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Effects of Piscivorous Predator Removal On Coral Reef Fish Community Structure

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The role of piscivorous predation in reef fish communities is poorly understood. Sale (1980) noted the lack of data about this problem. Here I examine the possibility that predation controls reef fish abundances. One predator model predicts that reduced predation would allow prey populations to increase (Paine, 1966; Menge and Sutherland, 1976). Eventually, increased competition should occur and then the best competitors should increase in abundance relative to poor competitors.

Here I compare an experimental reef that has small piscivorous predator populations with two control reefs with abundant predator populations. Spearfishing was primarily responsible for differences between predator populations on experimental and control reefs. Results reported here show that (1) piscivorous predator populations are significantly smaller on reefs impacted by spearfishing and (2) the abundance of some remaining species on the experimental reef differs significantly from control reefs.

Study Area

The experimental reef was Looe Key Reef (LKR), located on the outer reef tract (Lat 24° 33' N and Long 81° 24' W) south of Big Pine Key, Florida. LKR is a large reef with well developed spur and groove formations which provide high vertical relief. Antonius, Weiner, Halas and Davidson (1979) reported that most large piscivorous predators were conspicuously absent from LKR because of spearfishing pressure. Spearfishermen particularly concentrate on the larger predator species and individuals because of their greater food and sport value. Spearfishing was legal at LKR until April, 1981.

Molasses Reef (MR) and French Reef (FR), located on the outer reef tract in the Key Largo Coral Reef Preserve, were selected as control reefs because they have been protected from spearfishing since 1960. They also represent two extremes in major reef development in Florida. MR (Lat

25° 1' N, Long 80° 23' W) is a large reef with high relief similar to LKR. FR (Lat 25° 2' N, 80° 21' W) is smaller and less well developed. Divers commonly visited all reefs. Hook and line fishermen visited much less frequently.

Methods

I used two types of visual census methods with SCUBA gear. I censused all observable fishes at random points with one method. With the second method I only censused piscivorous predators during 15 minute search periods. Clear waters made visual censusing ideal for coral reef fishes. The methods were non-destructive and provided data suitable for statistical treatment. Traditional sampling techniques utilizing ichthyocides, trawls or blasting were not possible or were undesirable because of potential damage to the reefs. Data were collected between June 1979 and June 1981 between the hours of 0930 and 1630 (Table 1).

Table 1. Summary of random point census results.

	LOOE KEY REEF	MOLASSES REEF	FRENCH REEF
Total Species Observed	105	102	92
Total Individuals Observed	35,500	19,422	8,382
Mean Species/Sample (+ s.d.)	21 + 4	24 + 3	21 + 5
Mean Individuals/SampTe (+ s.d.)	273 + 145	309 + 164	212 + 133
Number of Samples	130	63	40
Boat Activity Index (\bar{X} + s.d.)	19 + 11	19 + 7	9 + 4
Number of Samples	13	9	5
Fishing Effort Index (\bar{X} + s.d.)	0.52 + 0.81	0.74 + 0.91	0.40 + 0.71
Number of Samples	126	58	40

Random Point Censuses

At random points on each reef, I recorded all species observed in five minutes within an imaginary cylinder extending from the surface to the bottom with an 8 m radius from the observer. Numbers of observed individuals of each species were counted and the mean and range of fork lengths were estimated for each species. A ruler held out perpendicularly at the end of a meter stick aided in making size estimates by reducing parallax errors. Size estimates of large fishes were made relative to the meter stick. Bohnsack (1979) found a high correlation ($r = 0.99$, $p < 0.01$) between estimated and measured fish lengths.

A rigorous sampling regime was used to avoid bias and prevent counting the same individuals more than once. All sample points were selected using a table of random numbers. I began each sample by facing seaward and listing all species within the field of view in the sample radius. When no new species were noted, new sectors were scanned by rotating to the left. New species were listed as observed. This process was continued for five minutes. Several complete rotations usually were made for each sample. Individuals were counted and size estimated immediately for species with few individuals (e.g. pomacanthids, chaetodontids, scarids) or for species not likely to remain in the sample area (e.g. carangids and *Clepticus parrai*). Species that were always present in the sample area (e.g. *Thalassoma bifasciatum* and *Abudefduf saxatilis*) and species not likely to leave the sample area (e.g. damselfishes) were initially listed as observed and counted later after the five minute

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sample period. At the end of the five minute sample period I would make one 360° revolution for each species in the latter two groups, during which data were collected. To avoid bias I would always work back up the list treating each species when reached. This procedure eliminated the tendency to count each species when it was particularly noticeable and abundant. With the addition of the last procedure, each point census took approximately 20 minutes to complete. Data collected should be considered a relative index of abundance and probably underestimate the true abundance of most species.

At each sample point bottom features were recorded and an index of fishing effort was made by counting the number of lost leaders observed in the sample area. A boat activity index was made by counting the maximum number of boats observed at any one time during each day on each reef. Divers accounted for most of the boats observed at all sites.

Predator Censuses

In addition to using community data described above, piscivorous predator populations were sampled independently during 15 minute search periods. Only piscivorous predators were censused. Each search covered a different area of bottom while swimming speed was held constant as much as possible. Unlike random point samples, likely hiding places for particular predators such as caves and ledges could be closely examined. Members of the following observed groups were considered piscivores: Aulostomidae, Belonidae (genus Tylosaurus), Bothidae, Carangidae (genus Caranx), Centropomidae, Elopidae, Lutjanidae, Muraenidae, Prichthidae, Scombridae, Serranidae (genera Epinephelus and Mycteroperca), and Sphyraenidae. Designation of a piscivore was based on stomach content analysis and on published reports (Randall, 1967; Starck, 1970). The effect of predation varies with the species of predator, the size of the individual, and the size of the prey items (See Starck, 1970).

Data Analyses

The null hypothesis being tested is that reefs subject to spearfishing are no different in fish composition from protected reefs. A non-parametric Kruskal-Wallis test (Sokal and Rohlf, 1981) followed as necessary by Dunn's multiple comparison procedure (Hollander and Wolfe, 1973) was used to analyze the boat activity index and the index of fishing effort (Table 1). Community structure of the sampled reefs was analyzed on the basis of similarity indices and abundance distributions.

Results and Discussion

Although this study deals with spearfishing, it is not intended nor should it be construed as a recommendation for a particular management policy.

Looe Key Reef, Molasses Reef and French Reef had a similar number of species (Table 1). Boat visitation was significantly less ($p < 0.05$) on FR versus LKR and MR. No statistical difference in boat visits was observed between LKR and MR. Sightings of lost fishing gear did not differ significantly among reefs ($p > 0.05$).

Total piscivorous predator populations were significantly different on the three reefs ($p < 0.001$) (Table 2). Significantly fewer predators were observed at LKR ($p < 0.05$) than on either control reef. However,

the two control reefs were also significantly different from each other ($p < 0.05$) with more predators observed at MR. I interpret this last result as a reflection of the difference in the physical structure between the control reefs.

Table 2. Analysis of variance of predator abundance. Data were normalized by a \log_{10} transformation.

Source of Variation	df	SS	MS	F-ratio	Significance
Among Reefs	2	11.803	5.902	33.26	($p < 0.001$)
Within Reefs	59	10.468	0.177		
Total	61	22.271			

The relative abundance of predator families was similar on all three reefs (Table 3). The lutjanids alone accounted for nearly 76% of all predators censused. Carangids and lutjanids comprised approximately 92% of all observed predators.

Table 3. Composition of all potentially piscivorous predators censused during predator searches.

Predator Group	Looe Key Reef	Molasses Reef	French Reef	Combined Total
Lutjanidae	67.60%	75.53%	92.53%	76.01%
Carangidae	26.19%	23.05%	4.04%	21.32%
Sphyraenidae	2.25%	0.67%	1.10%	1.06%
Serranidae	2.25%	0.19%	1.18%	0.67%
Aulostomidae	0.64%	0.44%	0.86%	0.53%
Other	1.05%	0.12%	0.29%	0.33%
Total Individuals	4,093	12,871	2,449	19,413
Mean Individuals	124	757	204	308
Total Species	24	21	21	28
Total Samples	33	17	12	62

Species composition within the lutjanids differed between experimental and control reefs (Fig. 1). The largest species were much rarer at LKR relative to control reefs, which I attribute to spearfishing pressure. Within a species, mean predator size was generally smaller at LKR, especially for intermediate sized species. Time and lack of space prevent statistical treatment of size data here.

Individual abundance of the serranid Epinephelus cruentatus was significantly greater at LKR than on control reefs ($p < 0.05$, mean = 0.58 ind./sample at LKR, 0.11 at MR, and 0.28 at FR). This species is usually too small to spear. The greater abundance of this species at LKR may be due to the reduced populations of other predator species. Thompson and Munro (1978) have shown the same pattern of increased abundance on reefs where populations of larger grouper have been reduced by trap fishing. Unfortunately, it is not clear from the data whether the density increase of Epinephelus cruentatus is in response to reduced predation or reduced competition from other predator species.

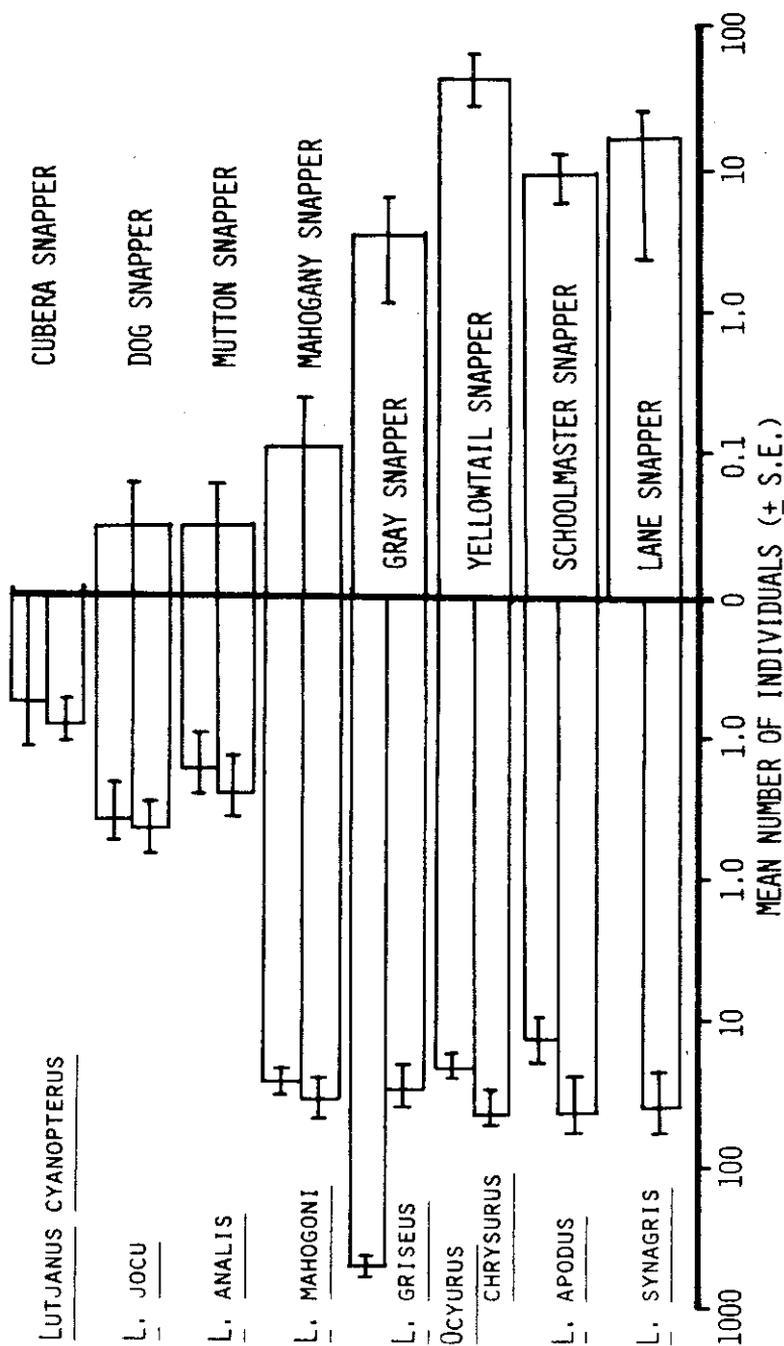


Figure 1. Abundance of snapper (Lutjanidae) compared on the experimental reef, LKR (right side), and control reefs, MR (left side, top bar) and FR (left side, bottom bar). Species are listed from top to bottom in approximate order of decreasing size. Species tend to be increasingly piscivorous from bottom to top. Sample size: 33 at LKR, 17 at MR, 12 at FR.

Community percent similarity indices show that the three reefs were broadly similar in terms of composition of individuals. Percent similarity indices were calculated based on the total individuals observed at each reef (Brower and Zar, 1977). The two control reefs were the most similar (65.8%). LKR was most similar to FR (63.5%) and least similar to MR (53.3%).

The total distribution of all species was analyzed using the G-test for goodness of fit (Sokal and Rohlf, 1981). Data were the number of species in different abundance categories (M. E. Crow, in prep.). The abundance patterns were not significantly different between reefs (Table 4). Although fewer species were found in the higher abundance classes at LKR, the G-statistic was not significant ($p = 0.22$). These results do not imply that each species was similarly distributed between reefs.

Table 4. Distribution of species into abundance categories.

ABUNDANCE CATEGORY	NUMBER OF SPECIES			
	Percent of Total Individuals	Looe Key Reef	Molasses Reef	French Reef
Greater than 5%		5	6	6
1.0% to 5%		9	10	12
0.5% to 1.0%		5	7	12
0.1% to 0.5%		21	22	23
0.05% to 0.1%		13	11	10
Less than 0.05%		52	46	29
Total Species		105	102	92
G = 10.38		$\chi^2 (0.05) = 14.07$		

The 25 most abundant species out of 132 total censused species accounted for over 91% of all censused individuals on all reefs (Table 5). The abundances of nine of these species (including six of the eight most abundant species) were significantly different ($p < 0.05$) between control and experimental reefs. The abundances on the two control reefs were similar ($p < 0.05$) for six of the nine species. The abundances for the three remaining species were different on all three reefs ($p < 0.05$), however, LKR was at one end of an extreme.

Among non-piscivorous species, the Haemulidae were examined (Fig. 2) because they were the most important family considering total biomass, number of species, and abundance. Their distribution (Fig. 2) is similar to that found in the Lutjanidae in that the largest species are rarest at LKR. This pattern is most easily explained as a consequence of spearfishing. However, smaller individuals of many of the missing species are not normally speared because of their small size. Their absence could be due to any of numerous autecological causes or it could be in part because of competition from the tomtate (Haemulon auro-lineatum) which achieves great density at LKR. At present I cannot support or refute either possibility. Note also (Fig. 2) that H. auro-lineatum almost completely replaces H. chrysargyreum at LKR. Inter-specific competition may be an important factor for these two species considering their similarity in taxonomy and appearance, or it may be of

no importance. Only carefully designed experiments can critically test such an hypothesis.

Table 5. A comparison of the distribution of the twenty-five most important species among reefs. Importance was based on mean proportion of individuals among reefs. Data were analyzed species by species using the Kruskal-Wallis test (Sokal and Rohlf, 1981). Dunn's multiple comparison procedure (Hollander and Wolfe, 1973) was used when appropriate. Data for five species that could be normalized by a log (x + 1) transformation were analyzed by analysis of variance (Sokal and Rohlf, 1981).

Species Ranked According to Decreasing Abundance	Percentage of Total Observed Individuals	Mean Individuals/Sample			Significance	
		LKR	MR	FR		
<u>Thalassoma bifasciatum</u>	18.11	68.88	29.81	35.28	**	1
<u>Eupomacentrus partitus</u>	17.10	46.13	58.60	32.30	n.s.	1
<u>Haemulon chrysargyreum</u>	8.56	0.17	57.21	15.50	*	
<u>Abudefduf saxatilis</u>	8.34	21.31	20.41	21.83	n.s.	1
<u>Haemulon aurolineatum</u>	6.06	72.66	0.00	0.00	**	
<u>Eupomacentrus planifrons</u>	5.35	19.33	12.11	10.58	**	1
<u>Lutjanus griseus</u>	2.89	0.04	25.05	1.15	*	
<u>Haemulon sciurus</u>	2.89	0.67	13.84	8.25	*	
<u>Caranx ruber</u>	2.17	3.06	16.06	0.33	a	
<u>Inermia vittata</u>	2.13	0.00	0.16	13.30	b	
<u>Ocyurus chrysurus</u>	1.92	4.00	6.29	4.75	**	
<u>Microspathodon chrysurus</u>	1.58	6.05	4.87	2.88	a	1
<u>Chromis multilineatus</u>	1.52	3.75	2.00	5.30	n.s.	
<u>Haemulon flavolineatum</u>	1.49	2.69	8.62	1.43	b	
<u>Acanthurus bahianus</u>	1.34	3.49	4.29	2.60	b	
<u>Halichoeres garnoti</u>	1.26	5.48	1.56	2.63	**	
<u>Clepticus parral</u>	1.18	4.00	4.41	2.23	n.s.	
<u>Mulloidichthys martinicus</u>	1.06	0.90	5.81	2.40	+	
<u>Halichoeres maculipinna</u>	1.06	2.98	1.90	3.03	n.s.	
<u>Scarus croicensis</u>	1.00	3.35	1.37	2.80	n.s.	
<u>Sparisoma aurofrenatum</u>	0.96	1.35	3.46	2.63	**	
<u>Lutjanus apodus</u>	0.87	0.69	1.06	3.43	n.s.	
<u>Pempheris schomburgki</u>	0.81	0.81	1.54	3.38	+	
<u>Acanthurus coeruleus</u>	0.81	0.91	2.29	2.83	+	
<u>Sparisoma viride</u>	0.80	1.20	3.24	1.93	a	

* LKR differed significantly from control reefs ($p < 0.05$) and control reefs were not significantly different ($p > 0.05$).

* All reefs were statistically different ($P < 0.05$) with LKR at one extreme.

+ LKR differed significantly from one control reef ($p < 0.05$) and the two control reefs were not statistically different ($p > 0.05$).

a LKR differed significantly from one control reef ($p < 0.05$) and the two control reefs were statistically different ($p < 0.05$).

b LKR did not differ significantly from either control reef ($p > 0.05$) although the two control reefs differed significantly ($p < 0.05$).

1 Analyzed by analysis of variance.

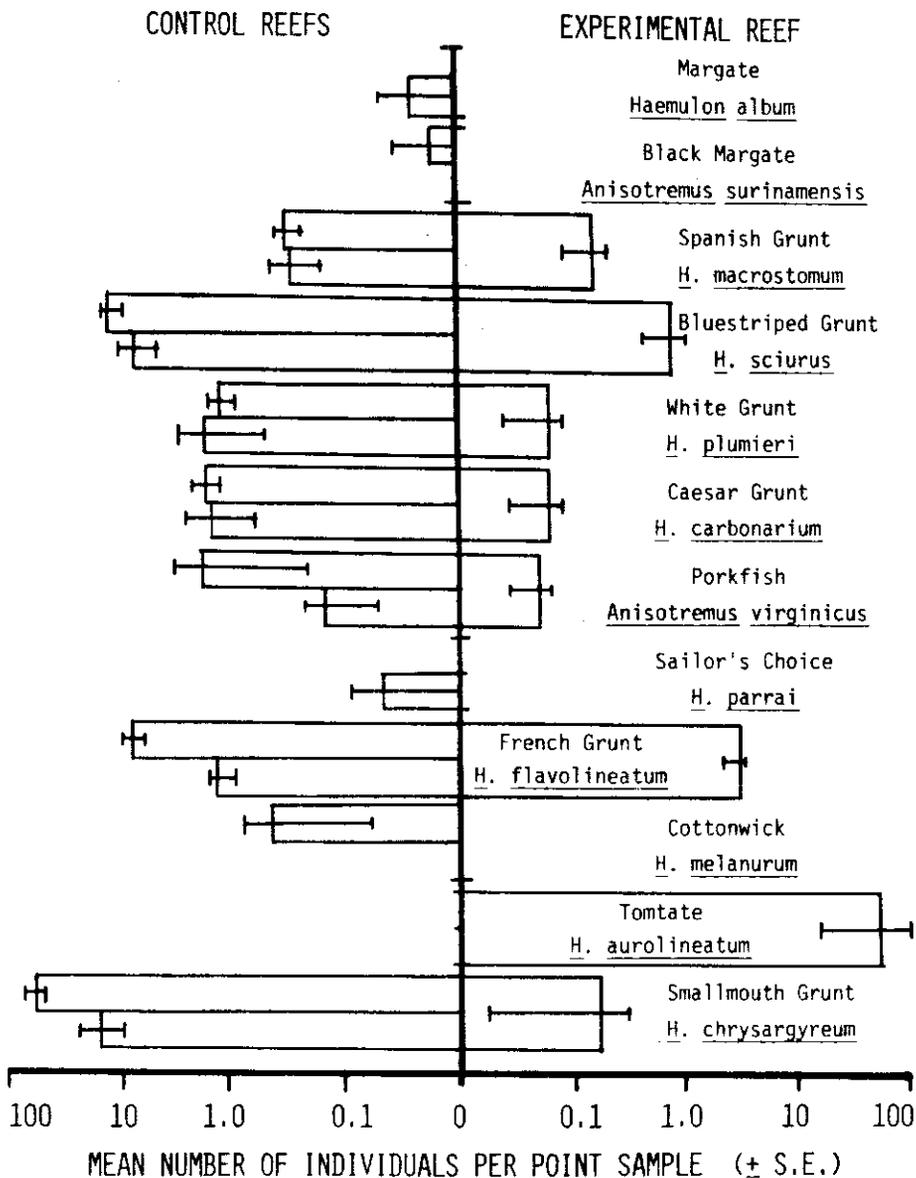


Figure 2. Abundance of grunt (Haemulidae) compared on the experimental reef (LKR, right side) and control reefs (MR, left side top bars; and FR, left side bottom bars). Species are listed from top to bottom in approximate order of decreasing adult size. Larger species are much more rare on the experimental reef. The tomtate, the most abundant grunt on the experimental reef, is absent in samples from control reefs. Sample size: 130 at LKR, 63 at MR, 40 at FR.

Results reported here are suggestive but not conclusive concerning the role of predation in determining relative abundances of reef fishes. The fact that the most abundant species, *Thalassoma bifasciatum*, was twice as abundant in samples from LKR (Table 5) appears to support the predator model. Likewise two very abundant and similar species of grunt, *Haemulon aurolineatum* and *H. chrysargyreum*, show complimentary distributions between control and experimental reefs (Fig. 2) which could be interpreted as support for the model. The same arguments could be made for other observed differences between experimental and control reefs. However, reduced predation or some other unrecognized factor or factors associated with LKR may be responsible for observed differences. Stating that piscivorous predation is an important factor controlling community structure of reef fishes based on present evidence would be premature. I expect ongoing monitoring of control and experimental reefs to help settle these alternative possibilities because in April 1981 LKR was designated the Looe Key Reef National Marine Sanctuary and spearfishing was prohibited. If predator populations increase on LKR and the observed differences between control and experimental reefs diminish, then the importance of predation will be supported. Otherwise other factors should be examined to account for differences between reefs.

Conclusions

Results showed that the total numbers of piscivores were smallest on the reef subject to spearfishing. Within the Lutjanidae, the largest species and individuals tended to be absent. One small species of grouper, *Epinephelus cruentatus*, showed greater density on the experimental reef which was apparently a response to the absence of larger predators. Community similarity indices and the distribution of species in abundance categories suggested broad similarities existed in community structure among reefs. However, several non-piscivorous species had significantly different abundance patterns between experimental and control reefs which could be interpreted as support for the importance of predation in structuring reef fish communities. Present data, however, are not sufficient to substantiate the predation model. Ongoing monitoring should help resolve this problem.

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