Appendix B. Data collected for field predation trials by Gorman, et al (1991).

Brittlestar on sponge combinations	depredated	survived
dark on maroon	4	2
pale on maroon	8	0
dark on lavender	6	2
pale on lavender	4	2

Appendix C. Combined data for field predation trials collected by Gorman, et al. (1991) and Burnaford, et al. (1992).

Brittlestar on sponge combinations	depredated	survived
dark on maroon	12	7
pale on maroon	21	0
dark on lavender	12	6
light on lavender	10	6

CORAL REEF FISH COMMUNITY STRUCTURE AS A FUNCTION OF SUBSTRATE COMPLEXITY

Joseph J. Bizzarro, Jeffry L. Dudycha and Alan B. Shabel

Abstract. We investigated the effect of substrate complexity on coral reef fish community structure in the fore reef and on the reef crest in Discovery Bay, Jamaica. Substrate rugosity and vertical relief, our estimates of spatial complexity, were determined for seven 3m x 3m plots. Diurnal and nocturnal fish censuses were then performed at each plot. Rugosity and vertical relief were highly correlated with both species richness and total number of individuals. The same was true for rugosity and species diversity, although the relationship was less strong. Nocturnal fish communities appear to be less complex than those active during the day. (ABS)

INTRODUCTION (ABS)

It is possible to divide the major resources used by coral reef fishes broadly as food and space (Sale 1984). Most reef fish rely on the physical substrate for both of these resources (Luckhurst and Luckhurst 1978), although space, rather than food, is generally agreed upon to be most limiting (Smith & Tyler 1972; Sale 1980).

Coral reef fish are remarkably sedentary once they complete their larval lives; the occupancy of a single shelter site for life is not uncommon (Sale 19??). Physically complex regions of the reef provide a greater number of living spaces for fish, as well as recruitment sites for algae and invertebrates on which fish feed. Based on this, we predicted that areas of high substrate and spatial complexity would support more complex fish communities.

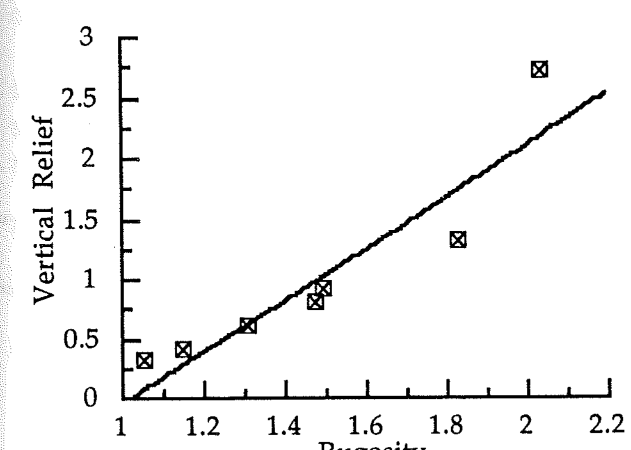

Figure 1. Scatterplot demonstrating the strong correlation between a plot's rugoisty and its vertical relief.

We tested this prediction in plots established in two reef zones: the reef crest and the fore reef. We estimated the spatial complexity of a site by measuring its vertical relief and substrate rugosity, the latter of which is essentially an estimate of total surface area (Luckhurst & Luckhurst 1978). We then performed diurnal and nocturnal censuses of all the fishes within each plot. We placed particular emphasis on locating cryptics because these species are the ones that are most often underestimated when assessing reef fish populations (Brock 1982).

Our censuses established the species richness, species diversity, and the total number of individuals at each site. These community parameters were then correlated with each plot's rugosity and vertical relief to determine what effect physical complexity has on fish community structure.

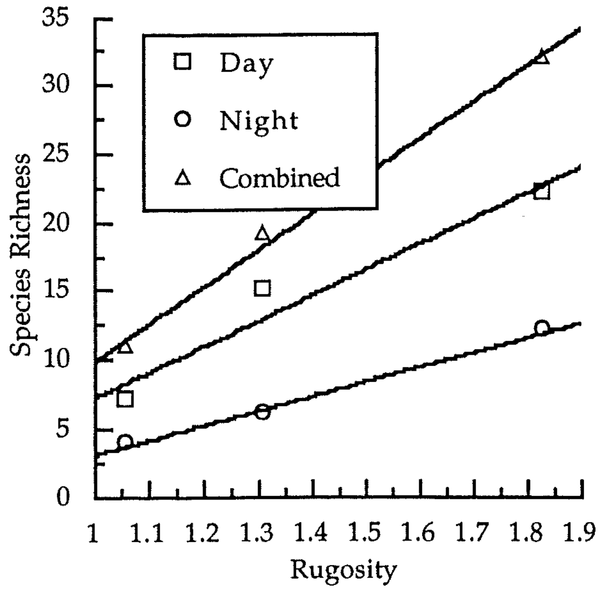

Figure 2. Species richness vs. rugosity on the reef crest.

Methods (JLD)

We conducted our study from 24 February to 4 March 1992 at the Discovery Bay Marine Laboratory in Discovery Bay, Jamaica. We established six 3m x 3m plots in two reef zones, the reef crest and the fore reef. Plots of similar substrate (coral and coral rubble) were chosen to be of varied complexity at approximately the same depth (within 3m). Four plots were located just south of Mooring 1, on the fore reef, and three were on the back reef edge of the west reef crest.

Measurement Of Physical Parameters. A rugosity index was calculated for each plot by dividing each plot into a grid and taking rugosity measurements along the grid lines (one grid line every 0.5m). A marked chain was conformed to the substrate along each grid line and its length was measured. This number was then divided by 3, the linear distance between two sides of the plot, to obtain the rugosity index. The ten measurements from each plot were averaged to estimate the rugosity index of the plot as a whole.

The vertical distance between the highest and lowest points in the plot was measured to determine vertical relief. The depth of each plot was recorded with a SCUBA depth gauge.

Fish Censuses. Fish were censused in the late morning (between 0900 and 1100) and also at night (between 2100 and 2300). Census methods varied based on location, but for all censuses two divers recorded fish species seen within the plot, and the number of individuals of each species seen. After each census, the minimum number of each species seen was determined. If only one diver recorded a species, this number was used. If a species was seen by both divers, either the number of individuals seen was averaged, or the greater number was used if the diver was certain that the fish were all separate individuals. The latter usually occurred only if the fish were seen in a school.

At the fore reef plots, the census consisted of hovering 3m above the plot for 3min, then moving to 1m above the plot for 3min, then making a close examination of the substrate and crevices for 4min in order to locate as many cryptic and hiding fish as possible. All fish within the plot up to a vertical height 0.5m above the highest point of the substrate were counted. Plots 1, 2, and 3 were censused on the same morning, plot 4 was censused 2 days later. Night censuses were made only on plots 1 and 2.

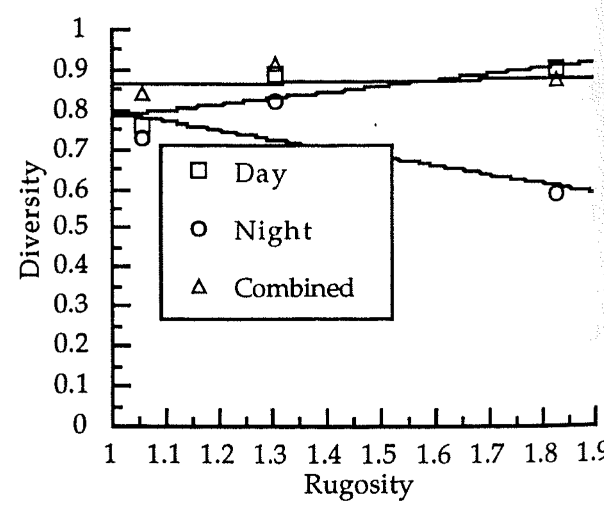

Figure 3. Community diversity vs. rugosity on the reef crest.

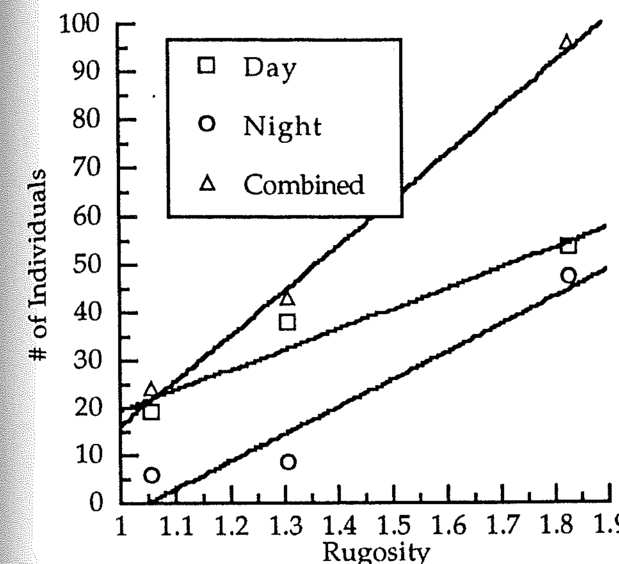

Figure 4. Number of individuals vs. rugosity on the reef crest.

Snorkeling equipment was used to census the reef crest plots. Each census consisted of 6 minutes of observation from outside the plot and then 4 minutes of close examination. All fish up to the surface were counted. All plots were censused in the morning and night on the same day.

Table 1. Comparisons of rugosity (student's t-test).

		t	p
Fore reef	plots 1 & 2	3.93	<0.001
	plots 1 & 3	4.84	<0.001
	plots 2 & 4	4.81	<0.001
	plots 3 & 4	4.99	<0.001
Reef crest	plots 1 & 2	2.99	<0.01
	plots 2 & 3	2.66	<0.01

Note: the plot designated with the higher number always has the higher index of rugosity.

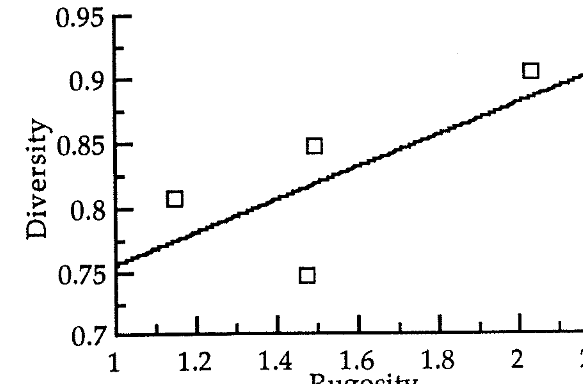

Figure 5. Community diversity at the fore reef during the day.

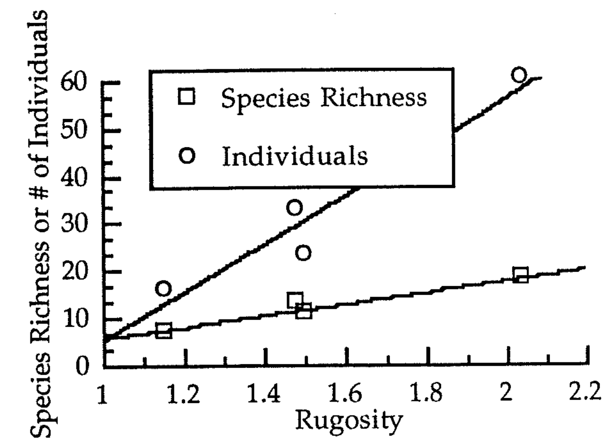

Figure 6. Species richness and # of individuals on the fore reef during the day.

Results (JLD)

We found significantly different rugosities in all of our plots with the exception of fore reef plots 2 and 3 (Table 1). We found that rugosity was positively correlated with vertical relief (r^2=.860, p<.001; Figure 1, Table 2). In general, we found that species richness and the number of individuals were positively correlated with rugos-

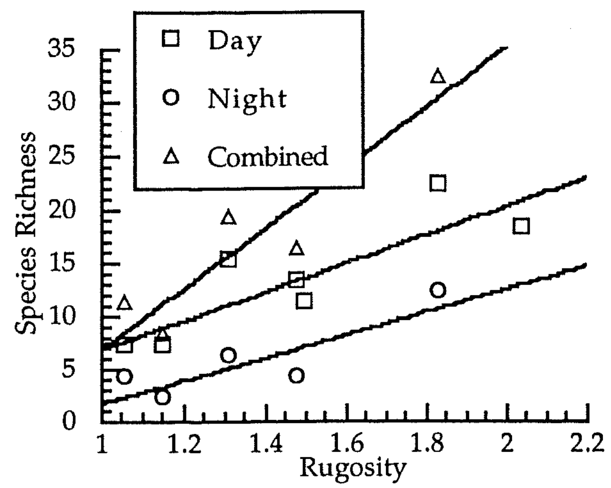

Figure 7. Species richness and rugosity: fore reef and reef crest plots.

ity (Table 3, Figures 2, 4, 6, 7, and 9). Diversity also appeared to be correlated with rugosity, though not as strongly (Table 3, Figures 3, 5, and 8). We also found that the number of individuals and the species richness were similar between the reef crest and the fore reef plots (Table 3). With our data, we can predict the community parameters of highly rugose areas at night for further testing.

A summary of all the fish observed appears in Appendix A.

Discussion (JJB)

Since the rugosities between plots at both the fore reef and reef crest were determined to be statistically different, and plots were established with depth and substrate type held constant (Table 2), any changes in community structure of fish probably are a consequence of differing substrate complexity. Tight correlations could not always be expressed statistically due to the low number of replicated plots. Data for the night census at the fore reef could not be tested because only two plots were censused. However, when sites or when day and night data were combined correlations were often statistically significant. Differences became more significant when more plots were included, as evidenced by lower r^2 values often resulting in greater significance (Table 4).

Table 2. Physical parameters of plots.

	Fore reef				Reef crest		
	#1	#2	#3	#4	#1	#2	#3
Depth (m)	10	8	8	7	1	1	1
Vert. Relief (m)	0.4	0.8	0.9	2.7	0.3	0.6	1.3
Rugosity Index	1.15	1.48	1.50	2.04	1.06	1.31	1.83

Table 3. Community parameters by plot

	Fore Reef				Reef Crest		
	#1	#2	#3	#4	#1	#2	#3
Number of species sighted							
Day	7	13	11	18	7	15	22
Night	2	4	–	–	4	6	12
Combined	8	16	–	–	11	19	32
Number of individuals							
Day	16	32.5	23	60	18.5	37.5	53
Night	2	4	–	–	5	8	47
Combined	18	36.5	–	–	23.5	42.5	95
Diversity †							
Day	.804	.744	.844	.903	.756	.883	.891
Night	.500	.750	–	–	.720	.813	.578
Combined	.827	.792	–	–	.836	.906	.864

†: Diversity calculated using Simpson's Index

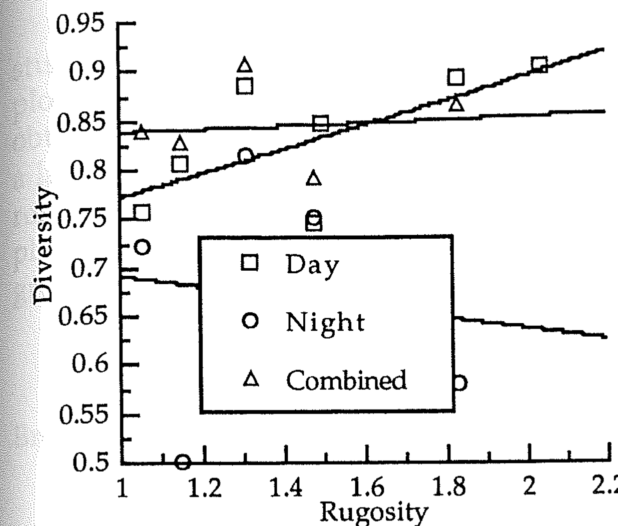

Figure 8. Diversity and rugosity: fore reef and reef crest plots.

As expected, higher numbers of individual fish were usually associated with greater substrate complexity. In the reef crest, numbers increased with increasing rugosity in both day and night censuses (Table 3, Figure 4). The same trends were evident at the fore reef (Table 3, Figure 6, Figure 10). However, although the correlations appear strong, only the data for the reef crest at night were significant statistically. When correlations were tested on the combined data for all sites, however, all trends were significant for both day and night (Table 4, Figure 9) regardless of time or location. Areas of high complexity provide more sites for shelter and a greater food base as a result of increased area for colonization by algae and demersal invertebrates (Luckhurst and Luckhurst 1978).

Table 4. Regression anaylysis data

Figure and Regression		r^2	t	p
1		.860	13.47	<0.001
2	day	.944	5.58	>0.1
	night	.993	9.64	>0.05
	combined	.996	6.37	>0.05
3	day	.614	6.21	>0.1
	night	.043	5.12	>0.1
	combined	.558	7.69	>0.05
4	day	.935	5.28	>0.1
	night	.934	6.05	>0.1
	combined	.996	6.39	>0.05
5	day	.481	10.45	<0.01
6	sp. richness	.950	9.09	<0.02
	# indivs	.928	9.87	<0.02
7	day	.728	54.51	<0.001
	night	.739	8.83	< 0.01
	combined	.858	9.86	<0.01
8	day	.452	12.91	<0.001
	night	.016	9.70	<0.01
	combined	.013	10.96	<0.01
9	day	.831	11.32	<0.001
	night	.733	9.85	<0.01
	combined	.867	1235	<0.001

The numbers of individuals found were comparable between the reef crest and fore reef (Table 3). We had expected to see higher numbers on the fore reef, based on previous observation. However, individuals on the reef crest consisted primarily of smaller species and a greater percentage of juveniles, making the total number of individuals similar although total biomass probably is much higher at the fore reef. The reef crest plots were dominated by small species such as cardinalfish, gobies, and wrasses, while the fore reef contained more large fish such as serranids and parrotfish. More fish were observed during diurnal censuses, a trend consistent with the results of a diel fish community study carried out earlier on the program. However, the entire community using an area is a combi-

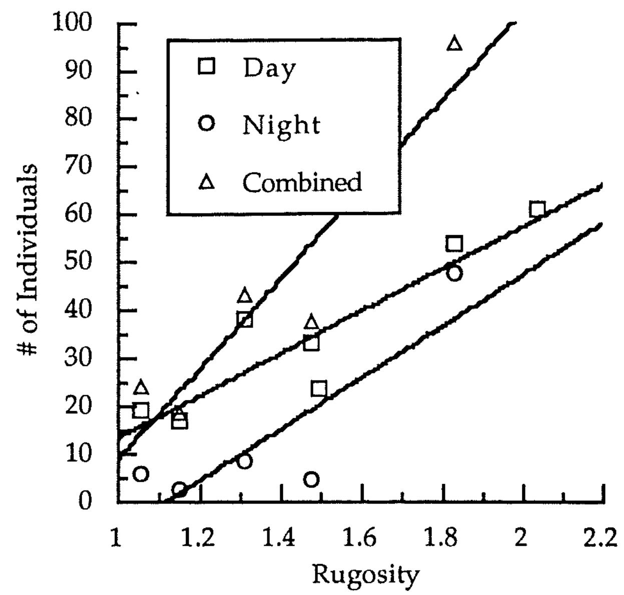

Figure 9. Number of individuals and rugosity: fore reef and reef crest plots.

nation of day and night censuses, since reef fish presumably seek shelter within their same home sites during periods of inactivity (Smith and Tyler 1972).

Like number of individuals, species richness tended to increase with increasing rugosity (Figures 2, 6, 7, and 10; Table 3). Species richness decreased at night in both the fore reef and reef crest. This is largely due to a decrease in the number of individuals at night resulting in less overall species (Table 3). Species richness also varied little between sites, in accordance with similar numbers of individuals noted. Species richness is directly linked to recruitment. Recruitment occurs largely on a random basis (Sale 1980). Most coral reef fish are also sedentary and occupy the same home site throughout their lives (Luckhurst 1978). Therefore, since many different species can settle in the same habitat type (Sale 1977), the variation in possible recruits is high, resulting in higher species richness within a more complex area due to more areas for settlement. Fifty-four species of 20 families were noted during the study in 63m^2 of substrate, exhibiting the high species richness of the reef fish community (Appendix A).

Diversity was also correlated positively with increasing rugosity, although not as tightly. Significant positive correlations were found during the day at the fore reef (Figure 5) and when areas were combined (Figure 8). However, negative correlations were shown nocturnally and when day and night data from different sites were combined (Figures 3, 5, 8, 10).

Simpson's diversity index combines number of individuals and species richness of an area. Therefore, although species richness showed a positive trend in all cases, diversity could be negatively correlated due to a disproportionally high number of one species. This was evident in the nocturnal reef crest census where 30 of 47 fish seen were of one species (Dusky Cardinalfish). This trend was consistent when data from the nocturnal fore reef census were added because, although species richness increased, the very low number of fish seen (6) was not enough to reverse the trend. Therefore, although diversity does not show as tight a correlation with rugosity as species richness or number of individuals, a larger sample pool of fish censused at night would probably show a similar positive correlation. Diversity should increase with substrate complexity largely as a function of increased overall numbers combined with increased species richness, as observed in all cases (Figures 2, 4, 6, 7, 9, and 10).

Suggestions for similar future studies include: establishing more plots, limiting the study to one site to obtain more definitive trends based on a larger sample size, and using vertical relief as a measure of substrate complexity since this method would save a great deal of time.

Literature Cited

Brock, R.E. 1982. A critique of the visual census method for assessing coral reef fish populations. *Bull. Marine Sci.*, 32 (1): 269-276.

Luckhurst, B.E., and Luckhurst, K. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Mar. Biol.* 49: 317-323.

Sale, P.F. 1980. The ecology of fishes on coral reefs. *Oceanogr. Mar. Biol. Annu. Rev.* 18: 367-421.

Sale, P.F. 1984. The structure of communities of fish on coral reefs and the merit of a hypothesis-testing. Manipulative approach to ecology. In: *Ecological Communities: conceptual issues and the evidence.* Princeton Univ. Press, Princeton, NJ.

Sale, P.F. 19??. (First chapter of book; editors unknown). Diversity of the tropics: causes of high diversity in reef fish systems.

Smith, C.L., and Tyler, J.C. 1972. Space resource sharing in a coral reef fish community. *Sci. Bull.* 14: 125-170.

APPENDIX A

Fish Sighted	Fore Reef			Reef Crest			
	1	2	3	4	1	2	3
Acanthuridae (surgeonfish)							
Acanthurus bahianus (Ocean Surgeonfish)		1				2	2
A. chirurgas (Doctorfish)		1					
A. coeruleus (Blue Tang)		1		1			
Apogonidae (cardinalfish)							
Apogon maculatus (Flamefish)						**1**	**1**
A. sp. (unidentified)						**2**	**1**
Phaeoptyx pigmentaria (Dusky Cardinalfish)		**1**			**2**	**2**	30
Blenniidae (combtooth blennies)							
Ophioblennius atlanticus (Redlip Blenny)							1
Chaetodontidae (butterflyfish)							
Chaetodon capistratus (Foureye Butterflyfish)							3
Cirrhitidae (hawkfish)							
Amblycirrhitus pinos (Redspotted Hawkfish)				1			
Clinidae (clinid blennies)							
Labrisomus guppyi (Mimic Blenny)							1
Malacoctenus gilli (Dusky Blenny)							2
M. macropus (Rosy Blenny)						1	1
M. triangulatus (Saddled Blenny)		**1**			2	3	2

Diodontidae (spiny puffers)							
Diodon holocanthus (Balloonfish)						1/**1**	**2**
D. hystrix (Porcupinefish)							**1**
Gobiidae (gobies)							
Bathygobius soporator (Frillfin Goby)							1
Coryphopterus glaucofraenum (Bridled Goby)					7.5	2	
Gnatholepis thompsoni (Goldspot Goby)						2	1
Gobiosoma prochilos (Broadstripe Goby)				4			
Grammidae (basslets)							
Gramma loreto (Fairy Basslet)				6			
Holocentridae (squirrelfish)							
Holocentrus adscensionis (Squirrelfish)		1/**1**		2.5			**1**
H. rufus (Longspine Squirrelfish)		1		4.5	**1**		**3**
Myripristis jacobus (Blackbar Soldierfish)				3.5			
Neoniphon marianus (Longjaw Squirrelfish)							**1**
Surgocentron vexillarius (Dusky Squirrelfish)	**1**				**1**	**1**	2/**3**
S. coruscus (Reef Squirrelfish)		**1**					
Labridae (wrasses)							
Bodianus rufus (Spanish Hogfish)			1				
Halichoeres bivittatus (Slippery Dick)						1	1
H. gamoti (Yellowhead Wrasse)	5		2	4			
Thalassoma bifasciatum (Bluehead Wrasse)	3	15.5	7	13	4	10	14.5
Monacanthidae (filefish)							
Cantherhines pullus (Orangespotted Filefish)				1			
Mullidae (goatfish)							
Pseudupeneus maculatus (Spotted Goatfish)			1		1		
Pomacentridae (damselfish)							
Abudefduf saxatilis (Sergeant Major)							3.5
Microspathodon chrysurus (Yellowtail Damselfish)				2			
Stegastes fuscus (Dusky Damselfish)			1	1		3/**1**	3/**2**
S. leucostictus (Beaugregory Damselfish)		1	1	4.5	2	3.5	
S. partitus (Bicolor Damselfish)	1	3.5					3
S. planifrons (Threespot Damselfish)				2	1	1	2
S. variabilis (Cocoa Damselfish)						2	1
Pomadasyidae (grunts)							
Haemulon flavolineatum (French Grunt)							1
H. sp. (unidentified)							1
Scaridae (parrotfish)							
Scarus iserti (Sriped Parrotfish)				2			
S. taeniopterus (Princess Parrotfish)	3	1.5	3.5	6	1	3	5
Sparisoma radians (Bucktooth Parrotfish)					**1**		1
S. viride (Stoplight Parrotfish)	2/**1**	1	3	1		2	
Sparisome aurofrenatum (Redband Parrotfish)	1		1	1			
Sciaenidae (drums)							
Odontoscion dentex (Reef Croaker)							1
Serranida (hamlets/seabass)							
Hypoplectrus indigo (Indigo Hamlet)						1	
H. puella (Barred Hamlet)		1	1				
Serranidae (grouper/seabass)							

Cephalopholis cruentata (Graysby)		2					
Serranus tigrinus (Harlequin Bass)	1		1.5				
Tetraodontidae (smooth puffers)							
Canthigaster rostrata (Sharpnose Puffer)		2					1
Unidentified							**1**
Open Water Planktivores							
Clepticus parrai (Creole Wrasse)			14				
Chromis cyanea (Blue Chromis)	1	8	20	2			
C. multilineata (Brown Chromis)		2					

Note: Numbers in **bold lettering** are from the night census.