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UTILIZATION BY FISHES OF SPACE AND FOOD RESOURCES ON AN OFFSHORE PUERTO RICAN CORAL REEF
 AND ITS SURROUNDINGS

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ABSTRACT

A cross-section of the fish community was studied on and near a coral reef 9.5 km west of Puerto Rico. Utilization of reef and off-reef habitat and diel activity cycle were observed for several diverse groups. The nature and degree of reef association were documented. Diet, based primarily on gut contents, was compared with quantitative benthic samples from the adjacent sand flat.

The reef-restricted scarids and Clepticus parrai (Labridae) were diurnally active, feeding respectively on benthic algae and zooplankton. Serranids appeared reef-restricted, but without clear diurnal/nocturnal pattern. Holocentrids and pomadasyids used reef protection by day and fed abroad at night, apparently mostly on the sand flat benthos. Opisthonema oglinum (Clupeidae), Caranx ruber and the mullids ranged widely day and night over reef and flats. The former fed mostly in mid-water, and the latter two apparently ate primarily sand flat benthos. Sphyraena and Synodus species were wide-ranging piscivores day and night, the former stalking in mid-water, the latter lying in wait on the bottom. Calamus (Sparidae) was a dominant exclusively sand flat species, feeding on the sand flat benthos day and night.

Herbivores, planktivores, piscivores and macro-invertebrate carnivores are all substantial components of the fish community. Feeding by macro-invertebrate carnivores on the sand flats provides an important energy input to the reef community. The sand flat benthos receives substantial energy from the water column. Most of the energy this group passes on to fish may come from detritus, much of which may be reef-derived.

KEY WORDS: Reef Fish Community, Habitat Usage, Diel Activity Cycle, Diet, Benthic Food, Trophic Level, Feeding Type.

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Introduction

Coral reefs typically provide a striking contrast to surrounding environments. In many regions reefs commonly occur as fringes or patches associated with extensive open, shallow areas of unconsolidated sediment. These "sand flats" may be almost featureless and of low apparent primary productivity, in sharp contrast to the complex physical structure and high productivity of the reef. For understanding the ecology of such areas, it seems important to determine how fishes use these very different substrates in their life activities.

Existing reef-related studies of fishes are numerous and diverse. However, few have dealt quantitatively with the trophics of a reef fish fauna (1,2,3,4,5,6). Often the data collection is not so spatially concentrated as to represent a fish community in any sense. Quantitative knowledge of available food is rarely obtained. There is probably no previous study in an open ocean tropical situation where food consumption of the fish community has been sampled concurrently with quantitative measurement of the local benthos. In the present study, saturation SCUBA diving from an underwater habitat permitted the use of a variety of collecting gear, combined with direct in situ observations over many hours in the water at all times of day, in a concentrated period of several days. Most of the quantitative data reported here are from the collections, but they are supported by the observations, especially in regard to fish locations. Thus, it was feasible to accumulate enough information on several important and diverse fish groups and the available benthic food to gain insights into how these fishes use the reef and off-reef areas for feeding and other life activities.

Study Area

The study was conducted at a 25 km² reef tract about 9.5 km off the west coast of Puerto Rico (18°5'50"N 67°17'20"W), due west of Punta Ostiones. A shallow bank occurs here, with depths restricted to 3-6 m by live and recent coral growth. Shoreward of the bank are extensive areas with 19-27 m depth. The study site was located at the seaward edge of this bank, where the steeply sloping face of living coral reef ends abruptly in an extensive, gently sloping sandy plain with sparse algal growth (7). The reef base is at 16.5 m depth. Excursions and regular collecting up to 10 m were possible. The sand flat was studied regularly for some 100 m seaward from the reef to depths of about 19 m. The reef consisted of a variety of living hexacorals and octacorals growing upon an open,

porous structural framework of dead coral. A diverse assemblage of other sessile invertebrates and low, encrusting and filamentous algae was present.

Materials and Methods

Monofilament gill nets with square mesh sizes from 13 mm (1/2 in) to 51 mm (2 in) were placed by divers on the reef face and the sand flat. Common Antillean fish traps with hexagonal wire mesh of 32 mm (1 1/4 in) opening across flats were also placed in both environments. Divers periodically removed fish from both types of gear. Most specimens were collected by these passive gear types, fishing continuously over periods of 7 1/2 to 10 days. Additional specimens were taken by spearing or other opportunistic means. Specimens were identified to species, measured and weighed, and gut contents were identified to the closest possible taxon and enumerated. For very abundant, primarily planktivorous or herbivorous species, only qualitative examination of about half the guts was made.

Benthic invertebrates were collected on the reef using a diver-operated drop net made by modification of a 1 m plankton net, employing poison within the net and an air-lift device to aspirate small organisms. Benthic invertebrates and algae were collected on the sand flat using a 61 cm diameter diver-operated coring device with a screened top and closable bottom and poisoning within. This sampler effectively collected nearly 100% of all organisms from the surface down to a depth of 12 cm into the sediment. Both samplers were effective in collection of highly mobile, surface-living forms, including small fish. For the homogeneous sand flat, the samples are probably representative of all the flora and the fauna in the size range from a few centimeters to 0.35 mm (the mesh size used for sieving the sediment). On the more heterogeneous reef surface, time and manpower did not permit adequate sampling for quantitative interpretation. Benthic specimens were identified to the closest possible taxon, enumerated and weighed dry.

Results

Major fish groups seem to be separable into the following types, based on their utilization of the available environments: reef surface, sand flat surface, and open water column.

Type A, reef-restricted: These fishes seldom leave the immediate environs of the reef, and only for very brief periods. Many are strongly demersal (e.g. most pomacentrids, chaetodontids, scorpaenids, muraenids, blenniids, gobiids and

clinids). Some species feed in mid-water, but normally only very close over the reef. To Type A fish the reef is extremely important as "home", both for shelter and feeding.

Type B, reef-related: These fishes normally use the reef part of every day. It appears to be important as cover, but they also regularly range off the reef. The extent of feeding on the reef is uncertain, but feeding off the reef appears to be important.

Type C, reef-indifferent pelagics: For these fishes, the reef is only a small part of the total daily range, and they move rather indifferently over various substrates. They do not appear to require bottom features for protection and feed either from the water column or on various bottom types. Many of the typically pelagic, surface-oriented species (e.g. some clupeids, engraulids, atherinids, belonids, hemiramphids and scombrids) were seldom or never collected or observed.

Type D, non-reef demersals: These fishes are strongly substrate oriented, but do not tend to associate regularly with reefs. The category would include cryptic sand-dwellers such as branchiostegids, opistognathids and the labrid group known as razorfishes. For these groups - poorly studied in this work - the sandy substrate offers both shelter and food. Wide-ranging demersals such as the sparids, which are more conspicuous and vulnerable to capture by passive gear, may also rely fully on the sandy substrate for feeding.

For some species of all the above types, sufficient numbers were collected to obtain some patterns for space usage. In most cases at least semi-quantitative conclusions regarding food type and source were possible. These results for these fishes are summarized in Table 1. Several species occupied different day and night locations, often synchronized with feeding activity, as shown in Table 1. Composition of the diet on a numerical basis is derived directly from counts of food items in guts. Composition on a weight basis uses these counts and the assumption that the average weight of an item in a given taxonomic category in the gut is the same as the average weight of that item in the sand flat benthos. This procedure gives a more ecologically meaningful estimate of food weight consumed than any attempt to estimate weights directly from the often fragmented gut contents.

Type A, reef-restricted

The abundant labrid, Clepticus parrai, was captured and observed only on the reef. Creole wrasse were seen and taken at all hours, but were more conspicuous and active in mid-water by day. No guts were found empty. Much of the gut contents was copepods, although a number of specimens contained larvae, including crab zoea.

Table 1

Classification of major groups collected and observed, with time, substrate and depth for most feeding and other activities and composition of diet (○, day; ●, night; ○, day and night; R-reef; F-sand flat; B-bottom; W-mid-water. Prey figures underlined are percent of total food consumption by weight; other prey figures are percent of total individual animals consumed by number. P indicates group is present in very small quantities. A indicates group is abundant).

Type	A		B		C				D		
Group	C. parrai	Scaridae	Serranidae	Holocentridae	Haemulon	O. ocellinum	C. ruber	Mullidae	Sphyracna	Synodus	Calamus
LOCATION	C	Scaridae	Serranidae	Holocentridae	Haemulon	O. ocellinum	C. ruber	Mullidae	Sphyracna	Synodus	Calamus
Feeding	○	○	●	●	●	●	●	●			
Substrate	R	R	R	F	F	R	R	R			F
Depth	W	B	B	B	B	W	W	B	W	W	B
Other	●	●	●	○	○	●	●	●	●	●	●
Substrate	R	R	R	R	R	R	R	R	R	R	F
Depth	B	B	B	B	B	W	W	B	W	B	B
PREY											
(% of total)											
Algae	~100										
Zooplankton	~100										
Mysidacea				P	P	A	A				
				9.1	1.3						
Benthic crustacea			P	29	64	P	P				21
				87	59						75
Natantia				44	40						7.8
				62	38						8.7
Reptantia				8.2	11		P				4.3
				4.4	3.8						1.8
Stomatopoda				46	12						2.3
				10	1.7						4.8
Isopoda				.25	1.2						1.0
				6.6	5.4						5.8
Tanaidacea				.22							.75
				1.7							6.3
Amphipoda				.03	.13						.36
				3.4	9.0						30
Ophiuroidea				20							9.6
				1.7							.37
Ascidacea				12							1.1
				27							2.9
Gastropoda				46	1.2						5.3
				.94	1.7						9.7
Pelecypoda				.10	1.3						1.1
				.31	2.6						2.9
Polychaeta				.16	.22		P				.75
				1.2	4.3						4.8
Fish									A		

A few possibly benthic or interface diet items were present in a few specimens, including the caridean shrimp, Leptochela, a genus inhabiting the sand flat. The habitat utilization, diel cycle and planktonic diet observed are consistent with observations of Randall (2).

The abundant Chromis species seemed to share a similar behavior. Other abundant, but nocturnal, Type A fishes with apparently similar feeding habits were the apogonids and the pempherids. Both groups were commonly seen within cavities in the reef by day and feeding in the water column by night. Neither was ever observed at any substantial distance from the reef nor abroad in daylight. No apogonids were collected; a few Pempheris schomburgki were taken in reef nets. Meager gut contents gave little information on diet. Earlier workers recorded similar behavior for these species (2,8,9,10).

Scarid species collected were Scarus croicensis, S. taeniopterus and S. vetula, Sparisoma aurofrenatum and Sparisoma viride. All specimens were taken on the reef except one Sparisoma aurofrenatum who entered a trap on the sand flat during daylight. Visual observations support the collections, indicating very little movement at any distance from the reef, strong daylight reef activity, and none after dark. All scarids taken by passive gear could have entered during daylight or the crepuscular hours. Some "sleeping" was observed, e.g. a Scarus vetula dormant inside a mucous envelope. No gut examined was empty. All contained substantial amounts of sediment (probably carbonate substrate taken in browsing algae from hard surfaces). Fragments identifiable as filamentous algae were common. The variety of other tiny organisms which were occasionally included could have been ingested incidental to algal browsing. These results on habitat, activity cycle and diet agree generally with most previous studies (1,2,6,10).

Smaller serranid species such as hamlets were numerous, seen only on the reef, and not collected. Three larger species - Epinephelus guttatus, E. striatus and Petrometopon cruentatum - were caught and commonly observed on the reef. All except one specimen (an E. guttatus) were taken on the reef. Sightings of groupers far off the reef were rare. Serranids were taken at all times of day, and no particular period could be considered most active. Meager and inconclusive gut contents included brachyuran crabs, caridean shrimp, a few other scattered small invertebrates, and possible fish remains. This behavior and diet are generally consistent with earlier studies (1,2,8,9,10).

Type B, reef-related

Holocentrid species collected were Myripristis jacobus, Holocentrus rufus, H. coruscus

and H. marianus (the last less important in numbers and food content). Squirrelfish appeared to be underrepresented in the catch, possibly in part because no finer mesh nets were set on the sand flat. They were typically numerous, sheltering close to the reef surface and in cavities by day. By night they ranged abroad over the flat to considerable distances. About 90% of all captures were made during the night or at dawn. Brachyuran and anomuran crabs, shrimp, stomatopods and isopods were important in the diet. The dominant xanthid crab was Micropanope lobifrons, the same species that dominated benthic samples from the sand flat. Similarly, the sand-burrowing anomuran, Callinassa, appeared prominently in both holocentrid guts and sand flat samples. Shrimp found in holocentrids and also in the sand flat samples included the penaeid, Trachypenaeus constrictus, and the carideans, Leptochela serratorbita, Periclimenes sp. and Alpheus sp. (particularly abundant in both). At least one stomatopod species - Gonodactylus oerstedii - was also present in sand flat benthos collections, along with unidentified juvenile gonodactylids. The stomatopods are night active residents of sandy substrates. A few polychaetes, amphipods, gastropods and ostracods were taken. Items that may have been taken in mid-water were a minor part of the diet. Mysids were fairly common; a few shrimp larvae and postlarvae, brachyuran megalops and anomuran postlarvae were present. In general, the diet appears to have been taken from the sand flat benthic fauna, reflecting a strong preference for stomatopods, shrimp, isopods and crabs. Other studies have indicated similar habitat use, diel activity cycle, and diet, except that Myripristis has often been considered a planktivore (1,2,3,8,9,10).

Lutjanids were not abundant except for Ocyurus chrysurus. Few were collected and gut contents were too limited to be definitive.

Among the numerous pomadasysids, Haemulon aurolineatum dominated collections and appeared to be similarly dominant in natural abundance. Other species collected were H. plumieri, H. flavolineatum, H. album and H. parrai. Nearly 90% of all specimens were collected on the reef. However, visual sightings and gut contents indicated that foraging on the sand flat is a regular habit. Such foraging appears to be mostly nocturnal, and groups of Haemulon were seen sheltering on the reef during the day. Of all grunts collected, 83% contained food. All species ate crabs; 44% of all H. aurolineatum individuals contained brachyurans and/or anomurans. Forty percent of all crabs in Haemulon guts were the dominant xanthid of the sand flat samples, M. lobifrons. Portunus spinicarpus and Portunus of uncertain species also occurred in both Haemulon guts and sand flat samples, as did Pinnixa. Shrimp occurred in all Haemulon species (47% of all specimens) and were frequently abundant. The very abundant caridean, Leptochela serratorbita, was also in sand flat samples, as were

Sicyonia and Latreutes. Alpheids were fairly common in the guts and numerous on the flat. Twenty percent of the Haemulon specimens contained stomatopods, including several Pseudosquilla ciliata, which was also collected in the sand flat benthos. Ascidiarians were common and abundant, occurring in 33% of Haemulon guts. Over 90% of these were the small, simple ascidian, Microcosmus helleri, which comprised 12% by number of all animals in sand flat samples. Pelecypods were fairly common in the diet, especially the mytilid, Musculus lateralis, which also represented 65% of sand flat pelecypods. Two other bivalves present in guts and sand flat samples were Tellina consobrina and Pitar sp. Several specimens contained ophiuroids; at least two had the sand flat genus, Ophiothrix, and two contained Ophiostigma isacanthum, which comprised 72% of all brittle stars in sand flat benthic samples. All species and most specimens of Haemulon contained amphipods, although they were not preferentially selected from the sand flat benthos. The most numerous amphipod in the guts was the small gammaridean, Chevalia aviculae - the most numerous animal in the benthos (30% of all animals). Half the Haemulon specimens contained polychaetes, although they were not preferentially selected. Fewer grunts had eaten isopods, but they were strongly favored. A few specimens contained tanaidaceans, including two cases of the strongly dominant species found in benthic samples. Earlier behavior and diet studies are consistent with these results for all species (2,8,9,10).

Type C, reef-indifferent

The large clupeid, Opisthonema oglinum, was commonly seen in all locations, apparently active abroad at all hours. Sixty percent of the reef catches and a third of the catches on the sand flat were in full daylight. Without regard to location, exactly half the specimens were caught in daylight and half during darkness or the crepuscular hours. Mid-water organisms strongly dominated the diet. These included many mysids, crab larvae, copepods, and a considerable number of fish larvae (possibly a clupeid species). Items of possible benthic origin included a few caridean shrimp, amphipods (including caprellids) and isopods. Although the thread herring has generally been considered a planktivore, and for the most part appears to be such in this study, some small fish and benthic diet items have been suggested (2,11).

Bar Jack

Caranx ruber was the only abundant carangid species. Capture locations agree with observations that the species commonly schools in all locations by day and night. Over half the bar jacks collected contained a little food, mostly Mysidacea. Benthic foods included caridean shrimp and traces of amphipods, isopods, ostracods and gastropods. Previous results agree with this observed behavior but indicate a strongly piscivorous diet (2,9).

The mullids were commonly seen on and off the reef at all hours, often foraging the sandy substrate using the barbels in tactile search. Mulloidichthys martinicus was present, but poorly collected and apparently less abundant than Pseudupeneus maculatus. The latter was taken both on the reef and sand flat by day and night, mostly in traps and dip nets. The goatfish collected contained very little food, mostly of benthic origin. The xanthid crab, M. lobifrons, and the polychaete, Arabella irricolor, were identifiable with the sand flat benthic samples. Earlier observations on habitat and diet are in agreement (1,2,3,8,9); some have emphasized strong diurnal feeding by P. maculatus.

Among top level carnivores, Sphyræna barracuda were occasionally present, while the smaller Sphyræna picudilla appeared to be regularly present. They were seen on and off the reef, by day and night. The few netted, at night or dawn on the reef, did not provide definitive diet information. All contained mostly fish, but a squid, amphipods and the shrimp, L. serratorbita, also occurred.

Synodontids were much in evidence on both reef and sand flat at all hours. Only Synodus intermedius were collected as adults; all were taken on the reef, despite their obvious presence on the flat. They were taken at several times of day, dark and light. None contained food. Other workers have confirmed the habitat and full-day activity of Synodus (1,2,3,9,11). The piscivorous habits of synodontids and sphyrænids are well documented (1,2,3,6,11).

sanddiver
- heard fish -

Type D, non-reef

The sparid, Calamus, was abundant and active about the flat at all hours. Porgies always oriented strongly to the sandy substrate while constantly ranging the flat without recourse to shelter. All except one sparid collected were Calamus pennatula. All specimens were taken on the flat except for one individual speared at the base of the reef just before dusk. Almost 70% of all Calamus ate crabs (mostly brachyurans), with 29% containing M. lobifrons. Portunids, including Portunus spinicarpus, were well represented in the guts and benthos. Pinnixa minuta also appeared to be present in the guts; it occurred prominently with other Pinnixa in the benthos. Shrimp in the diet included L. serratorbita and alpheids, both represented in benthic samples. Over 35% of all Calamus ate stomatopods, mostly Pseudosquilla ciliata, a species from the sand flat samples. Isopods were not numerous in guts but were strongly selected. Nearly all the amphipods eaten were C. aviculae, the strongly dominant benthic species. All of the very few tanaidaceans were the same unidentified species that composed 98% of all benthic sample tanaids. Seven species of gastropods were eaten. Pelecypod numbers were minor, but all were the common benthic mytilid,

M. lateralis. Numbers of ascidians, sipunculids and ophiuroids were also minor; for ascidians, one of three species, and for the other groups, the only species present, also occurred in the benthic samples. The habitat and diet agree generally with previous work (1,2,9); diurnal and possibly nocturnal feeding are reported.

Discussion

Fish collections were, of course, neither complete nor fully representative of the fish fauna present. A number of abundant species of small adult size (e.g. many pomacentrids, small labrids, gobies, blennies, many eels) and most young juveniles would not be retained by the mesh sizes used nor caught by the other methods employed. Other species could avoid capture for behavioral reasons. The principal range of several common species was shallower than the collecting activity. In spite of the bias in the data on collected species, in view of the obvious abundance, large biomass and probable ecological importance of several of them, it seems useful to consider these fishes as a group.

A trophic organization of the major fishes collected is shown in Table 2. In all, 32% are Type A, 21% Type B, 31% Type C and over 6% Type D. Thus, 53% have some dependence on the reef as "home." Of these, 34% feed mainly in mid-water and 36% feed importantly on the benthos of the sand flat. Less than 30% could be restricted to feeding on the reef benthos. Based on the collections only, 10 1/2% of the total fish fauna are piscivores, about 38% are macro-invertebrate carnivores (of which 90% apparently feed in the sand flat), 34% feed in the water column as planktivores, and 10% are benthic herbivores. Another 3% is composed of plectognaths known to be omnivores.

The scarids feed mainly on the encrusting and filamentous algal growth on the reef. Planktivores can be presumed to be nourished from three major sources: herbivorous zooplankton (primary consumers), carnivorous zooplankton (typically secondary consumers), and the larvae of benthic invertebrates, much of which must originate on the flats and represent various trophic levels. The fish that sustain the piscivores probably come largely from within the local system; some piscivorous trophic chains may contain four or more links. Based on analysis of gut contents and benthic samples, the macro-invertebrate carnivores appear to operate mainly as secondary and tertiary consumers. Seventy-two percent of the benthic faunal biomass of the sand flat is composed of primarily herbivorous filter feeders. Of these, ascidians are fairly important to some fishes (e.g. the pomadasyids). Pelecypods are minor prey, and the biomass of the remaining water filterers is small. Benthic particulate feeders (e.g. detritivores) comprise about 15% of all sand flat benthos. Some of these groups - e.g.

Table 2

Trophic organization and abundance in collections of major groups (N-numerous; M-moderately abundant; O-occasionally seen; B-bottom; W-mid-water. Fish type designations are as in text and Table 1).

Species/Group	Visual abundance	% of all specimens collected	Location of food source	Fish type by habitat utilization
HERBIVORES				
Scaridae	N	10	B	A
PLANKTIVORES				
<u>Clepticus parrai</u>	N	18	W	A
<u>Opisthonema oglinum</u>	N	12	W	C
<u>Caranx ruber</u>	N	7.7	W	C
MACRO-INVERTEBRATE				
CARNIVORES				
Serranidae	M	3.6	B	A
Holocentridae	N	4.5	B	B
Lutjanidae	O	Negl.	B	B
<u>Haemulon</u>	N	14.5	B	B
<u>Caranx ruber</u>	N	7.7	B	C
Mullidae	N	5	B	C
<u>Calamus</u>	N	6.3	B	D
PISCIVORES				
Serranidae	M	3.6	W*	A
<u>Lutjanus jocu</u>	O	Negl.	W*	B
<u>Caranx latus</u>	O	Negl.	W	C
<u>Sphyaena</u>	O	1.4	W	C
<u>Synodus</u>	M	4	W*	C

*Prey is probably taken very near the bottom.

some ophiuroids, macrurans and anomurans - are either fairly abundant or strongly favored by fish predators. About 2% of the benthos are primarily scavengers and 11% predators. In both groups, most members (e.g. Reptantia, Natantia, Stomatopoda) are reasonably abundant and strongly favored, making them very important food sources. Feeding by fishes upon these high invertebrate trophic levels results in long food chains. This carnivorous trophic pattern is in contrast to the dominant herbivory reported for oceanic atolls (3,5) and is more similar to the trophic situation described for coastal island fringing reefs of East Africa (4).

The major sources of primary productivity supporting the sand flat benthos are not obvious. Macroalgal biomass equal to 170% of the total animal biomass was measured, but it is largely calcareous forms such as Halimeda which seem unlikely to be heavily grazed. Many benthic filterers make direct use of planktonic microalgae and profit indirectly from microalgal water column production through the zooplankton they consume. The water column thus appears to make a substantial input to supporting the benthic standing crop. However, the filtering groups that would be consumed by much of the remaining

benthos are not abundant enough to support this community. A large fraction of the remaining benthos probably consume detritus, either by filtering fine particles or handling larger debris. Sediment samples contained much non-descript organic detritus. Some of this may come from pelagic production. Important amounts may come from the distant shore, from shallower, more productive regions, or from the reef tract. Certainly much material of reef origin is found in the flat. Thus, reef detritus may enrich the adjacent sand flats, supporting an invertebrate fauna upon which reef-related fishes feed.

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