971. It merely passed by the television without responding to it or the surroundings. This species is easily recognized by its generally pallid color and the black margins on the soft dorsal, caudal, and anal fins. It may or may not show large quadrate blotches on the upper sides.

6. *Mycteroperca venenosa* (Linnaeus): The yellowfin grouper is distinguished from the black grouper by its spotted pattern and from other groupers by shape. This is the most common *Mycteroperca* in the Bahamas. It was seen only in March and June, 1970, and June, 1971, a total of seven sightings.

The yellow margin of the pectoral fin, conspicuous in life, is not particularly noticeable through the television.

7. *Mycteroperca interstitialis* (Poey): The yellowmouth grouper is not common in the Bahamas, and it was seen at the television only twice, once in June, 1970, and

again in December, 1970. In each instance it passed by the television without stopping.

8. *Trachinotus goodei* Jordan and Evermann: The palometa is a distinctive pompano that is often seen in small schools over sandy bottoms near shore. We have only a single record of it near the television, in June, 1970.

9. *Elegatis bipinnulata* (Quoy and Gaimard): A school of about 20 rainbow runners was seen twice in June, 1970. On June 8 a group of five individuals swam past at 1913 hours and on June 9 about 15 were around the television between 0806 and 0830. In both cases the rainbow runners were in a mixed school with yellowtail snappers (*Ocyurus chrysurus*). On June 9 we also observed this species on a reef about 100 yards north of the television site, again accompanied by yellowtail snappers. On the last occasion the school was actively feeding on small fishes affected by our rotenone operation.

10. *Lutjanus analis* (Cuvier): The mutton snapper was recorded once in June, 1970, and 11 times (13%) in June, 1971. It is easily recognized by its size, shape, and small dark spot between the lateral line and the soft dorsal fin. On each occasion it was swimming slowly within a meter of the bottom.

11. *Ocyurus chrysurus* (Bloch): The yellowtail snapper was seen in June, 1970, and in December, January, and June, 1971, but it was not consistently present, occurring in only 6 to 13 percent of the sweeps. This is a streamlined fast-swimming species that travels in schools of five to 20 or more individuals. On two occasions it was seen in mixed schools with *Elegatis bipinnulatus*. It is a voracious piscivore.

12. *Haemulon striatum* (Linnaeus): During June, 1970, large aggregations of juvenile striped grunts of approximately 40 mm. length were seen during 75 percent of the sweeps. Counts of more than 300 were recorded, although these certainly did not represent the entire schools. Identification was confirmed by specimens rotenoned on a nearby reef. This species was not recorded again and we did not observe it near the television camera while we were diving.

13. *Calamus* sp?: Porgies of this genus were seen in only 2 to 11 percent of the sweeps in March and June, 1970, and June, 1971. Identification is uncertain, but we suspect they were *C. pennatulula* Guichenot, the pluma, which is the commonest species of the genus in the Bahamas.

14. *Chaetodon striatus* Linnaeus: The banded butterflyfish was recorded only during June, 1970, when a single individual was observed in the manatee grass during one series of sweeps in sections 9, 10, and 11. The color pattern is distinctive.

15. *Pomacanthus arcuatus* (Linnaeus): Large gray angelfish, often in pairs, were present in 12 to 33 percent of the sweeps during all observation periods except that of May, 1970. This species appears to have a wide home range, although we are not sure that the same individual returned to the site each time. The closely related *Pomacanthus paru* (Bloch), the French angelfish, was seen near the television site but was not recorded during our standard sweeps.

16. *Holacanthus ciliaris* (Linnaeus): The queen angelfish is most easily recognized by the intense blue ring that forms an ocellated spot on the forehead. It was usually present as a single individual during all six observation periods in 15 to 26 percent of the sweeps. We are not sure whether it was the same individual patrolling a home range or more numerous nomadic individuals passing the site. On rare occasions we saw two individuals at the same time and we are inclined to believe that this species is nomadic.

17. *Clepticus parrai* (Bloch and Schneider): The creole wrasse is a common mid-



water or suprabenthic species of the outer shelf, often occurring in schools, especially along the edge of the drop-off. The sporadic occurrence of single individuals, especially late in the evening, suggests that these were wanderers on forays away from their normal home in deeper water.

18. *Lachnolaimus maximus* (Walbaum): Solitary individuals of the hogfish appeared during four of the observation periods in 5 to 13 percent of the sweeps, but it was not recorded during the January or May, 1971, periods. This wrasse is recognized immediately by its shape and by the trailing dorsal fin spines. Through the television it appears pale with a dark bar from the mouth through the eye and onto the anterior edge of the dorsal fin, as well as by the dark caudal fin margin and dark dorsal fin base.

19. *Scarus coeruleus* (Bloch): The blue parrotfish occurred singly or in wandering groups of several individuals. It was recorded in March and June, 1970, and June, 1971, in 4 to 7 percent of the sweeps and was most frequently seen between 0700 and 0900 in the morning and between 1700 and 1800 in the afternoon.

20. *Scarus croicensis* Bloch: Striped parrotfishes present a severe problem in identification to divers and especially to UTV observers, but most of the striped juveniles around the television appeared to be juvenile *Sparisoma aurofrenatum* (Valenciennes), the redband parrotfish. Some, however, undoubtedly were either this species or *Scarus taeniopterus* Desmarest, the princess parrotfish. Such parrotfishes were recorded during all six observation periods in 2 to 40 percent of the sweeps.

21. *Scarus guacamaia* Cuvier: Groups of rainbow parrotfish occasionally passed the television. The size and pattern of dark and light blotches distinguish this large species. Winn, Salmon, and Roberts (1964) showed that this species has definite home sites along the shoreline of Bermuda, but we saw it only rarely at the UTV site (4 to 11% of the sweeps during March, June, and December, 1970, and June, 1971). Possibly the UTV site is near the periphery of their large home range so that it was visited only infrequently.

22. *Sparisoma viride* (Bonnaterre): Spotted juveniles, females, and occasional high males of the stoplight parrotfish were seen in June, 1970, and May and June, 1971, in 10 to 15 percent of the sweeps. Color patterns of each of the phases are distinctive.

23. *Acanthurus coeruleus* Bloch and Schneider: The blue tang is easily recognized by its deep body and light (yellow) caudal spine. It was much less common than *A. bahianus* Castelnau, the ocean surgeon (see Benthic residents). The blue tang was recorded in 23 to 35 percent of the sweeps during all observation periods except May, 1971, at which time it was not recorded.

24. *Acanthurus chirurgus* (Bloch): The doctorfish resembles *A. bahianus* but usually has a series of narrow vertical lines on its side that were clearly visible through the television. It was seen only in March and June, 1970, in 7 to 13 percent of the sweeps.

25. *Bothus lunatus* (Linnaeus): Large peacock flounders occasionally wandered past the television. They often stopped moving for many minutes at a time, and on several occasions were observed resting motionless with the head and anterior part of the body upraised on an object such as a concrete block. It was not seen in December, 1970, or January and May, 1971, but it occurred in 7 to 15 percent of the surveys during the other observation periods.

26. *Acanthostracion quadricornis* (Linnaeus): The scrawled cowfish was a frequent

visitor but did not remain in view for more than a few minutes at a time. It was recorded during June, 1970, and June, 1971, in 7 and 13 percent of the sweeps. Recognized by the cephalic "horns" and color pattern, it is the more common of the two species of the genus in the Caribbean.

27. *Acanthostracion polygonius* Poey: The honeycomb cowfish, identified by its distinctive color pattern was seen only on one occasion, during June, 1971.

28. *Lactophrys triqueter* (Linnaeus): The smooth trunkfish was distinguished from *L. trigonus* (see below) by its deeper, more robust body and smaller size. Sometimes its color pattern of pale spots was visible. It was seen during 25 percent of the sweeps in March, 1970, and in 21 percent of the sweeps during June, 1970, but not at all during the other periods. This suggests that individuals of this species are wanderers, as is probably true of the other two species of this genus.

29. *Lactophrys trigonus* (Linnaeus): The trunkfish was identified mainly on the basis of its size and shape. It was recorded in 1 to 2 percent of the sweeps during June, 1970, December, 1970, and June, 1971. It is probably a wide-ranging nomad.

30. *Lactophrys bicaudalis* (Linnaeus): The spotted trunkfish was identified by its color pattern and backwardly directed spines on the posteroventral part of the body carapace which can easily be seen through the television. It was present in 2 to 6 percent of the sweeps during June and December, 1970.

31. *Balistes vetula* Linnaeus: The queen triggerfish was present in 38 percent of the December, 1970, sweeps, and in 9 percent of those during June, 1970, and June, 1971. This species is probably a resident with a large home range rather than a true nomad, but on the basis of its infrequent appearance we place it with the benthic nomads until more data can be gathered on its habits. It was often observed picking at organisms on the bottom.

32. *Cantherhines pullus* (Ranzani): The orangespotted filefish was recorded only during December, 1970, but it was also seen in the area at other times while we were diving. Like *Sparisoma aurofrenatum* and *Chromis multilineatus* it has a conspicuous white saddle-shaped spot at the posterior end of the dorsal fin base. Longitudinal stripes on the sides of the posterior part of the body and caudal peduncle were sometimes visible.

33. *Monacanthus tuckeri* Bean: Small filefish believed to be this species (slender filefish) were seen only during March, June, and December, 1970, in 6 (December) to 49 (June) percent of the sweeps. Through the television it appeared rhomboidal in shape sharply divided into a darker dorsal half and a lighter ventral half. Although one individual may remain in the area for some time, as evidenced by its consistent occurrence during the June observation period, it does not appear to have a definite home, and we have classed it as a nomad.

## ARTIFICIAL REEF HABITATS

On March 4, 1970, two reefs of 10 by 20 by 40 centimeter concrete blocks (the standard 4 by 8 by 16-inch builder's units) were built in the camera field, one in sectors 2 and 3, designated Reef East and the other in sectors 10 and 11, designated Reef West. Figure 5 shows the design of these two reefs. Both were in areas that previously had only a sandy bottom with some turtle and manatee grass. The reefs originally were oriented so as to be in full view of the camera, with the openings so arranged that the

observer could see through most of the apertures in each of the reefs. The cement blocks were locked with large nails slipped through holes that had been drilled before emplacement.

Within one-half hour after the two artificial reefs were set in place, a small graysby, *Epinephelus cruentatus*, had moved into Reef East and stayed in the general vicinity for the remaining three days of that observation period. By June, 1970, the artificial reefs were covered with a thin growth of filamentous algae and were being utilized by numerous species of fishes.

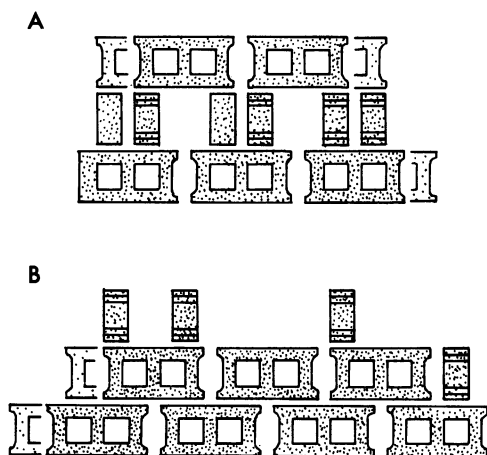


FIG. 5. Concrete block artificial reef structures. A. Reef West. B. Reef East.

By December, 1970, there was a dense growth of *Padina* algae, which increased in density until the following May. By June, 1971, however, there was a general regression of the *Padina* and in December, 1971, this algae was sparse, but some small stony corals were growing on the reef. The reefs remained upright until the week of January 18, 1971, when currents caused by a severe storm undermined the sand on which they rested and Reef East tipped over. At that time the blocks and nails pinning them together were sufficiently cemented together by natural factors so that the structures remained intact. By May, 1971, Reef West also had tipped over, from unobserved causes. On June 27, 1971, the artificial reefs were treated with emulsified rotenone in an attempt to collect all the fishes dwelling within the structures. Some difficulty was encountered, for the rotenone was not effective and the current was particularly strong; nevertheless 13 species were collected from Reef East and eight species from Reef West. Their presence demonstrates that cement block artificial reef structures are acceptable habitats for at least some fishes that are typically inhabitants of living coral reefs.

## FISHES COLLECTED FROM THE ARTIFICIAL REEFS

1. *Urolophus jamaicensis* (RW)
2. *Kaupichthys hyoproroides* (RE)
3. *Moringa edwardsi* (RE)
4. *Gymnothorax moringa* (RE)
5. *Pseudogramma bermudensis* (RE)
6. *Serranus tigrinus* (RW)
7. *Pomacentrus partitus* (RE, RW)
8. *Thalassoma bifasciatum* (RE, RW)
9. *Halichoeres garnoti* (RW)
10. *Starksia nanodes* (RE)
11. *Gnatholepis thompsoni* (RE, RW)
12. *Coryphopterus glaucofraenum* (RE, RW)
13. *Coryphopterus eidolon* (RE)
14. *Coryphopterus thrix* (RE)
15. *Coryphopterus dicrus* (RE)
16. *Quisquilius hipoliti* (RE, RW)
17. *Diodon holacanthus* (RW)

## DENSITY OF BENTHIC RESIDENTS

Table 1 gives the average number of individuals observed per sweep during the observation periods. These cannot be considered exact counts for undoubtedly there were some individuals consistently missed, and this was probably only partly compensated for by those that were counted more than once during each sweep. The main use of these figures is as an estimate of the relative abundance, consisting of occurrence and seasonal changes in the benthic fishes that use the suprabenthic zone.

LIMITS AND STABILITY OF THE  
SUPRABENTHIC FISH COMMUNITY

Although benthic residents, midwater visitors, and suprabenthic nomads all utilize the suprabenthic zone, it appears that the suprabenthic nomadic species can be treated as a distinct community. They are surely influenced more by each other than by members of either of the other two assemblages, simply because the potential for competition is greater. Midwater visitors, except during their short forays into the suprabenthic zone, occupy a different volume of water and their influence must be slight, although they may be important predators of suprabenthic fishes that stray too high in the water column. Some benthic resident species are undoubtedly important competitors of the suprabenthic species. The goatfish, for example, feed on about the same prey—interstitial invertebrates—that the sand-sifting rays do. The goatfish, however, appear to

TABLE 1  
DENSITY OF BENTHIC RESIDENTS  
(Average number seen per sweep.)

	March, 1970 <sup>a</sup>		June	Dec.	Jan.	May	June
	Before	After	1970	1970	1971	1971	1971
<i>Holocentrus ascensionis</i>	—	—	0.8	—	—	—	—
<i>Serranus tabacarius</i>	0.1	1.8	0.9	2.5	3.5	0.8	1.3
<i>Serranus tigrinus</i>	0.1	0.3	0.2	0.38	0.1	0.2	0.03
<i>Epinephelus fulvus</i>	—	—	—	—	—	0.8	0.9
<i>Epinephelus cruentatus</i>	—	0.4	1.0	0.38	0.8	0.8	0.2
<i>Epinephelus striatus</i>	0.2	0.6	0.3	0.6	1.0	0.1	0.2
<i>Haemulon album</i>	0.3	0.2	0.2	1.3	0.9	0.4	0.5
<i>Malacanthus plumieri</i>	1.3	1.8	0.9	3.6	2.1	1.9	0.8
<i>Pseudupeneus maculatus</i>	1.3	4.1	8.3	6.4	7.3	2.1	12.5
<i>Equetus lanceolatus</i>	—	—	—	—	—	—	0.5
<i>Pomacentrus partitus</i>	7.9	13.5	13.9	35.3	19.3	38.0	29.4
<i>Chromis multilineatus</i>	1.7	2.4	1.3	3.9	1.9	0.6	1.5
<i>Chromis cyaneus</i>	—	2.7	1.0	3.7	2.9	4.5	2.9
<i>Thalassoma bifasciatum</i>	3.9	5.8	3.3	8.0	6.9	4.6	8.5
<i>Bodianus rufus</i>	0.4	0.3	0.1	0.06	—	—	0.01
<i>Halichoeres garnoti</i>	1.2	3.3	1.6	2.4	1.6	0.7	1.8
<i>Halichoeres maculipinna</i>	0.1	0.1	0.5	2.3	1.9	0.6	0.9
<i>Halichoeres bivittatus</i>	3.6	5.0	2.5	1.8	1.9	0.5	1.2
<i>Sparisoma aurofrenatum</i>	0.1	0.04	0.7	1.05	1.3	1.4	3.4
<i>Opistognathus aurifrons</i>	—	—	0.5	1.7	—	—	0.06
<i>Acanthurus bahianus</i>	2.4	3.5	1.6	2.9	3.8	1.8	3.7
<i>Canthigaster rostrata</i>	1.1	1.5	0.8	1.1	0.5	1.5	1.7
Number of Sweeps	14	24	55	52	8	10	86

<sup>a</sup> The first and second columns are data taken during March, 1970, before and after the artificial reefs were built.

have definite home ranges and so the nomadic rays can avoid competition with the goatfishes merely by moving away from them.

The potential for interaction, it seems to us, is an aspect of community definition that is often overlooked or at least underemphasized. It appears that the most important kinds of interaction are competition (for food, space or nesting/courtship sites) and predator-prey relationships. A community, then, consists of *a group of species whose potential for interacting with one another is greater than their potential for interacting with other species.* At the same time, however, the members of the community must be mutually adapted for sharing the available resources, thus limiting competition. These criteria are especially pertinent when the community

is considered in an evolutionary context. The resource sharing mechanisms must have evolved in response to potential competition from other species and therefore only those species among which competition was possible could have had any influence on the directions the evolution of resource sharing mechanisms would take.

Each community must fit into its ecosystem and will have many kinds of interactions with physical and chemical factors and with other organism communities. We contend, however, that it is appropriate to study individual communities as we have defined them here because these are the unit "building-blocks" of ecosystems and the compartments on which systems ecology eventually can be based.

Observations through the television permit identification of the species that are suprabenthic nomads but they do not yield data as to the relative abundance of those species. Stability of the community can therefore only be measured in terms of when the fishes were seen at the UTV site. The patterns of occurrence are summarized in table 2.

Four reliable census periods are noted when we combine observations made before and after construction of the artificial reefs in March, 1970, and ignore the January and May observations because they are so incomplete. Eight species occurred in all four, nine in three, nine in two and seven were seen only during a single period. In other words, only about one-fourth of the nomads were seen during all observation periods but nearly 80 percent were observed during at least half of the observation periods. This is a minimum estimate of consistency because some other species may have been overlooked but it is unlikely that any were erroneously reported to be present.

In general, more species were recorded in both June samples than in the December sample and this may indicate that the fish move about more during June. Census data from June, 1970, June, 1971, and December, 1970, the three extensive observation periods, provide a measure of the consistency of the faunal composition of the community of fishes using the space around the television camera. For comparing the faunal lists of these observation periods we have used the following index of resemblance:

$$R = .5 \left( \frac{C}{T_1} + \frac{C}{T_2} \right)$$

Where C = the number of species recorded from both samples (censuses),  $T_1$  = total number of species in the first sample,  $T_2$  = total number of species in the second sample. This index is an average of the proportion of common species in the two samples and assumes equal sampling effectiveness.

TABLE 2  
PERCENTAGE OF SWEEPS CONTAINING SPECIES OF SUPRABENTHIC NOMADS

	March, 1970 <sup>a</sup>		June	Dec.	Jan.	May	June
	Before	After	1970	1970	1971	1971	1971
<i>Dasyatis americanus</i>	—	—	1.8	4.0	—	—	3.5
<i>Urolophus jamaicensis</i>	7.1	20.8	7.3	6.0	25.0	20.0	7.0
<i>Synodus</i> sp.	—	4.2	5.5	—	—	—	1.2
<i>Dactylopterus volitans</i>	—	4.2	—	—	—	—	—
<i>Mycteroperca bonaci</i>	7.1	4.2	—	2.0	—	10.0	—
<i>Mycteroperca interstitialis</i>	—	—	3.6	4.0	—	—	—
<i>Mycteroperca venenosa</i>	7.1	—	5.5	—	—	—	3.5
<i>Trachinotus goodei</i>	—	—	1.8	—	—	—	—
<i>Elegatis bipinnulata</i>	—	—	3.6	—	—	—	—
<i>Lutjanus analis</i>	—	—	1.8	—	—	—	12.8
<i>Ocyurus chrysurus</i>	—	—	10.9	13.0	12.5	—	5.8
<i>Haemulon striatum</i>	—	—	74.5	—	—	—	—
<i>Calamus</i> sp.	—	4.2	1.8	—	—	—	10.5
<i>Chaetodon striatus</i>	—	—	1.8	—	—	—	—
<i>Pomacanthus arcuatus</i>	—	33.3	12.7	12.0	12.5	—	16.3
<i>Holacanthus ciliaris</i>	21.4	16.7	25.5	15.0	25.0	20.0	23.3
<i>Clepticus parrai</i>	—	—	—	6.0	12.5	20.0	14.0
<i>Lachnolaimus maximus</i>	7.1	12.5	7.3	6.0	—	—	4.7
<i>Scarus coeruleus</i>	7.1	—	3.6	—	—	—	7.0
<i>Scarus croicensis</i>	57.1	37.5	36.4	8.0	12.5	40.0	2.3
<i>Scarus guacamaia</i>	—	8.3	7.3	4.0	—	—	10.5
<i>Sparisoma viride</i>	—	—	14.5	—	—	10.0	12.8
<i>Acanthurus coeruleus</i>	—	16.7	34.5	19.0	12.5	—	23.3
<i>Acanthurus chirurgus</i>	7.1	12.5	12.7	—	—	—	—
<i>Bothus lunatus</i>	7.1	4.2	14.5	—	—	—	4.7
<i>Acanthostracion</i>							
<i>quadricornis</i>	—	—	7.3	—	—	—	12.8
<i>Acanthostracion</i>							
<i>polygonus</i>	—	—	—	—	—	—	1.2
<i>Lactophrys triqueter</i>	7.1	25.0	3.6	—	—	—	—
<i>Lactophrys trigonus</i>	—	—	1.8	2.0	—	—	1.2
<i>Lactophrys bicaudalis</i>	—	—	5.5	2.0	—	—	—
<i>Balistes vetula</i>	—	12.5	9.1	38.0	—	—	9.3
<i>Cantherhines pullus</i>	—	—	—	2.0	—	—	—
<i>Monacanthus tuckeri</i>	—	8.3	49.1	6.0	—	—	—

<sup>a</sup> The first and second columns are data taken during March, 1970, before and after the artificial reefs were built.

RESEMBLANCE INDEXES BASED ON: (1) All species; (2) only the suprabenthic nomadic species; (3) only benthic residents:

	(1) ALL	(2) SUPRABENTHIC NOMADS	(3) BENTHIC RESIDENTS
Between June, 1970, and June, 1971	.863	.792	.928
Between June, 1970, and December, 1970	.759	.655	.975
Between December, 1970, and June, 1971	.773	.629	.952

The two June (1970, 1971) samples had more suprabenthic species in common with each other than either did with the December, 1970, sample. However, the list of benthic residents present in June, 1970, was more similar to that of the December, 1970, sample than to that of the June, 1971, sample, which indicates that there is seasonal variation in suprabenthic species but not in resident benthic species.

Precise quantitative data on the abundance and fluctuations of suprabenthic fish species are unlikely to become available in the foreseeable future. It is, however, our subjective impression from limited observations during the past eight years that the population levels of these fishes are quite stable and that long-term changes in relative abundance are far less than short-term annual or seasonal fluctuations due to seasonal movements, time of recruitment, etc.

### MECHANISMS THAT CONTRIBUTE TO COMMUNITY HOMEOSTASIS

There is ample evidence that the behavioral ecology of every fish species is adaptable to changing environmental conditions. The mode of living is fixed within certain limits, of course, but the precise reaction of individuals to a given situation can be altered by the presence of other species. One can therefore imagine that if a habitat were occupied by only one species of fish, the behavior of those individuals would be quite different from their behavior in a multispecies assemblage. This we believe is an important aspect of the origin and maintenance of diversity and community structure because the presence of other species as competitors or potential predators serves to restrict each species to the niche (in the broadest sense) for which it is best adapted.

In the following discussion we have attempted to analyze some of the interactions between the species of the suprabenthic community and also their interaction with certain other aspects of the suprabenthic zone. We have not considered purely chemical factors nor have we dwelt with such physical parameters as light, temperature, and turbidity because it is apparent that those conditions are within the tolerance limits of all the species present. The currents of the Gulf Stream assure adequate water flow at all times so that chemical conditions are quite stable along the



western edge of the outer shelf of the Great Bahama bank. This water movement also transports larval fish and planktonic eggs, thus insuring that the young stages of many species have free access to all microhabitats. On the other hand, there are many Bahamian fishes that do not live on the outer shelf, not because they never have access to it but because the environment does not meet their needs. The restricting factors could be physical or chemical in nature or they could be predators that feed on the colonizers as fast as they arrive, or they could be competitors that deny them adequate food or shelter. In other words, the faunal composition, i.e., the list of species, of the region is maintained by rejection of recruits that find the environment unsuitable or already fully occupied.

It is clear that every habitat has an upper limit as to the biomass of fishes it can support and that this limit is imposed ultimately by the energy and materials available, both from local primary productivity and imported from other habitats. Just how this biomass is apportioned among the species, however, is not fully understood. Smith and Tyler (1972), have postulated a sequence of increasing specialization throughout evolutionary time that has led to greater compartmentalization of available food and space. They believe that new forms can be added to the community as residents only if they are able to use the resources in ways that the other species already present cannot. In other words, late arrivals must have specializations that are not already being used by an established member of the community.

Smith and Tyler also postulated that the numbers of individuals, and hence the biomass, of any given species is limited by direct competition between members of the same species. In the presence of other species each individual is compelled to use whatever special adaptations it possesses and this puts it into direct competition with its own conspecifics. This reasoning leads us to the conclusion that relative abundance (diversity) is maintained by interactions between species. Our understanding of the mechanisms that maintain diversity can only be as good as our understanding of these interactions.

It is important to realize that we are concerned with exchange of information that is not necessarily synonymous with the exchange of energy or materials. For example, the approach of a predator will cause *Pomacentrus partitus* to move down in the water column closer to shelter sites in the bottom. Thus, the predator has modified the behavior of this species without any actual predation. If there are too many damsel fishes, competition for the available shelter results and some individuals eventually will be preyed upon because they had to remain in relatively exposed positions. Thus, the population of damsel fishes is limited by the available

shelter sites, but only when there are predators around to make shelter necessary.

In the suprabenthic fish community we recognize the following factors as being of primary importance:

- I. Space. Fishes use space for hunting, shelter, reproduction (courtship and nesting), waste disposal, and residual activities.
- II. Food. Three limiting aspects of food are kind, quantity, and availability.
- III. Symbiotic partners. Symbiosis is widespread in coral reef communities. We recognize three major types of symbiosis: shelter symbiosis in which fish take shelter in sponges, sea cucumbers, and coral surfaces; cleaning symbiosis; and feeding symbiosis.

Information transfer can proceed in the following ways:

1. **FLOW:** One factor or species exerts a direct, unidirectional influence on another. For example, a fish that feeds by straining sand substrate can only feed where there is sand present. In this case the sand is transferring information to the fish.

2. **FEEDBACK:** When two species interact so that each influences the other there is feedback. For example, a large predator may feed on a smaller predator but the small predator can also eat the young of the large predator.

3. **COMPETITION:** Interspecific competition because it is between two separate gene pools is basically an unbalancing phenomenon. Each generation will see an increased unbalancing until the less fit is eliminated. For this reason interspecific competition can only influence the community composition by keeping out those species that would be in direct competition with the species present. At times there may be intense competition from members of other communities as occurs when predaceous midwater fishes enter the suprabenthic zone to crop fishes that would normally be preyed upon by nomadic suprabenthic or benthic predators. This kind of competition would be so varied and erratic that it is unlikely to be a selective factor that would lead to the development of a new adaption. Intraspecific competition, however, is probably a major influence in limiting the populations of many of the species.

4. **PREDATION:** Although predation is probably the chief cause of death, it is only selective information when a particular predator species preys on a particular prey species often enough to be a selective factor forcing the prey to develop new defensive adaptations.

5. **CO-ADAPTATION:** This refers to specializations that permit one species to utilize resources that others cannot. In the evolutionary context these specializations must have arisen in response to competition from other

species. For this reason we call them co-adaptations rather than simply adaptations.

We are recognizing here three types of co-adaptations: (1) temporal; (2) microdivision; (3) sharing of resources that are never in short supply. Organisms that use the same resources at different times, whether these are diurnal or seasonal differences, must be behaviorally and perhaps structurally specialized in different ways than those that use different parts of the resource at the same time. This is not to claim that it is any more difficult to develop one kind of specialization than the other, but merely that the difference between the two types is important.

In the accompanying diagrams, temporal specializations are indicated by a wavy line representing cycles, and microdivisional specializations are represented by a series of short vertical dashes indicating fine compartmentalizations. A single solid line indicates sharing of abundant food and space resources. In these cases, it is not clear how the competitive exclusion principle applies to these species, although we suspect that more precise data will resolve such questions.

#### FOOD SHARING

Using the stomach content analysis data of Randall (1967), we have assigned the nomadic fishes to seven somewhat arbitrary food compartments: planktivores, benthic predators, suprabenthic predators, sand sifters, scrapers, browsers, and pickers. These assignments are not entirely satisfactory, for there is a great deal of food overlap and nearly every species could at times be placed in one or more of the other compartments. Our judgments are made on the basis of observations of how the fishes hunt and (sometimes) feed, obvious anatomical specializations for feeding in a particular way, and, finally, on literature records of actual stomach contents.

Figure 6 shows verified food pathways within this community. A pathway is considered to have been verified wherever there is a definite record (usually that of Randall, 1967) of at least one species of one compartment having fed on at least one species from the donor compartment. In figure 7 we have summarized the relative importance of food and space sharing between the several compartments.

Although we have assigned individual species to each compartment it must be recognized that different life-history stages may belong in different compartments. For example, juvenile *Pomacanthus arcuatus* are benthic resident parasite pickers, whereas the adults are nomadic sponge browsers.

**PLANKTIVORES (FIG. 8):** Two species, *Clepticus parrai* and juveniles of *Haemulon striatum*, are primarily plankton croppers, hovering above the

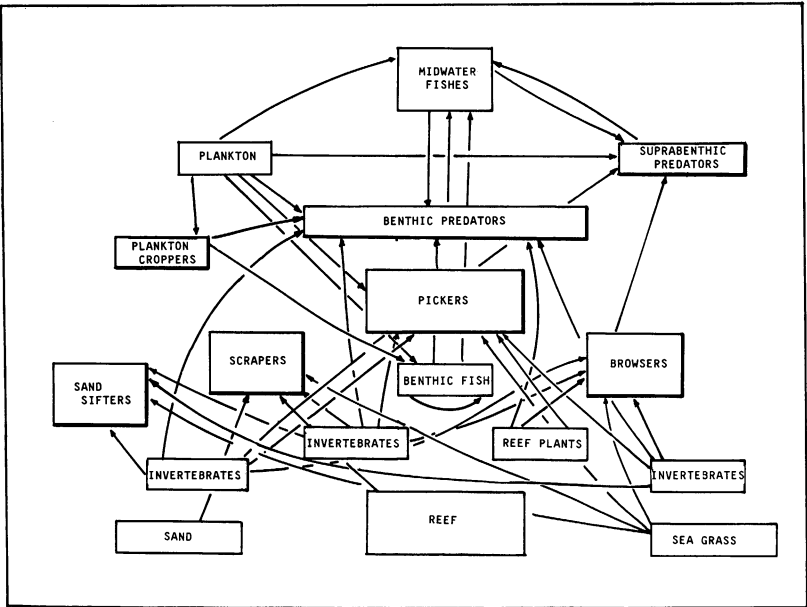


FIG. 6. Confirmed food pathways in the suprabenthic zone. Data from Randall, 1967.

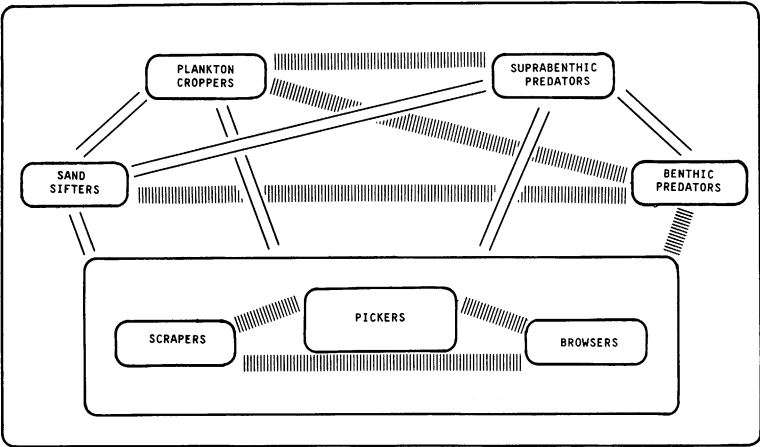


FIG. 7. Relative importance of food and space sharing among suprabenthic nomadic fishes. Dashed line indicates food specializations are most important. Open line indicates space separation is most important.

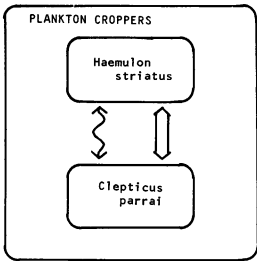


FIG. 8. Resource sharing among plankton croppers.

bottom and chasing individual plankters. The *Haemulon* are seasonal. In fact, they were only seen during June, 1970, but *Clepticus* was nearly always present in small numbers. We believe that there are both temporal and compartmental space-sharing adaptations because *Clepticus* is more abundant farther out on the reef and *Haemulon* is abundant closer to shore.

**BENTHIC PREDATORS (FIG. 9):** Five species are assigned to this category. The largest species, the groupers *Mycteroperca venenosa*, *M. bonaci*, and *M. interstitialis* are bottom stalkers. *Synodus* sp. feeds by short rushes to capture fishes somewhat off the bottom. *Bothus lunatus* usually feeds near the bottom, but Randall (1967), found *Jenkinsia* sp. and *Selar crumenophthalmus* in *Bothus* stomachs and this indicates that this flounder, at least on occasion, leaves the bottom to feed when the prey comes close enough. *Bothus* also fed on stomatopods and octopods, and this indicates that *Bothus* and *Synodus* eat somewhat different foods. The three species of *Mycteroperca* have similar

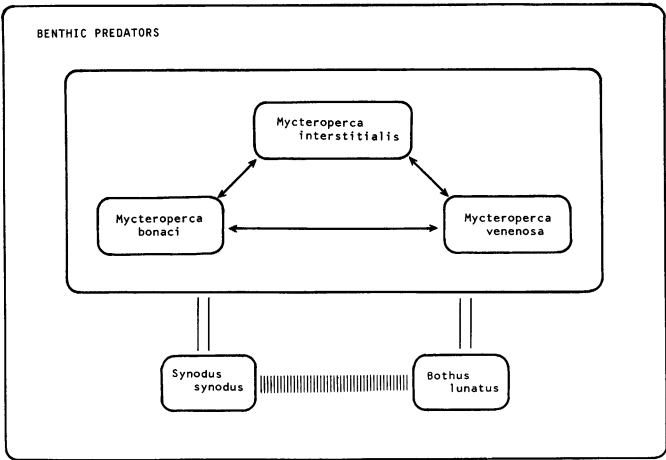


FIG. 9. Resource sharing among benthic predators.

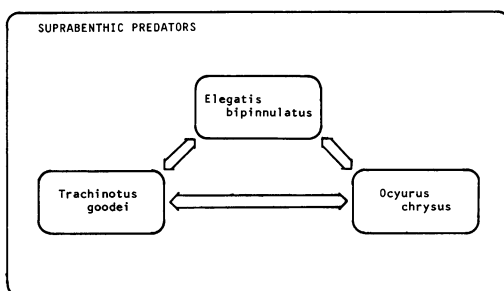


FIG. 10. Resource sharing among suprabenthic predators.

habits. All of these groupers fed almost exclusively on fishes. Randall (1967) found that of 51 *M. venenosa* with stomach contents, 48 had fed mostly on fishes, one had fed on shrimp, and two had eaten squids. In view of the abundance of small fishes in this area and the fact that we almost never saw them together, we concluded that these groupers were adapted for feeding on an abundant food resource and avoided competition by feeding in different areas or at different times.

**SUPRABENTHIC PREDATORS (FIG. 10):** Three species are placed here, all of which feed slightly off the bottom but still within the suprabenthic zone. All three are schooling predators: *Trachinotus goodei*, *Ocyurus chrysurus* (adults), and *Elegatis bipinnulata*. There seems to be marked food and space compartmentalization among the three although all appear to feed on a wide variety of animal food. Young *Ocyurus chrysurus* feed on plankton, and even bottom detritus, but larger individuals take a greater proportion of fish. *Trachinotus goodei* often move into shallow water to feed on sand-dwelling mollusks stirred up by bathers or other fishes. Their typical food, however, is fish. *Elegatis bipinnulata* was described by Hiatt and Stasburg (1960) as more or less pelagic, which may indicate that our observations are unusual. Its food habits are not well known. Thus, both space and food are divided to avoid competition. Although *Elegatis* and *Ocyurus* were feeding together at the time of our observations we believe this to be a temporary association.

**SAND SIFTERS (FIG. 11):** These are species that feed by sifting through unconsolidated bottom deposits to obtain the small infaunal organisms. Some species take in large amounts of sand and sort out food materials with their pharyngeal apparatus. Others blow the sand away to expose the food. Three species are: *Dasyatis americana*, *Urolophus jamaicensis*, and *Dactylopterus volitans*. The two rays probably utilize the same food resource and the same hunting grounds. Both feed by fanning the sand to expose their food. *Dasyatis* also feeds on fish to some extent, but the food habits of *Urolophus* have not been studied in detail. Apparently these species are

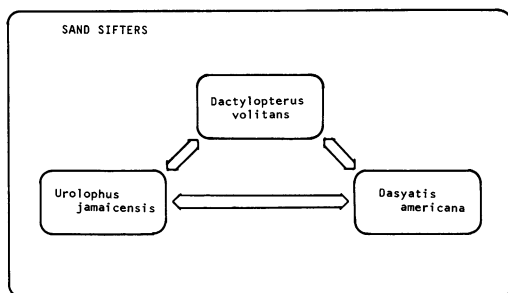


FIG. 11. Resource sharing among sand sifters.

limited by some factors other than food or space, possibly reproductive factors, since both are viviparous and have relatively few offspring. *Dactylopterus* feeds mainly on crabs, with other crustaceans, pelecypods, and fishes making up smaller proportions of the diet. Randall has postulated that it uses the free anterior rays of the pectoral fins to scratch in the sand. It is a rare species that is probably limited by some factor other than food or space.

**SCRAPERS** (FIG. 12): The four species of parrot fishes are grouped together as scrapers because they normally remove a part of the substratum while feeding on attached plants or animals. *Scarus coeruleus* and *S. guacamaia* travel in larger groups and appear to be nomadic in the area of the television, although they may have home sites elsewhere. *Scarus croicensis* and *Sparisoma viride* appeared as small groups or solitary individuals and were rare enough to be considered wanderers. However, they too may have homes to which they frequently return. We doubt that food competition is important to these fishes.

**BROWSERS** (FIG. 13): Browsers are fishes that feed on parts of attached plants and animals without consuming the entire organisms or colonies

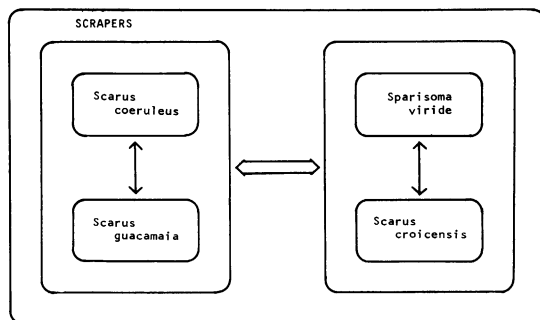


FIG. 12. Resource sharing among scrapers.

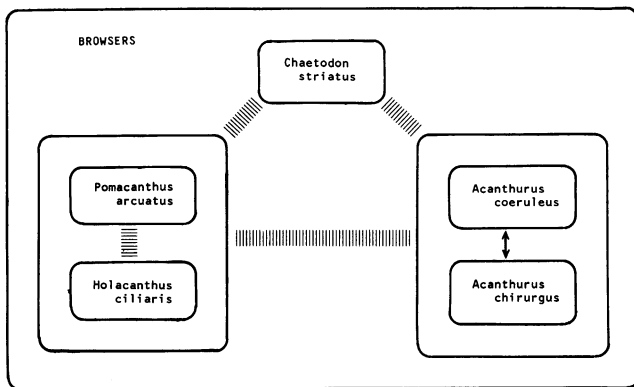


FIG. 13. Resource sharing among browsers.

and without scraping away the substrata. At the television site three chaetodontids (*Pomacanthus arcuatus*, *Holacanthus ciliaris*, and *Chaetodon striatus*) and two acanthurids (*Acanthurus coeruleus* and *A. chirurgus*) were browsers. The acanthurids feed mainly on algae and organic detritus and there is almost complete food overlap. *Chaetodon striatus* feeds mostly on tentacles of polychaets and anthozoans, but the two angelfishes fed largely on sponges. Both angelfishes are parasite pickers when young and sponge feeders when adult. They seem to have extensive food overlap throughout their lives.

**PICKERS (FIG. 14):** The distinction between browsers and pickers is that pickers most often crop entire benthic organisms, whether sessile or free living, whereas browsers usually nip off only part of the organism or colony. The distinction is not particularly sharp but we think it is important, and it is often reflected in the patterns of dentition.

*Lachnolaimus maximus* feeds (again according to Randall, here and elsewhere) chiefly on mollusks (82%), with crustaceans a poor second (about 13%). *Calamus pennatula* feeds on a variety of invertebrates including crabs, wrasses, and mollusks, but there is no particular dominance of any one taxon. *Balistes vetula* feeds chiefly on echinoids (73%), with the remainder of the diet made up of 18 other groups of bottom-dwelling organisms. *Cantherhines pullus* feeds on algae and organic detritus (43%), sponges (31%), and a variety of other plants and animals. *Monacanthus tuckeri* feeds on small crustaceans and other organic materials. *Lutjanus analis* feeds on crabs (45%), fishes (30%), and miscellaneous smaller invertebrates.

There may be some differences in hunting grounds among the species of trunk fishes . . . "*Acanthostracion quadricornis*, *Lactophrys bicaudalis* and



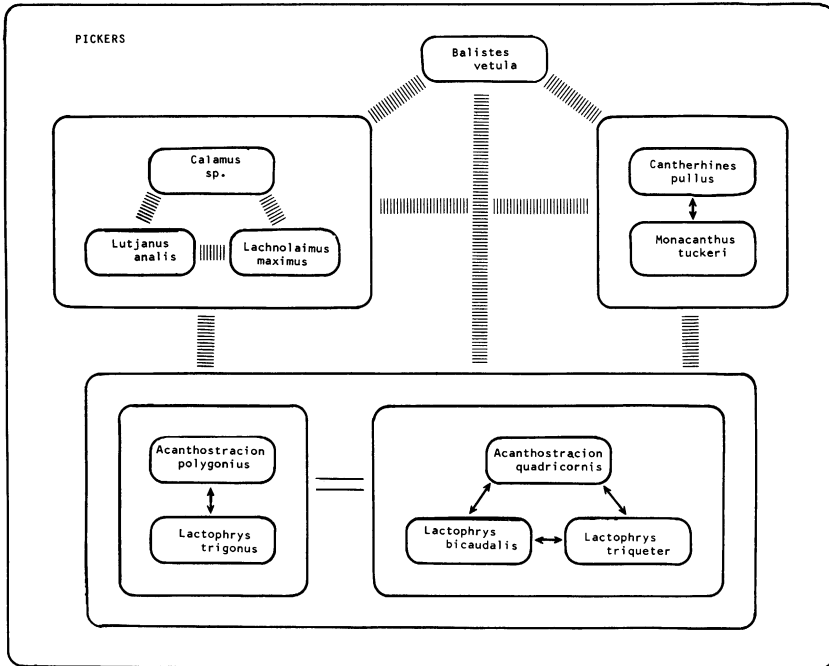


FIG. 14. Resource sharing among pickers.

*L. trigonus*, are most often seen in exposed areas such as seagrass beds and even sand flats . . ." (Randall, 1967, p. 812). *Acanthostracion polygonius* and *L. triqueter* are reef dwellers. Much of their food consists of attached animals but they also feed on free living organisms.

Figure 7 summarizes the relative importance of space and feeding microspecializations as mechanisms by which the suprabenthic nomads avoid competition for food.

Pickers, grazers, and scrapers all feed on the reef surface and would be in competition except that they feed on different foods or at least in different ways so that the foods are differentially available to them. Thus, we have indicated that food compartmentalization is the primary competition avoiding mechanism. Benthic predators also feed close to the reef much of the time but they feed mainly on fishes rather than plants and invertebrates. When feeding over sand, benthic predators avoid competition with the sifters by feeding on fishes rather than interstitial invertebrates. Planktivores feed in the same area as midwater and benthic predators but again on different foods.

The other groups are largely adapted for using different parts of the environment. Sifters, because they require unconsolidated sediments, occupy a different microhabitat (open sand) from any of the other groups except (sometimes) benthic predators. There is some food overlap with all groups but competition is minimized by space specializations (in this case hunting area).

Similarly, planktivores and midwater predators use the space above the bottom and do not compete with the benthic piscivores, browsers, pickers, or scrapers.

For a few pairs and triads of species there seems to be complete overlap of space and food. These are: *Scarus guacamaia* and *Scarus coeruleus*; *Scarus croicensis* and *Sparisoma viride*; *Acanthostracion polygonius* and *Lactophrys trigonus*; *Acanthostracion quadricornis*, *Lactophrys triqueter*, and *L. bicaudalis*; *Monacanthus tuckeri* and *Cantherines pullus*; *Acanthurus coeruleus* and *A. chirurgus*; *Mycteroperca interstitialis*, *M. venenosa*, and *M. bonaci*.

We suspect that more careful and detailed analysis will reveal differences in food or space utilization, or both, that we have not detected. Hynes (1970, p. 376) has emphasized that similarity of diet means that species are not competing for food.

#### SPACE SHARING

In categorizing the species as midwater visitors, benthic residents, and suprabenthic nomads we have already considered the gross aspects of space sharing. The residents make intensive uses of a small amount of space and the nomads roam over large areas without using any one part of it intensively. It is also noteworthy that most of the species we have considered nomads do not appear to show marked diel activity cycles, although we have not investigated this point thoroughly as television cannot be used for night observations. The only nomadic species mentioned here that we are aware of having a definite activity cycle are *Clepticus parrai* and *B. vetula*. *Balistes vetula*, in holding pens at the Lerner Marine Laboratory, retires to the bottom at sunset and remains inactive during the hours of darkness (Clark, 1950, and personal observ.). Various groupers, *Haemulon album*, *Ocyurus chrysurus*, and *Lutjanus analis*, are probably active both during the day and at times throughout the night (Smith and Tyler, 1972).

#### SYMBIOTIC PARTNERS

During the June, 1971, observation period several fish species visited a cleaning station in section 10 where a half-buried cinder block was

resting on its side. From June 24 through June 29 we observed the following species at this station being cleaned:

NOMADS	RESIDENTS
<i>Calamus</i> sp.	<i>Pseudupeneus maculatus</i>
	<i>Epinephelus fulvus</i>
<i>Pomacanthus arcuatus</i>	<i>Sparisoma aurofrenatum</i>
	<i>Haemulon album</i>

Observations during a dive to the site confirmed that there was a sea anemone at one edge of the cavity of the block and that several (four to six) individual cleaner shrimps, *Periclemenes pedersoni*, were living among the tentacles of the anemones. These were undoubtedly the cleaners at this station. Other cleaner shrimps of the same species were found with anemones in the artificial reefs.

INFORMATION FLOW AND COMMUNITY EVOLUTION

In figure 15 some of the information pathways of the suprabenthic zone are illustrated diagrammatically. Materials flow, i.e., food pathways, have already been summarized in figure 6 and are not repeated. In this diagram spatial relationships are indicated by double lines, for example the reef provides space for benthic fishes, planktivores (when they are inactive), and so on. Symbiotic relationships between reef-dwelling invertebrate parasite pickers and fishes are indicated by dashed lines. Competition and predation between nomads and components of other communities are indicated as shaded lines.

In a community as complex as even this suprabenthic assemblage of fishes with only 33 species there is a very large number of possible pathways through which information can be transferred, and yet repeated samplings and observation, indeed just the continued coexistence of large numbers of species, suggests that the net effect of all this information leads to stability rather than randomness. The overall effect of so many pathways through which each individual receives information is precise channelization and there is strong selection against individuals with deviant structural or behavioral characteristics.

It appears then that the trend in community evolution is toward ever higher diversity because as the member species become more specialized they limit the acceptable variation in life modes of other species. Increasing specialization, then, decreases random variation, which leads to more rigorous specialization and even more complex information webs.

Highly complex information webs enhance community stability in two ways. First of all, the availability of a wide variety of prey species has a stabilizing effect on both predators and prey as the predators feed on



dispersal mechanisms (planktonic eggs and larvae or wandering adults) there will invariably be new species coming into the habitat. Most of these are unable to become established, hence the community is restricted by rejection of unacceptable colonizers.

2. The only newcomers that can become part of the community are those that have special adaptations that allow them to utilize the available resources without competition with species that are already established members of the community. (This is in an evolutionary sense—generations of co-existence—not in the sense of a single point in time).

3. As new species are accepted by the community they become part of the information network and force the established species into ever narrower niches. We can imagine a community with one herbivorous species that is best adapted to feeding on fleshy algae. In the absence of competitors this species might also eat filamentous algae but when a form that is well adapted for feeding on filamentous algae is present the original species will be restricted to the food for which it is best adapted.

4. The channelizing effect of a complex information net favors the development of ever more precise specializations (narrower niches) and these effective and specific adaptations make it possible for the fish to invade other communities as highly specialized potential competitors. Thus, Darwinian natural selection is an adequate driving force favoring the development of high diversity communities. The only individuals acceptable to the community, and therefore most apt to survive to reproduce, will be those that are specifically adapted to a niche not occupied by another species.

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