An Analysis of the Fish Assemblages on a Coral Patch Reef in Puerto Rico

RALPH G. TURINGAN and ALEJANDRO B. ACOSTA
Department of Marine Sciences
University of Puerto Rico
Mayaguez, Puerto Rico 00709

ABSTRACT

The fish assemblages on a coral patch reef in Puerto Rico were visually censused 30 times over three years. The structure of the assemblages, in terms of species numbers, numbers of fishes, and species composition for fishes 5 cm total length or larger was determined from five 200 m2 - transects set at predetermined locations within the reef. A total of 72 fish species belonging to 22 families were recorded on the reef. However, only an average of 55 individuals of 11 species were present at any one census. The fish abundance of Corona de Laurel reef was numerically dominated by the families Acanthuridae, Pomacentridae, Labridae, and Scaridae which accounted for about 70% of the total number of fishes observed during the study. Diversity of the fish fauna was more influenced by the number of species than by the distribution of individuals among taxa. Percent similarity between any two transects was low, indicating that species composition and abundance varied within the reef. Seasonal patterns of fish abundance were not clearly evident.

KEY WORDS: Community Structure, Coral-reef Fishes, Patch Reefs, Puerto Rico, Visual Census.

INTRODUCTION

Assemblages of fishes on coral reefs are characterized by high numbers of individuals and species. Proposed mechanisms for maintaining high diversity of coral-reef fishes include competition for food and space (Smith and Tyler, 1972, 1973, 1975; Risk, 1972; Belk, 1975) and random variations in colonization and mortality (Russell *et al.*, 1974; Sale, 1974, 1976, 1977; Sale and Steel, 1986).

Several studies have demonstrated a relationship between fish species diversity and substrate topographic complexity (Risk, 1972; Luckhurst and Luckhurst, 1978; Sale and Dybdahl, 1975, 1978; Bell and Galzin, 1984). Talbot (1965) postulated that more complex coral fauna provides more ecological niches than a habitat consisting of a single coral species. Emery (1973) found that the type of substrate was particularly important in determining the abundance of pomacentrids in Florida reefs. Furthermore, habitat characteristics exhibit a very strong influence on the recruitment processes of coral-reef fishes (Sale *et al.*, 1980; Luckhurst and Luckhurst, 1977; Shulman, 1984, 1985a,b).

This study describes the community structure of the fish assemblages on a coral patch reef in terms of species composition, number, and seasonality of fish.

MATERIALS AND METHODS

The study site, known as Corona de Laurel, is an entirely submerged patch reef separated from the main reef (Arrecife de Laurel) by a channel 5 m deep. This reef is located about 2 km off La Parguera on the southwest coast of Puerto Rico. The physiography and hydrography of Laurel Reef has been described by Glynn (1973).

Five 50 m line transects were established on the reef (Figure 1). Each transect was marked by nylon twine stretched along the bottom and weighted with stones. Fishes within 2 m on either side of the transect line were counted (see Recksiek *et al.*, 1991 for detailed description of how the boundaries were maintained).

Visual inspection of the reef using SCUBA was undertaken to establish sites for the transects. The transects were set at locations which appeared to represent different habitats within Corona de Laurel reef. Transect 1, characterized as a high relief site, was set on the southwest corner of the reef. The average depth at this site was 7 m and the substratum consisted almost entirely of dead coral boulders and rubble and numerous holes and crevices. Transect 2 was set on the western edge of the reef where the substrate is similar to that of transect 1 except for fewer dead corals, holes and crevices, and lesser relief. Transects 3 to 5 were set on the backreef where the substrata consisted mainly of soft coral colonies (*Eunicia* spp. and *Pseudopterogorgia* spp.), small patches of live coral and sand. Transect 3 included more sand and patches of seagrass than transects 4 and 5. Among these transects, transect 5 had the most live coral cover and coral rubble patches.

Fishes on each transect were visually censused 6 times (one every 3 days) per year during February and March 1987, 1989, and 1990. One monthly census (during the first quarter moon phase) was also conducted on each transect for a period of 1 year (May, 1989 - April, 1990). During each census the diver slowly swam the transect once while attempting to record all fishes that were at least 5 cm total length or larger.

Species diversity was computed using the Shannon-Wiener Diversity formula (Pielou, 1966a,b):

$$H' = -(Ni/N)*Ln(Ni/N)$$

where N is the total number of fishes for all species, Ni is the number of individuals of the ith species (i = 1 to S, the total number of species), and Ln is natural logarithm. Two components of the diversity index were also computed:

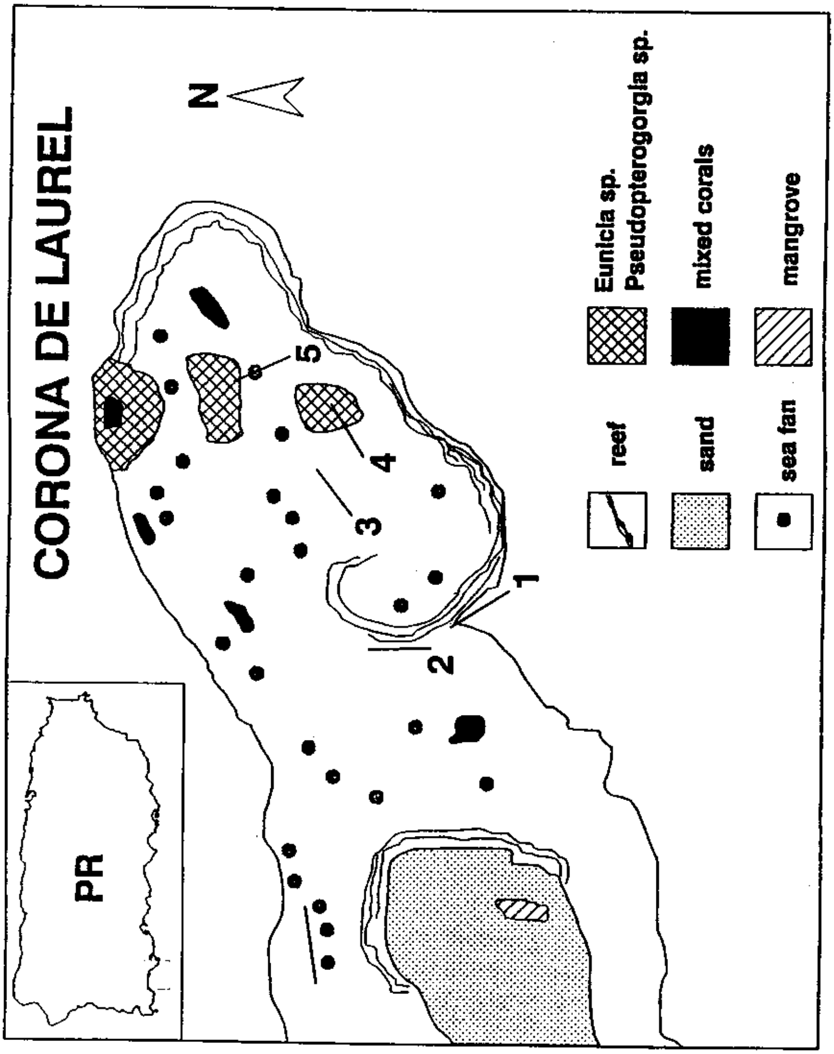

Figure 1. The study site, Corona de Laurel reef, located on the southwest coast of Puerto Rico. The map is not drawn to scale.

$$H_{max} = Ln(S)$$

the maximum diversity attainable in each transect, assuming that all species were represented by the same number of individuals; and species evenness,

$$J = H'/H_{max}$$

a measure of how individual fishes were distributed among species.

To examine spatial variation in community structure of the fishes on Corona de Laurel, all 30 visual censuses on each transect were considered when comparing assemblages among transects. Temporal variation in community structure over a year's period was examined by comparing monthly diversity indices computed as averages of visual censuses on all 5 transects (*i.e.*, N = 5). Furthermore, faunal similarities between transects during one season or within transects across seasons were measured using the "Percent Similarity" formula: $PS = \min(Pi_a \text{ or } Pi_b)$, where Pi_a is the percentage of species i in transect a, Pi_b is the percentage of species i in transect b (Hillman *et al.*, 1977). For these comparisons, monthly censuses were pooled into seasons (*i.e.*, Winter = January, February, and March; Spring = April, May and June; Summer = July, August, and September; Fall = October, November, and December).

RESULTS

The Fauna

A total of 72 species of fish belonging to 22 families was observed during the entire study period (Table 1). Only 21 species (29% of the total) were common to all 5 transects. Most of these occurred consistently in low abundances (average of 1-4 individuals per transect) in all five transects (*e.g.*, *Aulostomus maculatus*). Sixty species of fishes (90% of the total) were observed in transect 1 while the remaining transects contained only about half of the species censused.

In terms of average numerical abundance, the fish fauna was dominated by 4 families (Figure 2): Acanthuridae (surgeonfishes), Pomacentridae (damselfishes), Labridae (wrasses) and Scaridae (parrotfishes) . These accounted for about 70% of the total number of fish observed during the study. Distribution varied among transects (Figure 2). Most of the surgeonfishes were observed in transects 1 and 2. Transect 1 contained most of the damselfishes while almost all of the wrasses were observed in transect 5. Parrotfishes were more abundant in transects 1 and 5 than any other transect. All these dominant families were observed in relatively low abundances in transects 3 and 4.

Because no single species of fish occurred in considerably high numbers in each of the 12 monthly censuses, we lumped fishes into family groups and totaled the abundance data for all transects to determine any seasonal differences

Table 1. List of fish species and their average abundances in each of five transects (TR) at Corona de Laurel patch reef.

	TR-01	**TR-02**	**TR-03**	**TR-04**	**TR-05**
ORECTOLOBIDAE					
Ginglymostoma cirratum	1				
SYNODONTIDAE					
Synodus sp.	1	2		1	1
MURAENIDAE					
Muraena sp.	1		1	1	1
AULOSTOMIDAE					
Aulostomus maculatus	1.44	1.4	1.14	1	2
HOLOCENTRIDAE					
Holocentrus adscencionis	15.14	2.56		1.67	1
Holocentrus rufus	7.95	1.5	1		4.64
Holocentrus marianus	3				
Myripristis jacobus	4.88	2			1.73
SERRANIDAE					
Hypoplectrus guttavarius	1.25			2	2.15
Hypoplectrus indigo	1.14				1
Hypoplectrus unicolor	1			1	
Hypoplectrus puella	1				
Serranus tigrinus	1.11	1			1
Epinephalus cruentatus	1				
Epinephalus guttatus	1.14	1.25	1	1.25	1.5
Epinephalus striatus	1				
Myctoreperca venenosa	1				
CARANGIDAE					
Caranx ruber	9.92	1.14	13.6	2.75	7.5
SCOMBRIDAE					
Scomberomorus maculatus	1	1	1	1	
LUTJANIDAE					
Lutjanus apodus	4.75	3			1.6
Ocyurus chrysurus	5.09	1.67	1.64	1.5	4.17

Table 1. (continued)

	TR-01	TR-02	TR-03	TR-04	TR-05
HAEMULIDAE					
Haemulon sciurus	3			1	
Haemulon plumieri	20.33		2		2.67
Haemulon flavolineatum	5.77	1.11			1.62
Haemulon chrysargyreum	2.62				1.12
Haemulon carbonarium	5.5				1
Haemulon macrostomum	1				
Anisotremus virginicus	2	2			
SPARIDAE					
Calamus calamus	1	1		1	
Calamus bajonado	3	1			
MULLIDAE					
Mulloidicthys martinicus	12.58			2.33	
Pseudupeneus maculatus	4	2.75	2.86	3.33	
CHAETODONTIDAE					
Chaetodon capistratus	2.77	2.12	2.7	3.38	5.85
Chaetodon striatus	1.82	2.58	1	1.2	1
POMACANTHIDAE					
Pomacanthus arcuatus	2.27	1.33			1
Pomacanthus paru	2	3.75		1	
Holocanthus ciliaris		1	1		
POMACENTRIDAE					
Abudefduf saxatilis	3.83	2.5			2
Chromis multilineatus	35.45	9.33			7
Chromis enchrysurus	6	4.6		5	
Microspathodon chrysurus	5.91	3.38	1.6	3.5	2.86
Pomacentrus fuscus	7.47	4.75	2	4.5	4.14
Pomacentrus planifrons	12.5	6	7.29	3.12	
Pomacentrus variabilis	6	5.2		10	
Pomacentrus partitus	11.66	5.24	9.43	10	13.5
Pomacentrus leucostictus	6.19	2.85	1	3	3.5
LABRIDAE Lachnolaimus maximus	1				
Bodianus rufus	1	1			
Halichoeres bivittatus	2	2.69	1.6	1.25	1
Halichoeres radiatus	5	3.62	2.12	2.5	
Halichoeres sp.	6	3.6	1.6	2	
Thalassoma bifasciatum	14.71	2.91	9.71	16.77	45

Table 1. (continued)

	TR-01	TR-02	TR-03	TR-04	TR-05
SCARIDAE					
Sparisoma viride	9.38	5.1	3.38	4	5.17
Sparisoma aurofrenatum	8.75	9.32	5.15	4.15	3.31
Sparisoma rubripinne	5	3	2.75		
Sparisoma chysopterum	3	2.14	2.25	1	1.67
Sparisoma sp.	2	2.54	2.82	4.75	
Scarus croicensis	12.56	9.86	1.33	10.33	
Scarus taeniopterus	7.12	3	1.2	5.875	10
Scarus vetula		1			
Scarus spp.(juveniles)	28.64			14.29	48.46
ACANTHURIDAE					
Acanthurus bahianus	6.67	9.04	5.37	4.27	3
Acanthurus chirurgas	5.67	8.21	5	6.25	1.25
Acanthurus coeruleus	9.68	3.11	1	2.5	1.78
BALISTIDAE					
Balistes vetula	1				1
MONACANTHIDAE					
Cantherhines pullus		1		1.5	
TETRAODONTIDAE					
Sphaeroides testudineus			1		
Sphaeroides spengleri	1				
Canthigaster rostrata	2.75	1.5	1.25	1	1
DIODONTIDAE					
Diodon holocanthus			1		1
Diodon histrix					1
Total Number of Species	65	48	32	41	42

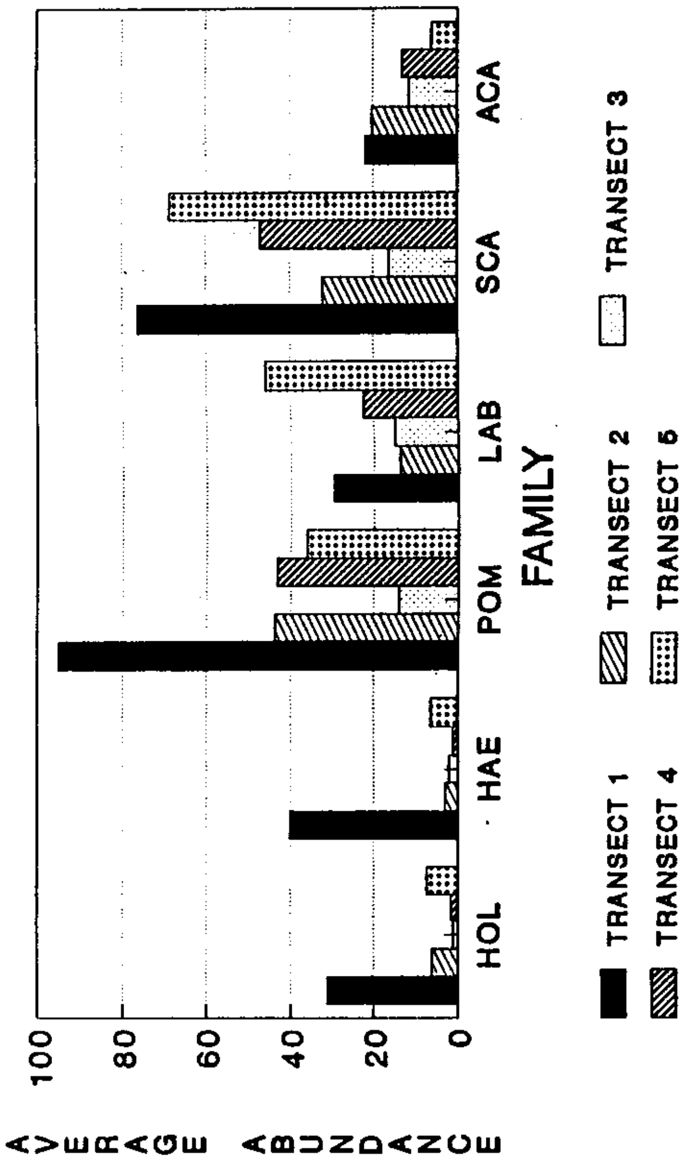

Figure 2. Average abundances of most common families of fishes on each transect at Corona de Laurel reef. Vertical bars depict 95% C.I. of the mean. Number of visual censuses per transect is N = 30.

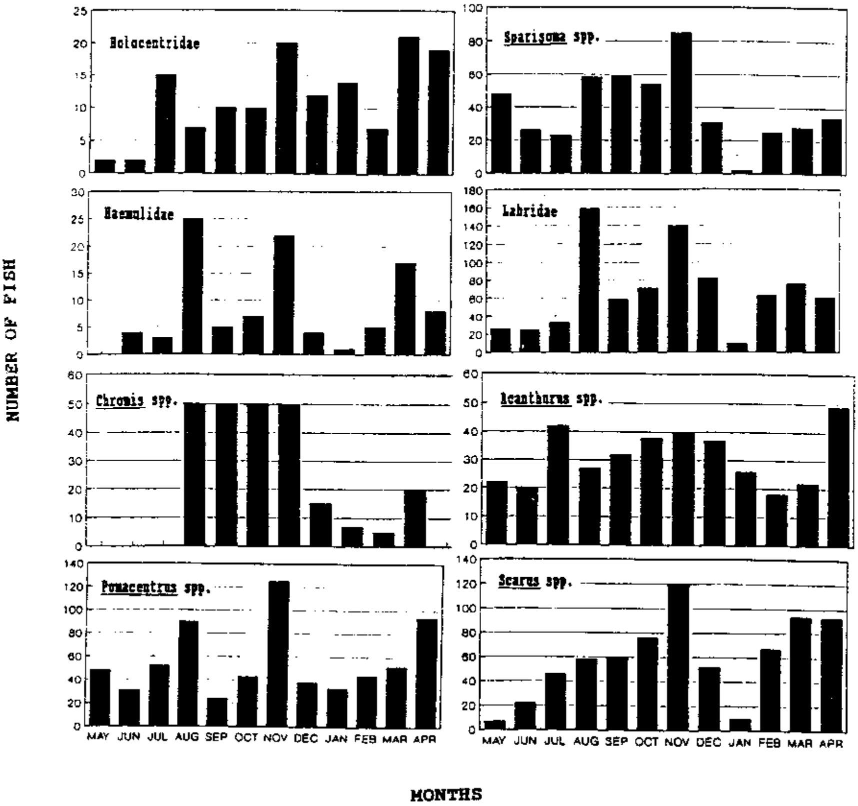

Figure 3. Comparison of monthly abundances of most common families of fishes on Corona de Laurel reef. Numbers represent sums of fish abundances for all transects; each transect was visually censused once a month.

in their abundance. The monthly abundance distribution of the four most abundant fish families is presented in Figure 3.

In general, more fish were observed during the summer and fall (July to December) than during the winter and spring (January to June) months. The families Pomacentridae and Scaridae showed peak abundances in November whereas the wrasses were most abundant in August. Although the number of surgeonfishes remained relatively low throughout the year, peak in abundance of these fish was apparent in July. It is noteworthy that these families of fishes appeared to have unusually low values in January.

Community Diversity Indices

The Shannon-Wiener species diversity and its components, Evenness (J) and Maximum Diversity (H_{max}), varied among transects (Figure 4). Transect 1 had the highest diversity among transects averaged across all censuses. This was generally attributed to the high number of species found in this transect. Although there were more species in Transect 5 than in Transect 2, species diversity was higher in the latter transect. In this case, the difference in H′ diversity between the two transects resulted from Transect 5 being dominated by two species, namely, *Thalassoma bifasciatum* and *Scarus* sp.; Transect 2 had relatively fewer species but individuals were more evenly distributed within each species (as indicated by a higher J index).

Monthly changes in diversity indices for the fish assemblages (Figure 5) during a year's sampling period were much less pronounced than those of fish abundance (Figure 2). However, the dip in fish abundance in January (Figure 2) corresponded with the lowest values for H′ and H_{max}. Diversity decreased during this month because of fewer species (as indicated by low H_{max}index) observed and recorded.

Percentage Similarity (PS) between any two pairs of transects was consistently low to moderate (Table 2), with the highest PS value (75%) being obtained in the fall for transects 4 and 5. Between-transect comparisons did not vary across seasons (One-way ANOVA, NS). Seasonal comparisons of percentage similarity within transects are given in Table 3. No seasonal patterns were evident. In general, within-transect percentage similarity between seasons (Table 3) was higher than between-transect percent similarity across all seasons (Table 2).

DISCUSSION

There is evidence that suggests the existence of highly structured fish assemblages on coral reefs in the Caribbean (Smith and Tyler, 1972, 1975; Gladfelter and Gladfelter, 1978; Gladfelter *et al.*, 1980; Anderson *et al.*, 1981;

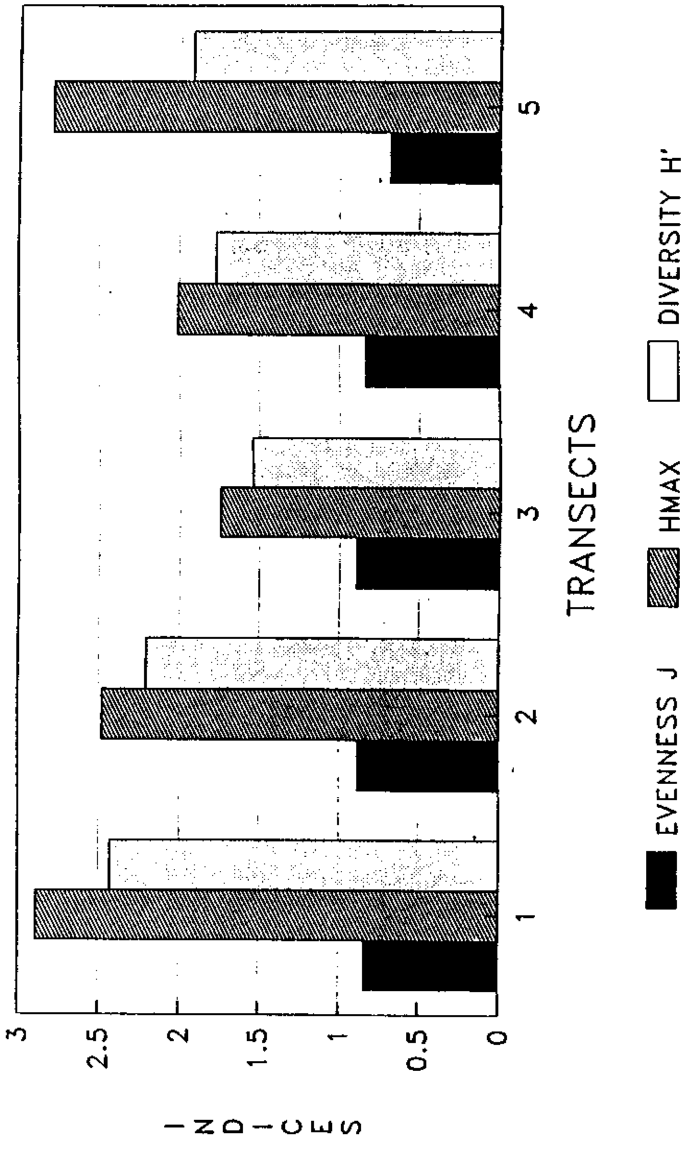

Figure 4. Average community indices for the fish assemblages on each transect at Corona de Laurel reef. Vertical bars depict 95% C.I. of the mean. Number of censuses per transect is N = 30.

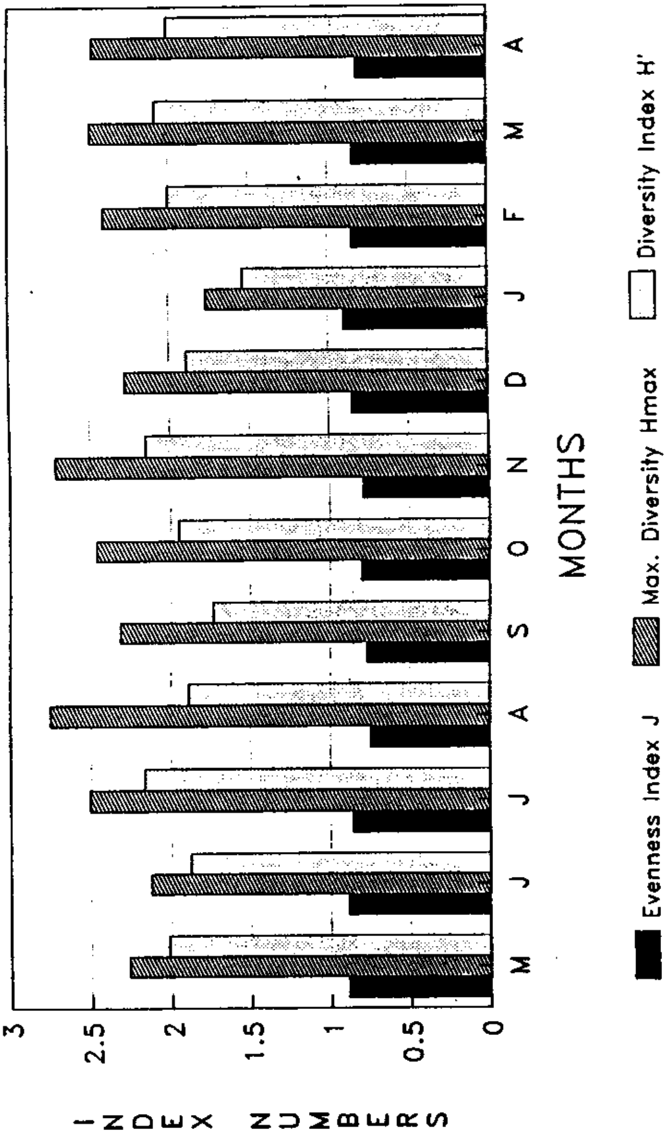

Figure 5. Comparison of monthly average community indices for the fish assemblages on Corona de Laurel reef. Numbers represent averages for all transects; each transect was censused once a month. Vertical bars depict 95% C.I. of the mean.

Table 2. Percentage Similarity values for comparisons between seasonal samples taken from five transect stations at Corona de Laurel patch reef.

Transects Compared	Winter	Spring	Summer	Fall
1 & 2	32.42	41.6	33.2	33.17
1 & 3	14.18	30.74	13.28	21.48
1& 4	37.98	49.92	41.3	38.18
1 & 5	55.72	35.68	41.05	47.47
2 & 3	44.34	38.37	51.99	52.59
2 & 4	33.13	46.28	40.06	35.07
2 & 5	27.1	19.78	26.14	31.46
3 & 4	40.03	38.55	29.63	13.9
3 & 5	10.46	17.31	5.01	11.63
4 & 5	50.03	39.37	47.58	75.01
Mean	34.54	35.76	32.92	36.00
S^2	14.46	10.50	14.86	19.02

Table 3. Similarity matrix comparing fish assemblages between seasons in each transect at Corona de Laurel reef, La Parguera, Puerto Rico.

	WINTER	SPRING	SUMMER
SPRING	56.13(T1)		
	64.39(T2)		
	61.88(T3)		
	53.18(T4)		
	80.49(T5)		
SUMMER	59.81(T1)	45.24(T1)	
	69.86(T2)	62.41(T2)	
	50.68(T3)	57.24(T3)	
	55.37(T4)	55.81(T4)	
	76.00(T5)	81.25(T5)	
FALL	65.66(T1)	50.43(T1)	70.13(T1)
	58.33(T2)	61.96(T2)	60.56(T1)
	63.24(T3)	62.61(T3)	69.43(T3)
	57.57(T4)	50.90(T4)	50.93(T4)
	72.71(T5)	74.76(T5)	77.76(T5)

Kaufman and Ebersole, 1984). These authors found that the characteristics of the reef environment, such as habitat microtopography or substrate complexity, and food availability play very important roles in determining the organization and structure of coral-reef fish communities. In considering the 5 transects as distinct habitat subdivisions within the reef, the differences in reef-fish diversity and low percentage fish- faunal similarity among transects demonstrate the existence of variable species assemblages in different habitats.

In this study variations in species composition and abundance were much greater over the small spatial scale examined than over the one-year time frame. This is evidenced by differences in percent similarity among transects versus within transects over time. These results, then, suggest that in general, variability in species composition and abundance of fishes on Corona de Laurel reef may be attributable more to spatial rather than temporal factors.

Several previous studies on coral-reef fishes also have pointed to the importance of spatial differences, in particular the degree of habitat complexity in structuring reef-fish communities. For example, Itzkowitz (1977), Gronnel (1980), and Waldner and Robertson (1980) have found that settlement, survival, and behavioral ecology of reef fishes are largely determined by the type and quality of the available substrata. Likewise, Shulman (1984, 1985a,b) demonstrated that recruitment and subsequent survivorship of several species of fish in the U.S. Virgin Islands were strongly limited by the number of refuges available. Although the relationship between habitat characteristics and fish community parameters was not quantified in the present study, there is evidence of increasing fish diversity with increasing habitat complexity. As described in the methodology, the order in which the transects could be arranged based on the degree of coral diversity and substrate complexity are Transect 1, 2, 5, 4, and 3 (*i.e.*, from highest to lowest). Fish species diversity and abundance were also observed to follow the same order (*i.e.*, from most diverse to least diverse [Figures 2 and 4]).

Seasonal changes in the community structure of the fish assemblages on Corona de Laurel reef were not clearly established. However, it was found that the most abundant fishes showed increased abundance in the summer and fall months (*i.e.*, August and November), and remarkably low abundances were observed in the winter (*i.e.*, January). Statistical verification of this trend was not possible because monthly censuses (only once a month per transect) were not replicated; however, because this trend was observed in a number of unrelated fish taxa, we feel that seasonal variations in abundances are indeed occurring. Smith and Tyler (1972) suggested that annual cycles in the numerical abundance of reef fishes would be expected as a result of seasonal recruitment. Our study was not sensitive to seasonal pattern of larval recruitment because it excluded fishes < 5 cm total length. The observed differences in monthly fish species diversity and abundance suggest either (i) that recruitment to Corona de Laurel reef continues well past the larval stage, (ii) that the effects of seasonal variation in larval recruitment are retained over time, or (iii) that factors other than recruitment are important, such as predation (Harmelin-Vivien, 1989; Sale *et al.*, 1984).

We conclude with a comment on the statistical methodology of this study and other similar studies. Such studies are subject to a shortcoming in statistical design. Many reef fishes are territorial and relatively long-lived (*i.e.*, 1 year); in replicate samples over time, there is a likely possibility that the same individual fish will be observed. This increases the probability that percent similarities within transects will be higher than in comparisons between transects. In assessing fish community structure on continuous habitats such as coral reefs using visual census techniques, probable violation of the statistical requirement of "representative" samples should not be overlooked. Thus we recommend that the results of any study of temporal variations in fish community structure based on repeated visual censuses on the same transect should be interpreted with caution. In the present study, we feel the results are robust, for two reasons. First, the magnitude in the percent similarity differences between spatial and temporal comparisons was large (Tables 2 and 3). Second, within-transect percent similarities showed no pattern over time, *i.e.*, we would expect similarities between winter and spring surveys to be greater than between winter and the following fall (Table 3) if pseudoreplication was strongly biasing the results.

ACKNOWLEDGEMENT

We are indebted to Richard S. Appeldoorn and 2 anonymous reviewers for their valuable comments and suggestions on the manuscript. We thank Angie McGeehee and Mario Tatcher for their commments on an earlier version of the manuscript. Our sincere gratitude goes to Steve Tuleveck for his assistance during one phase of the data collection and to Dave Jones for drawing Figure 1. Partial funding for this research was made available through Sea Grant research grants to Richard S. Appeldoorn, University of Puerto Rico (Project Number R/RR-30-10) and Conrad Recksiek, University of Rhode Island (Project Number M/PD-8716).

REFERENCES CITED

Anderson, G. R. V., A. H. Ehrlich, P. R. Ehrlich, J. D. Roughgarden, B. C. Russel, and F. H. Talbot. 1981. The community structure of coral reef fishes. *American Naturalist* **117**:476-495.

Belk, M. S. 1975. Habitat partitioning in two tropical reef fishes Pomacentrus lividus and P. albofasciatus. *Copeia* **1975**: 603-607.

Bell, J. D. and R. Galzin. 1984. Influence of live coral cover on coral-reef fish communities. *Marine Ecology Progressive Series* **15**: 265-274.

Emery, A. R. 1973. Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentridae) at Alligator Reef, Florida Keys. *Bull.Mar. Sci.* **23**: 649-770.

Gladfelter, W. B. and E. H. Gladfelter. 1978. Fish community structure as a function of habitat structure on West Indian patch reefs. *Revista de Biologia Tropical* **26**(Suppl.1): 65-84.

Gladfelter, W. B., J. C. Ogden, and E. H. Gladfelter. 1980. Similarity and diversity among coral reef fish communities: a comparison between tropical Western Atlantic (Virgin Islands) and Tropical Central Pacific (Marshall Island) patch reefs. *Ecology* **61**(5): 1156-1158.

Glynn, P. W. 1973. Ecology of a Caribbean coral reef. The Porites reef-flat biotope: Part I. Meteorology and hydrology. *Marine Biology* **20**: 297-318.

Gronnel, A. 1980. Space utilization by the cocoa damselfish *Eupomacentrus variabilis* (Pisces: Pomacentridae). *Bulletin of Marine Science* **30**: 237-251.

Harmelin-Vivien, M. L. 1989. Reef fish community structure: an Indo-Pacific comparison. pp. 21-60, In: M.L. Harmelin-Vivien and F. Bourlière (Eds.). *Vertebrates in Complex Tropical Systems.* Ecological Studies, Volume 69. Springer-Verlag, New York.

Hillman, R. E., N. W. Davies, and J. Wennemer. 1977. Abundance, diversity, and stability in shore-zone fish communities in an area of Long Island sound affected by the thermal discharge of a nuclear power station. *Estuarine and Coastal Marine Science* **5**: 355-381.

Itzcowitz, M. 1977. Spatial organization of the Jamaican damselfish community. *Journal of Experimental Marine Biology and Ecology* **28**:217-241.

Kaufman, L. S. and P. Ebersole. 1984. Microtopography and the organization of coral reef fishes in the West Indies. *Journal of Experimental Marine Biolo gy and Ecology* **28**:217-241.

Luckhurst, B.E. and K. Luckhurst. 1977. Recruitment patterns of coral reef fishes on the fringing reef of Curacao. *Canadian Journal of Zoology* **55**:681-689.

Luckhurst, B. E. and K. Luckhurst. 1978. Analysis of the influence of substrate variables on coral reef fish communities. *Marine Biology* **49**: 317-232.

Munro, J. L., V. C. Gaut, R. Thompson and P. H. Reeson. 1973. The spawning seasons of Caribbean reef fishes. *Journal of Fish Biology* **5**: 69-84.

Pielou, E. C. 1966. Shannon's formula as a measure of specific diversity, its use and misuse. *American Naturalist* **100**: 463-465.

Pielou, E. C. 1966b. The measurement of diversity in different types of biological collections. *Journal of Theoretical Biology* **13**: 131-144.

Recksiek, C. W., R. S. Appeldoorn, and R. G. Turingan. 1991. Studies of fish traps as stock assessment devices on a shallow reef in southwestern Puerto Rico. *Fisheries Research* **10**: 177-197.

Risk, M. J. 1972. Fish diversity on a coral reef in the Virgin Islands. *Atoll Research Bulletin* **153**: 1-6.

Russell, B. C., F. H. Talbot, and S. Domm. 1974. Patterns of colonization of artificial reefs by coral reef fishes. *Proceedings of the Second International Coral Reef Symposium*, Brisbane, Australia **1**: 207-215.

Sale, P. F. 1974. Mechanisms of coexistence in a guild of territorial fishes at Heron Island. *Proceedings of the Second International Coral Reef Symposium*, Brisbane, Australia **1**: 193-206.

Sale, P.F. 1976. Reef fish lottery. *Natural History* **85**: 60-65.

Sale, P. F. 1977. Maintenance of high diversity in coral reef fish communities. *American Naturalist* **111**(97): 337-359.

Sale, P. F. and R. Dybdahl. 1975. Determinants of community structure for coral reef fishes in an experimental habitat. *Ecology* **56**: 1343-1355.

Sale, P. F. and R. Dybdahl. 1978. Determinants of community structure for coral reef fishes in isolated coral heads at lagoonal and reef slope sites. *Oecologia* (Berlin) **34**: 57-74.

Sale, P. F., P. J. Doherty and W. A. Douglas. 1980. Juvenile recruitment strategies and the coexistence of territorial pomacentrid fishes. *Bulletin of Marine Science* **30**: 147-158.

Sale, P. F., P. J. Doherty, G. J. Eckert, W. A. Douglas, and D. J. Ferrel. 1984. Large-scale spatial and temporal variation in recruitment to fish populations on coral reefs. *Oecologia* **64**(2): 191-198.

Sale, P. F. and W. J. Steel. 1986. Random placement and the distribution of fishes among coral patch reefs. *Marine Ecology Progressive Series* **28**: 165-174.

Shulman, M. J. 1984. Resource limitation and recruitment patterns in a coral reef fish assemblage. *Journal of Experimental Marine Biology and Ecology* **74**: 85-109.

Shulman, M. J. 1985a. Variability in recruitment of coral reef fishes. *Journal of Experimental Marine Biology and Ecology* **89**: 205-219.

Shulman, M. J. 1985b. Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* **66**(3): 1056-1066.

Smith, C. L. and J. C. Tyler. 1972. Space resource sharing in a coral reef fish community. *Bulletin of the Natural History Museum of Los Angeles County* **14**: 125-170.

Smith, C. L. and J. C. Tyler. 1973. Direct observations of resource sharing in coral reef fish. *Helgoländer Wis Meeresunters* **24**: 264-275.

Smith, C. L. and J. C. Tyler. 1975. Succession and stability in fish communities of dome-shaped patch reefs in the West Indies. *American Museum Novitates* **2572**: 1-18.

Talbot, F. H. 1965. A description of the coral structure of Tutia reefs (Tanganyika, East Africa) and its fish fauna. *Proceedings of the Zoological Society of London* **145**: 431-471.

Waldner, R. E. and D. R. Robertson. 1980. Patterns of habitat partitioning by eight species of territorial Caribbean damselfishes (Pisces: Pomacentridae). *Bulletin of Marine Science* **30**: 171-186.