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Resilience of predators to fishing pressure on coral patch reefs

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Abstract

Numbers and biomass of piscivorous fish and their predation on other fish may often be high in undisturbed coral reef communities. The effects of such predation have sometimes been studied by removal of piscivores (either experimentally or by fishermen). Such perturbations have usually involved removal of large, highly vulnerable, mobile piscivores that are often actively sought in fisheries. The effects of fishing on smaller, demersal, semi-resident piscivores have been little studied. We studied such effects on the fish communities of patch reefs at Midway atoll by experimentally removing major resident, demersal, piscivorous fishes. First, four control reefs and four experimental reefs were selected, their dimensions and habitats mapped, and their visible fish communities censused repeatedly over 1 year. Census of all control and experimental reefs was continued for the following 39 months, during which known piscivores were collected repeatedly by hand spearing. Records were kept of catch and effort to calculate CPUE as an index of predator density. Spearfishing on the experimental reefs removed 2504 piscivorous fish from 12 families and 43 taxa (mostly species). The species richness of the catch did not show an overall change over the duration of the experiment. Spearman rank correlation analysis showed some unexpected positive correlations for density in numbers and biomass of major fished piscivorous groups (especially lizardfish) over the experiment. Only two relatively minor fished piscivorous taxa declined in abundance over the experiment, while the overall abundance of piscivores increased. Visual censuses of fish on the experimental reefs also failed to show reduction of total piscivores over the full experimental period. No significant trend in the abundance of lizardfish censused over the full period was apparent on any of the control reefs. The high resilience of piscivores on these experimental reefs to relatively intense fishing pressure could result from their protracted recruitment seasons, high immigration rates, cryptic habits, or naturally high abundances. A major factor was the high immigration rates of lizardfish, replacing lizardfish and other less mobile piscivores removed from the reefs by spearing. On the fished reefs, the removed lizardfish population replaced itself >20 times during the experiment; other piscivorous taxa replaced themselves only 5 times.

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Keywords: Experimental fishing; Fish density; Midway atoll; Piscivores; Reef fish; Undisturbed coral reef communities

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1. Introduction

Piscivorous fishes are numerous and trophically important in many coral reef fish communities (Grigg et al., 1984; Hixon, 1991; Polunin and Roberts, 1996). Piscivores constituted 11% of the fish community biomass from Tanzania (Talbot, 1965) and 54% from the Great Barrier Reef (Goldman and Talbot, 1976). Friedlander and DeMartini (2002) reported that more than 54% of the total fish biomass in the Northwestern Hawaiian Islands (NWHI) consisted of “apex predators”. Near the opposite end of the Hawaiian archipelago (where fishing is intense), they found that only 3% of the biomass consisted of “apex predators”. In this southeast portion of the chain, at Kaneohe Bay on Oahu, piscivores made up 15% of the fish biomass of a patch reef community (Brock et al., 1979). These authors used various criteria to identify species as piscivores or “apex predators”, and apparently included all the biomass of these “piscivores” in the estimates of percent of the total fish biomass. On lagoonal patch reefs in the NWHI (the region of the present experiment), Norris and Parrish (1988) estimated the numbers and biomass of piscivores, weighted these abundance measures by the percent of fish in the diet of each predator species, and determined that the level of total piscivory was high in these communities: 52 of 126 reef fish species, 8% of the total fish community by numbers of individuals, and 20% by fish biomass.

Some species of upper trophic level predators (e.g., medium–large piscivores such as groupers, snappers and jacks) are often prime targets of coral reef fisheries. They are often vulnerable to capture, and their populations may be especially sensitive to overfishing (Russ, 1991; Watson and Ormond, 1994; Roberts, 1997; Russ and Alcala, 1998, Pauly et al., 2002). In several studies, fishing on coral reefs has been shown to strongly depress the population density, biomass, catch-per-unit-effort (CPUE), and average size of such large reef predators, apparently because of certain life-history characteristics (e.g., low recruitment, slow growth, late maturity) (Adams, 1980; Jennings and Lock, 1996; Jennings and Kaiser, 1998; Russ and Alcala, 1998). The effects of fishing on smaller, demersal, semi-resident piscivores have previously been little studied (Carr and Hixon, 1995). The purpose of our study was to examine the response of populations of demersal fish predators (piscivores)

to repeated, long-term experimental fishing on previously undisturbed patch reefs, compared to populations of these piscivorous species on similar control reefs. This experiment was part of a broader investigation on the effects of predators on the structure of coral reef fish communities (Schroeder, 1989).

2. Materials and methods

2.1. Study area

Field work took place within Welles Harbor, in the SW quarter of Midway atoll (28°12'N, 177°24'W) of the Northwestern Hawaiian Islands (Fig. 1). The lagoon averages 10 km in diameter and is surrounded by an emergent barrier reef except along the NW side. The patch reefs studied were among many scattered within the SW section (~2 km W of Sand Island and ~2 km E of the western barrier reef) of the shallow (5–10 m), sand-bottom lagoon. This section of the lagoon had experienced no known human disturbance or fishery, either commercial or recreational, for decades. Water temperatures measured throughout the year on study reefs of this subtropical atoll ranged from 17 °C in February to 28 °C in August. Currents were usually from the south, negligible to slight. Large oceanic swells from the NW often created strong bottom surge during winter. Underwater horizontal visibility was usually 10–20 m, except after rare storms, which dispersed sand and debris into the water column, greatly reducing visibility.

2.2. Control and experimental reefs

The design for the experiment included eight patch reefs, four of which were controls. The eight reefs selected appeared to be broadly similar in terms of size, vertical relief, water depth, isolation across open sandy area, nature of the substrate, and apparent general composition of the fish assemblage. Prior to the study, all reefs were in natural condition (i.e., had experienced no known recent human disturbance). During the first year (May 1981–1982), all reefs remained undisturbed, and the fish were visually censused in all seasons as a baseline. Piscivorous predators were repeatedly removed from the four experimental removal reefs from June 1982 to August

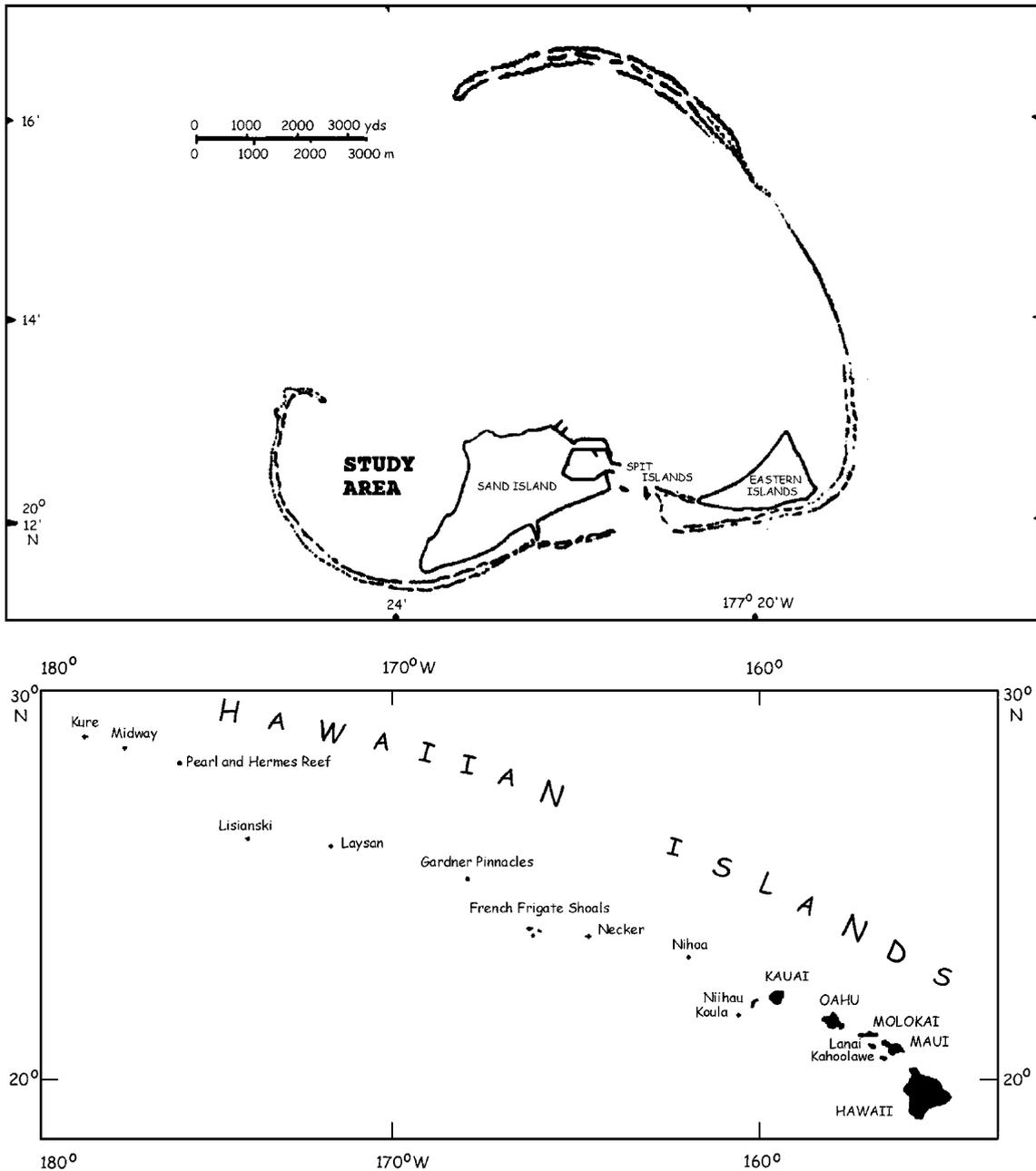


Fig. 1. Midway atoll (top), with the site of the study indicated, and the Hawaiian archipelago (bottom).

1985. At the start of the experiment, we believed that the experimental removal reefs were sufficiently isolated from control reefs to assume that fishing on them did not affect natural abundances of piscivores on the control reefs. All control and experimental

removal reefs were separated by some tens of meters of open sand from each other and from all other patch reefs. The range of distances separating control reefs was 70–132 m (mean 94 m). Inter-reef isolation (to nearest neighbor patch reef) for removal reefs ranged

from 20 to 100 m (mean 51 m). Fishes on all eight reefs were visually censused repeatedly throughout the experiment. The average minimum number (e.g. excluding recruitment pulses) and species richness ranged from about 50 fish from 15 species on the smallest patch reef (12 m²), to about 200 fish from 50 species on the largest (186 m²) reef. Detailed bathymetric maps were made of each reef at the beginning of the study and repeated during the final sampling period. From these maps, the projected surface area (two-dimensional footprint) of exposed hard substrate was estimated and used to aid in the interpretation of results (e.g., total fish abundance declined on patch reefs experiencing major reduction in size from shifting sand) (Schroeder, 1989).

2.3. Total fish collections

At the end of the experiment, all fishes on the study patch reefs were collected using the chemical ichthyocide rotenone. The entire patch reef was first surrounded by a 1-cm square mesh barrier net, from the sea surface to the sand bottom just beyond the perimeter of the reef, and the net was left in place throughout the entire process. A team of divers used collapsible plastic containers to disperse rotenone powder dissolved in seawater around the reef in quantity sufficient to achieve a target concentration of 1.0 ppm (calculated from the strength and amount of powder used relative to the total volume of seawater enclosed within the barrier net). This concentration has been found sufficient to achieve an effective total kill in similar situations (J.D. Parrish, unpublished data). Current was negligible to slight, allowing the treatment to last 10–20 min. Divers then collected all fish of all species until no more could be found after moving rocks, digging in holes, and sifting sand around the reef base. Other divers snorkeled at the surface to collect any floating fish. All fish collected were stored on ice, measured, and then frozen.

2.4. Experimental fishing on predators

Resident demersal piscivorous fishes were removed from experimental reefs by fishing with pole spears at a roughly bi-daily frequency within each of 17 major cruises. (A “major cruise” was a continuous sampling period [seas permitting] of 1–4+wk, i.e.

Jun82, JA82, Nov82, D/J83, Mar83, MJ83, JA83, Nov83, D/J84, Mar 84, JJ84, Aug84, ON84, Jan85, MA85, May85, JA85). Piscivores were also removed during 11 minor cruises (each ~1 week) between these major cruises. No attempt was made to remove large roaming predators in the water column.

The target set of piscivorous species (Table 1B) was determined from extensive diet analysis of most of the common reef fish species from similar reefs in the NWHI (J.D. Parrish, unpublished data; Parrish et al., 1985; Norris and Parrish, 1988; Schroeder, 1989) and from other nearshore Hawaiian locations (Hobson, 1974). The largest piscivorous impacts were expected from members of the families Muraenidae (moray eels), Synodontidae (lizardfish), Congridae (conger eels), Labridae (wrasses), Scorpaenidae (scorpionfish), Holocentridae (squirrelfish), Priacanthidae (bigeyes) and Cirrhitidae (hawkfish), based on their biomasses and the importance of fish in their diets (Norris and Parrish, 1988). These species, with few exceptions, were regarded as primarily benthic/demersal and sufficiently site attached to be considered resident on the patch reefs where they were collected, based on our previous observations and visual censuses on NWHI reefs and available literature on their habitat associations.

All four removal reefs were fished at least monthly throughout the experiment, and bi-daily within each of the major cruises, with rare exceptions. During each collection period, fish were speared for about 30 min by a pair of scuba divers (about 1 spear-h of effort a day) at each reef. An average of seven days of spearfishing occurred at each reef on each major cruise. Fishing effort and catch data were recorded for each collection. Data included species richness, and for each piscivorous species collected, numerical abundance, biomass and CPUE. Changes in these variables over the 3 years of fishing were quantified for major groupings of taxa using Spearman rank correlation coefficients (r_s). The significance of these correlations was based on the experimentwise error rate of r_s for the designated groups (Miller, 1981).

2.5. Censused predator populations

The total-count underwater visual census method was used to assess abundance and temporal variability of resident piscivorous fish populations for the control

Table 1

Taxonomic composition (A) by family and (B) by lower taxa of the total quantity of predators removed from the set of experimental reefs, June 1982–August 1985

(A) Family	% N	% Kg	(B) Species	% N	% Kg
Synodontidae	46.53	41.77	<i>Synodus ulae</i>	38.22	37.65
Scorpaenidae	38.14	14.93	<i>Dendrochirus barberi</i>	11.30	0.90
Muraenidae	6.43	17.99	<i>Sebastapistes ballieui</i>	11.02	2.14
Bothidae*	2.00	1.38	<i>Scorpaenodes littoralis</i>	6.99	0.88
Aulostomidae*	1.88	0.48	Syndontid spp	6.47	2.21
Labridae	1.24	10.28	<i>Gymnothorax steindachneri</i>	3.79	9.07
Antennariidae	1.28	0.77	<i>Scorpaenopsis diabolus</i>	3.04	9.01
Congridae	0.60	7.05	<i>Sebastapistes coniora</i>	3.15	0.35
Cirrhitiidae	1.28	1.89	<i>Bothus mancus</i> *	1.20	0.89
Fistulariidae*	0.36	1.15	<i>Aulostomus chinensis</i> *	1.76	0.46
Ophidiidae	0.24	2.30	<i>Saurida gracilis</i>	1.76	1.86
Carangidae*	0.04	0.02	<i>Gymnothorax eurostus</i>	1.84	2.36
			<i>Scorpaenopsis cacopsis</i>	1.04	1.21
TOTAL N and Kg (100%)	2504	136.90	“All others” ^a (combined)	9.48	31.82
			TOTAL N and Kg (100%)	2504	136.90

Abundance is given for numbers (%N) and biomass (%Kg). Taxa <1%N each are pooled in “all others”^a (29 taxa, values in Schroeder (1989)). Taxa that probably lack strong attachment to patch reefs are indicated by *.

^a *Thalassoma ballieui*, Scorpaenid spp., *Bothus pantherinus**, *Paracirrhites forsteri*, *Antennarius commersonii*, *Conger cinereus*, *Cirrhites pinnulatus*, Bothid spp.*, *Taenianotus triacanthus*, *Pterois sphex*, *Bodianus bilunulatus*, Antennariid spp., Muraenid spp., *Cirrhitops fasciatus*, *Fistularia commersonii**, *Fistularia* spp.*, *Brotula multibarbata*, Aulostomid spp.*, *Gymnothorax undulatus*, *G. hepaticus*, *G. meleagris*, *G. flavimarginatus*, *G. pindae*, *Enchelycore pardalis*, *Ariosoma bowersi*, *Cheilinus unifasciatus*, *Pseudocaranx dentex**, *Synodus variegatus*, *S. binotatus*.

and experimental patch reefs (Brock, 1954; Schroeder, 1989 [Chap. 1]). We attempted to record all diurnally observable individuals present, as follows: Each patch reef was divided symmetrically into quadrants. During the first replicate of a set, one diver censused the quadrants on one side, while another diver censused the other side. The two divers then switched sides and conducted a second replicate. Caves and crevices were scrutinized closely. Quadrant counts were checked by a total reef count for highly mobile and conspicuous species, to avoid duplication. The total number of individuals per species observed in each quadrant was recorded. This method is reasonably accurate for quantifying most diurnally exposed fish on the reef (Sale and Douglas, 1981; Brock, 1982; Schroeder, 1989 [Chap.1]; Friedlander and Parrish, 1998). The standard length (SL) of each fish observed was estimated visually and recorded as a size class (which permitted conversion to estimates of biomass).

Censuses were conducted during the 20 major cruises during May 1981–August 1985 (i.e., MJ81, JA81, Jan82, MJ82, JA82, Nov82, D/J83, Mar83, MJ83, JA83, Nov83, D/J84, Mar84, JJ84, Aug84, ON84, Jan85, MA85, May85, JA85). During each

cruise, two to ten replicate censuses were conducted on each reef between 08:00 and 17:00 h, with rare exceptions (e.g. burial of some reefs by shifting sand). On days when both census and spearing were performed on removal reefs, censuses were conducted immediately before spearing. Changes in numbers for major groups of piscivorous taxa were quantified using Spearman r_s . The significance of these correlations was also based on the experimentwise error rate of r_s for designated groups (Miller, 1981).

3. Results

3.1. Study reefs

Detailed physical measurements of the patch reefs were taken at the beginning and end of the study. The experimental removal reefs ranged in initial projected surface area (two-dimensional footprint) from 15 m² to 154 m² (mean 61 m²). Control reefs ranged in initial area from 12 m² to 186 m² (mean 58 m²). Considerable temporal change in reef size occurred at irregular intervals throughout the experimental period,

when shifting bottom sand either exposed or buried hard reef substrate (Schroeder, 1989 [Chap. 4]). Changes were most dramatic during winter months, following events of large swells and seas. For example, sand movement, analogous to wind-driven terrestrial dunes, reduced water depth from 10 m to 5 m in less than two months in some sections of the lagoon. Reefs that showed a net increase in area over the duration of the study were 2R (+201%), 3R (+9%), and 4R (+12%), whereas reefs that decreased in size were 1R (−45%), 1C (−10%) and 2C (−55%). Two control reefs were completely buried by sand during the winter of 1983–1984 and were replaced with similar patch reefs (3C [+34%] and 4C [−19%]). These changes in the sizes of patch reefs prevented straightforward analysis and comparison of different reefs on the basis of fish density.

3.2. The natural piscivore community

Piscivores made up about 9.5% by numbers and 19% by biomass of the entire natural community of patch reef fishes collected with rotenone. Piscivorous groups, in decreasing order of numerical importance, were scorpaenids, muraenids, synodontids (mainly *Synodus ulae*, Schultz, 1953), piscivorous labrids, and cirrhitids (Table 2), based on all individuals collected with rotenone on the four control reefs at the end of the experiment. Visual census of these same control reefs, over the course of the study, indicated that 9% of all individual fish were piscivorous. In visual censuses, piscivores included 37% small scorpaenids, 16% muraenids, 11% synodontids, 17% piscivorous

Table 2

Numerical (% N) and biomass (% Kg) abundance for predator families in total ichthyocide collections from the set of four control reefs pooled, at the end of the study (August 1985), and % N censused on the same four reefs pooled, immediately before collection

Family	Defaunated (Ichthyocide)		Censused
	% N	% Kg	% N
Scorpaenidae	47	9	37
Muraenidae	22	42	16
Synodontidae	11	6	11
Labridae	4	29	17
Cirrhitidae	2	5	15
Other	14	9	4
TOTAL piscivores (100%)	547	20.1	295

Table 3

Spearman rank correlation coefficients (r_s) relating number of piscivore species collected per day with collection date, over the 3 years of fishing: June 1982–August 1985

Reef	Mean±SD	N	r_s	P
1R	1.51±1.04	106	0.251	0.0096*
2R	1.82±1.26	117	0.251	0.0063*
3R	3.42±1.77	122	0.090	0.3269 ns
4R	2.93±1.54	125	−0.009	0.9177 ns

Mean±SD=number of species collected per day; N=total collection dates during the 17 major cruises; significance level of r_s : * $P<0.0127$; ns, not significant.

labrids, and 15% cirrhitids. Less cryptic or more exposed piscivores (e.g. labrids, cirrhitids) made up a relatively higher proportion of the total fish censused because visual counts under-represented the numerous cryptic piscivores.

3.3. The fished piscivore community

Spearfishing on the four predator removal reefs from June 1982 to August 1985 produced a total of

Table 4

Spearman rank correlation coefficients (r_s) relating number of piscivore individuals collected per day with collection date, over the 3 years of fishing (all cruises with $N>4$ dates), considering various groupings of taxa

Taxa	Reef	Mean±SD	N	r_s	P
All (pooled) piscivores	1R	3.14±2.18	64	0.281	0.0244 ns
	2R	2.95±2.17	74	0.431	0.0001***
	3R	7.70±5.18	86	0.361	0.0006**
	4R	6.05±4.40	93	0.188	0.0711 ns
All (pooled) synodontids	1R	1.47±1.26	64	0.162	0.2021 ns
	2R	1.28±1.47	74	0.501	0.0001***
	3R	2.88±2.83	86	0.525	0.0001***
	4R	2.81±3.51	93	0.334	0.0009***
All (pooled) non-synodontid piscivores	1R	1.67±1.78	64	0.252	0.0447 ns
	2R	1.66±1.42	74	0.126	0.2852 ns
	3R	4.81±3.77	86	0.090	0.4108 ns
	4R	3.25±2.47	93	−0.128	0.2221 ns
<i>Synodus ulae</i>	1R	1.36±1.29	64	0.189	0.1349 ns
	2R	1.20±1.46	74	0.486	0.0001***
	3R	2.73±2.73	86	0.465	0.0001***
	4R	2.45±3.43	93	0.316	0.0020**

Significance levels of r_s for the bracketed groups: for a group of 4, * $P<0.0127$, ** $P<0.0025$, *** $P<0.0003$; for a group of 8, * $P<0.0064$, ** $P<0.0013$, *** $P<0.0001$; ns, not significant.

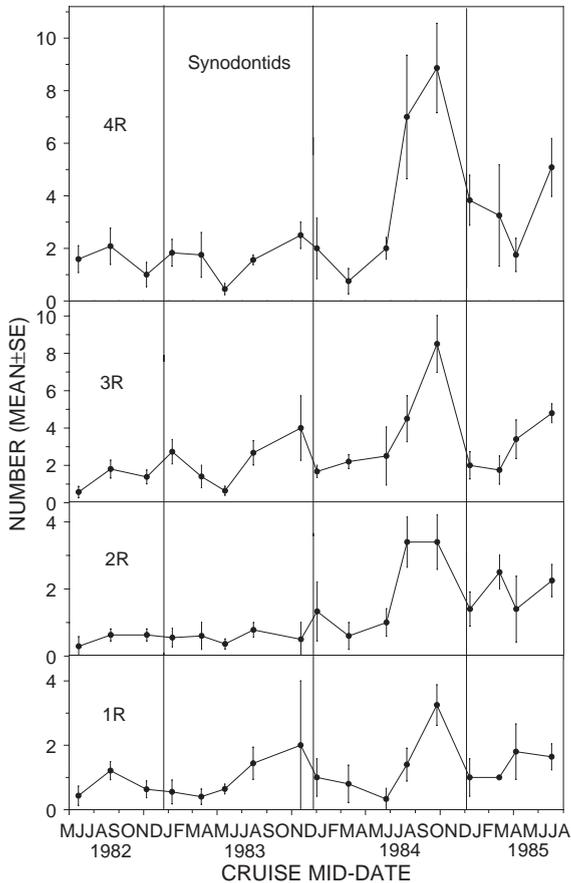


Fig. 2. Temporal variability in the number of individuals collected of all (pooled) synodontids from 4 experimental patch reefs. Number is mean (\pm SE) number of fish collected per spear-h ($N=2-17$ replicate collections).

2504 piscivorous fish (136.9 kg biomass) from 12 families and 43 taxa (mostly species) (Table 1). The total numbers and biomass of fished piscivores increased with reef size (Schroeder, 1989). Synodontids (predominantly *S. ulae*) accounted for ~47% by numbers (~42% by biomass) of the total catch. Scorpaenids were ~38% by numbers (~15% by biomass), and muraenids were ~6% by numbers (~18% by biomass).

The species richness of the catch did not show a consistent, overall change through the duration of the experiment. Spearman r_s relating the mean number of piscivore species with the collection date, over the 3 years of fishing, were low or insignificant for all reefs (Table 3). Temporal variability in species richness was considerable; values were usually

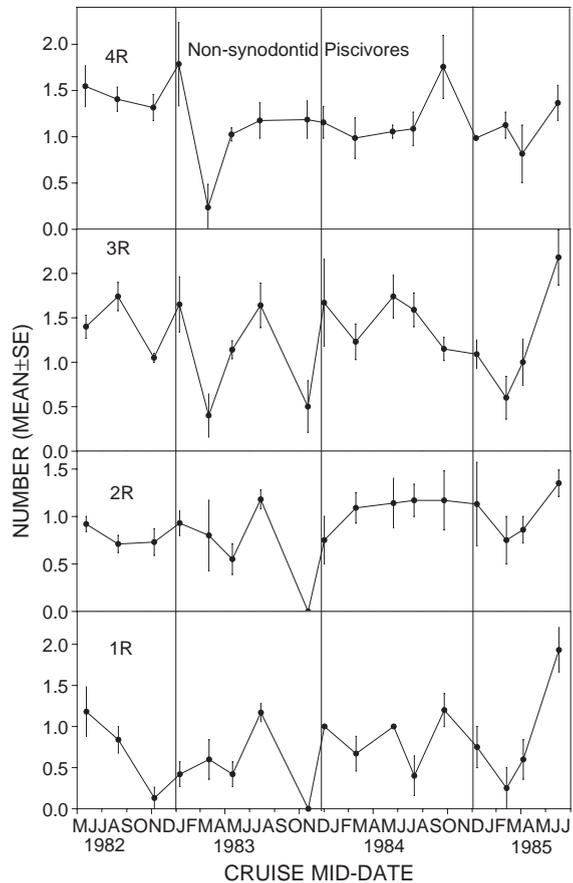


Fig. 3. Temporal variability in the number of individuals collected of all (pooled) non-synodontid piscivores from 4 experimental patch reefs. Number is mean (\pm SE) number of fish collected per spear-h ($N=2-17$ replicate fishing collections).

highest in summer or fall, following the peak recruitment season (Schroeder, 1989 [Chap. 5]). The average collection (per spear-h of effort) over the whole experiment, among the four reefs, consisted of three to eight piscivores from two to three species (Tables 3 and 4).

The number of piscivore individuals in a collection on each patch reef was used as an index of resident piscivore population size on that reef at the time of the collection, assuming negligible migration to or from patch reefs. Spearman rank correlation analysis, relating number of piscivores collected with the collection date over the 3 years of fishing, produced diverse results among the major groups of taxa (Table 4). Some significant positive correlations were found for all (pooled) piscivores, all (pooled)

synodontids and *S. ulae*. All these increases in catch over time can be attributed primarily to *S. ulae*, which accounted for over 80% of all synodontids, and synodontids (Table 1) accounted for nearly half of all piscivores caught. The peak in numbers of synodontids during the latter half of 1984 consisted primarily of adults (Fig. 2). The major changes in reef size occurred a year earlier (winter 1983–1984). Throughout the fishing experiment, there was no consistent trend in lizardfish size changes. The number caught for all other (non-synodontid) piscivores (pooled) (Fig. 3) exhibited considerable temporal variability, but did not show a consistent, overall increase or decrease with time over the full 3-year period (Table 4). Muraenid, scorpaenid and labrid piscivores (pooled by family) also showed no significant Spearman r_s over the full period. Similar results were found for all the above taxonomic groupings using Spearman r_s for daily collections of piscivore biomass and CPUE (kg/spear-h) (Schroeder, 1989 [Chap. 5]).

3.4. Censused predator populations

Of the resident piscivorous fishes censused over the years of experimental fishing, scorpaenids predominated: 42.7% of the total of control and removal reefs (Table 5A). The majority were small (<6 cm

estimated standard length) species, e.g., *Sebastapistes coniorta*, Jenkins, 1903, *Scorpaenodes littoralis*, (Tanaka, 1917), *Dendrochirus barberi*, (Steindachner, 1900), and *Sebastapistes ballieui*, (Sauvage, 1875) (Schroeder, 1989 [Chap. 5]). Synodontids accounted for 12.8% of the piscivorous community censused across all eight reefs (Table 5A). Precise species identification for this family was often difficult during underwater census, but the majority were *S. ulae* (Schroeder, 1989 [Chap. 1]).

For each piscivorous family, the percent it represented of all resident piscivore individuals was compared from the initial (baseline) year (Table 5B) to the final (fished) year (Table 5C), on both control (pooled) and removal (pooled) reefs. The only groups showing a major reduction during fishing were hawkfish (Cirrhitidae) and frogfish (Antennariidae), the latter of which occurred in very small numbers. During the final year (Table 5C), the numerical abundance of cirrhitids on the fished set of reefs was 93% lower than that on the control set of reefs, as compared to only 24% lower during the baseline year (Table 5B). During all (pooled) years of fishing, the censused percent for each main cirrhitid species on the predator removal set of reefs was only a fraction of that on the control set: 3.3% for *Cirrhitops fasciatus*, (Bennett, 1828), 6.7% for *Paracirrhites forsteri*, (Bloch and Schneider, 1801), and 6.9% for *Cirrhitus*

Table 5

Percent (relative to the total) of all resident piscivores censused on all reefs combined during: (A) the years of experimental fishing on predator removal reefs (June 1982–August 1985); (B) the initial baseline (prefished) year (May 1981–May 1982); and (C) the final (fished) year (October 1984–August 1985) of the study

Family	(A) All fished years reef treatment		(B) Baseline year reef treatment		(C) Final year reef treatment	
	Control %	Removal %	Control %	Removal %	Control %	Removal %
Scorpaenidae	27.30	15.36	25.99	18.29	22.64	17.15
Muraenidae	11.74	2.30	9.36	2.49	14.13	2.95
Labridae	11.29	3.19	10.19	3.08	10.11	3.11
Cirrhitidae	11.26	0.65	10.59	8.07	7.40	0.54
Synodontidae	8.16	4.65	6.07	3.69	11.65	5.98
Ophidiidae	1.39	0.06	0.86	0.43	0.97	–
Aulostomidae	0.53	0.61	0.22	0.18	1.15	0.27
Antennariidae	0.18	0.16	0.09	0.25	0.06	0.06
Bothidae	0.13	0.23	0.06	0.06	0.09	0.33
Congridae	0.13	0.08	–	–	0.21	0.09
Fistulariidae	0.10	0.41	–	0.03	0.18	0.63
Serranidae	0.10	–	–	–	0.24	–
TOTAL %	72.30	27.70	63.42	36.58	68.84	31.16
TOTAL <i>N</i>	5783	2216	2060	1188	2280	1032

Two of the control reefs were different, larger reefs in the final year, since the original ones were buried by sand.

Table 6
Spearman rank correlation coefficients (r_s) relating number of resident piscivores censused per replicate (N =total census replicates) with cruise mid-date, for various groupings of taxa, June 1982–August 1985

Taxa	Reef	Mean±SD	N	r_s	P
All (pooled) piscivores	1C	6.21±2.62	78	-0.096	0.4042 ns
	2C	25.11±9.19	80	0.042	0.7080 ns
	3C ₁	6.91±4.06	34	-0.772	0.0001***
	3C	16.85±8.98	40	0.523	0.0005**
	4C ₁	19.55±4.93	38	-0.358	0.0274 ns
	4C	25.50±7.90	36	0.513	0.0014**
	1R	2.64±2.69	76	0.263	0.0218 ns
	2R	3.53±2.81	79	0.271	0.0158 ns
	3R	11.97±7.03	76	0.009	0.9378 ns
	4R	16.52±9.21	50	0.659	0.0001***
All (pooled) non-synodontid piscivores	1C	5.18±2.27	78	-0.202	0.0756 ns
	2C	23.85±8.92	80	0.009	0.9401 ns
	3C ₁	6.50±3.65	34	-0.756	0.0001***
	3C	11.95±8.36	40	0.541	0.0003**
	4C ₁	18.37±4.70	38	-0.283	0.0851 ns
	4C	19.47±5.62	36	0.372	0.0255 ns
	1R	1.84±2.52	76	0.163	0.1595 ns
	2R	2.47±2.65	79	0.071	0.5327 ns
	3R	10.24±6.83	76	-0.101	0.3843 ns
	4R	14.62±8.40	50	0.602	0.0001***
All (pooled) Synodontids	1C	1.03±1.30	78	0.217	0.0563 ns
	2C	1.26±1.48	80	0.086	0.4460 ns
	3C ₁	0.41±0.66	34	-0.557	0.0006**
	3C	4.90±2.84	40	0.196	0.2256 ns
	4C ₁	1.18±1.16	38	-0.325	0.0466 ns
	4C	6.03±4.81	36	0.361	0.0306 ns
	1R	0.80±1.05	76	0.166	0.1515 ns
	2R	1.06±1.40	79	0.177	0.1187 ns
	3R	1.74±2.19	76	0.374	0.0009**
	4R	1.90±2.28	50	0.534	0.0001***
Following considers only the baseline year (May 1981–May 1982) and first year of fishing (June 1982–March 1983):					
All (pooled) Synodontids	1C	1.11±1.04	44	-0.156	0.3106 ns
	2C	2.21±1.97	48	-0.648	0.0001***
	3C ₁	1.25±2.04	44	-0.297	0.0505 ns
	4C ₁	2.07±2.50	42	-0.029	0.8550 ns
	1R	0.78±1.25	46	-0.326	0.0272 ns
	2R	1.42±1.66	36	-0.551	0.0005**
	3R	0.64±0.90	36	-0.230	0.1780 ns
	4R	2.29±3.22	17	-0.856	0.0001***

Significance levels of r_s for the bracketed groups: for a group of 4, * P <0.0127, ** P <0.0025, *** P <0.0003; for a group of 6, * P <0.0085, ** P <0.0017, *** P <0.0002; ns, not significant. C₁=initial control reefs buried by sand and replaced.

pinnulatus (Bloch and Schneider, 1801) (Schroeder, 1989). Except for cirrhitids, no clear reduction in populations accompanying experimental fishing was apparent for any dominant piscivorous family.

Comparing the initial baseline year to the first year of fishing on predator removal patch reefs (Table 6, last section), the abundance of synodontids was significantly reduced on two of the four reefs, while on control reefs, the only significant decrease occurred at reef 2C, which was greatly reduced in size by drifting sand. Subsequently (Fig. 4), higher abundances of synodontids were censused on the removal reefs, as fishing continued over time, compared to high variability with no apparent pattern on the control reefs.

4. Discussion

4.1. The fished piscivore community

Decreases in CPUE of piscivores by number of individuals, weight, and possibly number of species were expected as the experiment progressed, reflecting the expected reduction of predators on the reefs by fishing. Decreased abundance or density of piscivores is common in coral reef fisheries and in fishing experiments (Russ, 1991; Watson and Ormond, 1994; Gaudian et al., 1995; McClanahan, 1995; Watson et al., 1996; Beets, 1997; Jennings and Polunin, 1996, 1997; Russ and Alcala, 1998). A lower diversity of target species in the catch from heavily fished reefs, compared to lightly fished or unfished reefs, has been reported from other tropical regions (Bohnsack, 1982; Munro and Williams, 1985; Russ, 1985; Koslow et al., 1988; McClanahan, 1995; Russ and Alcala, 1998). However, the species richness of all piscivores removed from the patch reefs in our study did not decrease overall, but was highly variable over the experimental period. A decrease in CPUE over time as fishing pressure continues is also common for reef fisheries (Smith and Dalzell, 1993; Gaudian et al., 1995; Polunin and Roberts, 1996; Russ and Alcala, 1998), which is often taken to indicate a decrease in the size of the fished population. However, with a short-term exception, this result was not found for the main piscivorous groups of taxa fished at Midway atoll. Conversely, groups composed largely or entirely of

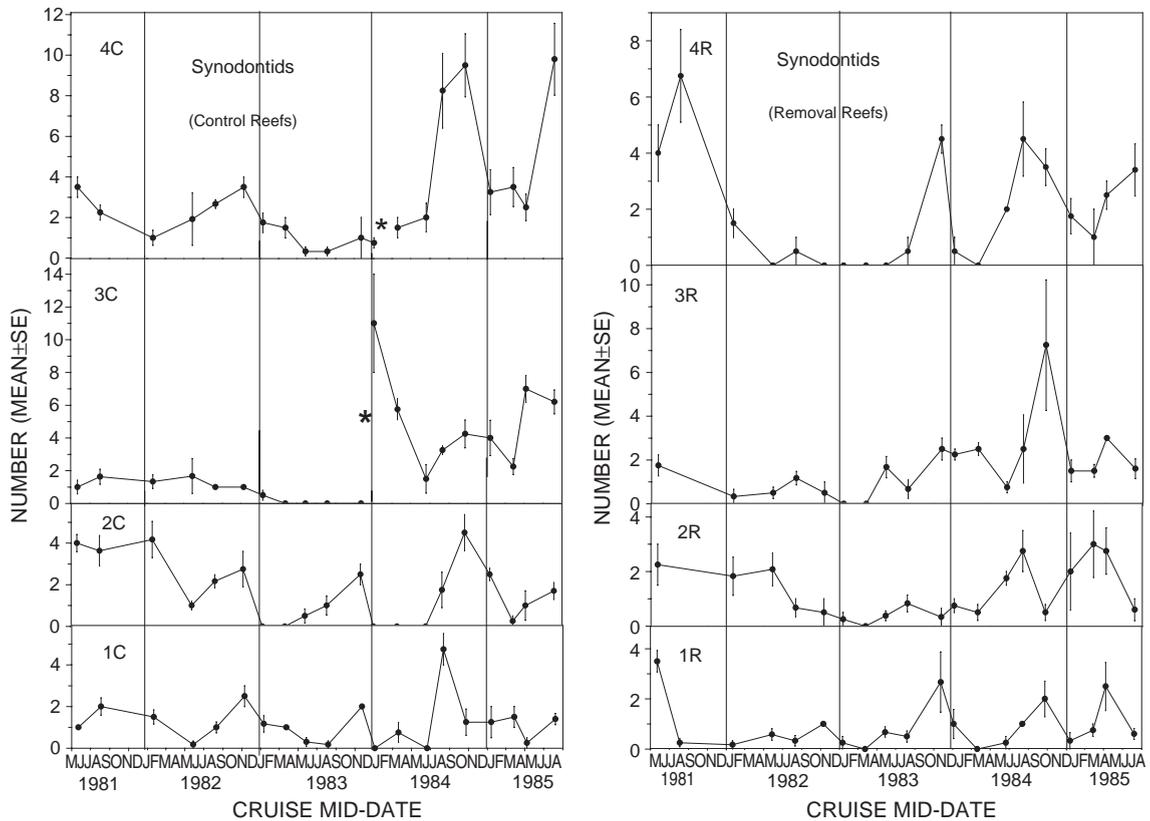


Fig. 4. Temporal variability in the abundance of all synodontids (pooled) on 4 natural patch reefs (C=Control) and on 4 experimental patch reefs (R=Removal). Number is mean (\pm SE) number of fish seen on a replicate census ($N=2-12$ replicate censuses). (*The original reefs 3C and 4C were lost under shifting sand during the winter of 1983–1984 and replaced with other, similar reefs.)

synodontids (predominantly *S. ulae*) increased in CPUE (by several appropriate measures, cf. Table 4) in response to continued fishing pressure.

Spearfishing applied to all resident, demersal, piscivorous taxa yielded a catch composition that differed greatly from their abundances in the patch reef fish community on control reefs (Tables 1 and 5). Synodontidae dominated the collections because of behavioral characteristics that render them more susceptible to capture. Also prominent in the catch were many small scorpaenids and fewer but larger muraenids that provided greater biomass. Shallow-water native species of snappers (Lutjanidae) and groupers (Serranidae) are common piscivorous taxa on reefs circumtropically, but are few and not populous in the shallow waters of the Hawaiian archipelago (Randall et al., 1993; Randall, 1996; Myers, 1999) and were seldom seen during the study.

Our experiment was not designed to reduce the abundance of large, transient piscivores (e.g., sharks, jacks). (Initial attempts to do so using large exclusion cages failed when the cages were wrecked by severe winter storms.) We recognized that the effects of large, transient predators on reef fish populations may be considerable (Sudekum et al., 1991; Carr and Hixon, 1995), but this did not appear to be the case on our study reefs. Values of an independent index of potential transient predation, based on sightings made while surveying control patch reefs, were 0.057 sharks/day and 0.043 jacks/day ($n=209$ field dates, May 1981–August 1985) (i.e. only one shark seen every ~ 18 days of underwater surveying and only one jack seen every ~ 24 days). Rates were artificially higher on removal reefs, where sharks and jacks were attracted to resident predators speared and wounded in the fishing experiment. We found the abundance of

sharks and jacks at Midway lagoon substantially below that reported by [Friedlander and DeMartini \(2002\)](#) for the Northwestern Hawaiian Islands overall. More recently, biomass densities of apex predators were found to be severalfold to an order of magnitude lower at Midway and Kure atolls at the extreme northwestern end of the archipelago, than from the central islands and banks of the NWHI ([DeMartini and Friedlander, 2004](#); [DeMartini et al., in press](#)).

Learned behavior may reduce the catchability of certain piscivores after frequent pursuit by spearfishermen. For example, we observed that *S. littoralis* (Scorpaenidae) and *C. fasciatus* (Cirrhitidae), which occurred in small numbers, became particularly skittish on the experimentally fished reefs, in contrast to their more complacent behavior on the control reefs. Others studies (reviewed in [Polunin and Roberts, 1996](#)) also found that spearfishing can alter reef fish behavior, which could reduce catchability and CPUE and also bias estimates by visual census. If such learned behavior was a factor in our study, it failed to cause a net reduction in CPUE for the major piscivores.

4.2. Censused predator populations

Repeated visual census of piscivores was conducted to determine whether they were reduced on experimentally fished reefs, compared to control reefs. No significant increases in the censused abundance of synodontids were apparent on any of the six control reefs over the full period ([Fig. 4](#) and [Table 6](#)); rather, synodontid abundances varied with no detectable pattern. The predominance of scorpaenids in the census data, in contrast to the predominance of synodontids in the catch records, probably reflects the higher catchability of synodontids. Synodontids were larger and easier to spear than the mostly small, quick scorpaenids. The actual numbers of synodontids on the reefs were underestimated by visual census (i.e., ichthyocide collections revealed significantly greater numbers; [Schroeder, 1989](#) [Chap. 1]). Spearfishing collections, where divers searched exclusively for predators, also provided higher estimates of synodontid numbers on experimental reefs, as compared to census counts, where divers searched for all fish on the reef without a focused “search image”. Estimates of numbers of muraenids, cirrhitids and piscivorous labrids were also

low (relative to the total of all piscivores) in both spearing collections and census on the fished reefs. The ability to sample a target fish community depends on the site and species considered ([Samoilys, 1992](#); [Watson et al., 1995](#); [Jennings and Polunin, 1995](#)). Augmenting conventional visual censuses with baited censuses has been suggested to improve the accuracy for cryptic piscivorous species ([Stewart and Beukers, 2000](#); [Willis and Babcock, 2000](#)). Some studies that have compared results from fishing CPUE and visual census methods suggest that they can produce similar estimates of relative abundance ([Kulbicki et al., 1987](#); [Kulbicki, 1988](#); [Gaudian et al., 1995](#)).

The fact that only one common family (Cirrhitidae) showed a major sustained decline in relative abundance suggests that repeated spearfishing had a limited effect in maintaining reduced numbers of total predators on the patch reefs. Numerically, cirrhitids accounted for only several percent of the natural piscivorous community ([Schroeder, 1989](#), [Chap.1]). In contrast to synodontids and scorpaenids, cirrhitids at Midway possess a particular combination of characteristics (e.g., low natural abundance, low recruitment, highly resident and sedentary behavior, and relatively small size) that may have contributed to the decline and continued low levels of cirrhitid populations on the reefs under the repeated experimental perturbation.

In spite of more than 3 years of repeated fishing on piscivores, significant long-term decreases in numbers or biomass were not observed for any other major predator group. At least on these small patch reefs in the vicinity of undisturbed reef areas, these piscivores were found to be highly resilient to fishing pressure. Factors responsible for this resilience could include protracted recruitment seasons (e.g., scorpaenids), high immigration rates (e.g., synodontids and piscivorous labrids), the cryptic nature of many piscivores (e.g., muraenids and scorpaenids), and their naturally high abundances ([Schroeder, 1989](#)). Attempts by other researchers to remove piscivores experimentally have also met with difficulties, including immigration ([Stimson et al., 1982](#); [Hixon, 1991](#)). [Shpigel and Fishelson \(1991\)](#) found that elimination of adult groupers resulted in replacement by other predatory fishes, largely of different taxa.

Temporal census data on piscivores also indicated that the fishing experiment was unable to maintain low

levels of piscivores relative to natural levels (Table 6). Differences in piscivore numbers between fished reefs and controls were confounded on some of the reefs by the strong effect of changes in reef size on fish abundance, due to shifting sand caused by storms. The spike in abundance of adult synodontids seen during the last half of 1984 may have indicated redistribution from neighboring patch reefs in response to such sand movement during winter storms. However, the largest sand disturbance occurred in the winter of 1983–1984, which was not followed by major changes in predator abundance on the study reefs. Overall, examination of time sequences of the data for control and removal reefs separately and for recruits (<6 cm SL) and larger (adult) fish separately, failed to show patterns of correlation that would suggest that either local recruitment or storm events provided the major forcing of patterns of abundance for synodontids on these patch reefs. The major dynamics of predator abundance may come from variable migration among these patches and their surroundings, based on cues presently unknown.

The most consistent long-term pattern discernible from these complex responses was for synodontids, which significantly increased on reefs subjected to repeated, long-term fishing pressure, in contrast to controls (Table 6 and Fig. 4). Further support for this result is shown by comparing the total number of synodontids removed from the experimental patch reefs (Table 1A) to the abundance of synodontids resident on similar control patch reefs as determined by total collection of fish at the end of the experiment (Schroeder, 1989, [Chap. 1]). On the fished reefs, the removed synodontid population replaced itself more than 20 times during the 39 consecutive months of the fishing experiment (i.e., a complete replacement in less than 2 months). This result contrasts with that from all other, non-synodontid piscivores, which replaced themselves only five times (i.e., 8 months for a complete replacement). Replacement of adult synodontids may have been even greater, relative to other piscivores, than these figures suggest. Replacement of non-synodontids included a considerable component of recruitment by juveniles (mainly small scorpaenids). For synodontids, recruitment appeared to be a much smaller component of total replacement. A very high immigration rate was primarily responsible for the

rapid replacement of synodontids (Schroeder, 1989). Because of the patchy distribution of coral reefs at many scales, movement of fish may significantly affect distributions, catch rates and fishery dynamics (Robertson, 1988a,b, 1998; Hilborn and Walters, 1992; Gaudian et al., 1995).

A possible explanation for the observed increased CPUE of synodontids with continued fishing follows: On natural (unfished) reefs, other resident piscivores (e.g., cirrhitids) competitively keep lizardfish off the reef, forcing them to remain on the sand/rubble periphery and surrounding sand (Schroeder, 1989). No direct evidence was found of competitive pressure against lizardfish or other species. However, if such pressure occurred on natural reefs, reduction in population of the established resident competitors, coupled with the high natural migration rate of lizardfish, could result in increased numbers of lizardfish on the experimental reefs. Lizardfish were observed migrating between patch reefs much more freely than most other demersal piscivores, and they frequently buried themselves in the sand. An opportunity to migrate to a position on a patch reef might provide the advantages of improved concealment and feeding opportunities for a transient piscivore.

Evidence consistent with the reef as preferred habitat for predators was found by Shulman (1983, 1985) and Sweatman and Robertson (1994), where fewer predators occurred at increasing distances from the reef. Webster and Hixon (2000) found that when larger planktivorous fish were removed from the edge of reef ledges, smaller individuals quickly occupied these prime feeding positions.

We suggest that when piscivores were fished from patch reefs in our experiment, the more migratory synodontids rapidly filled the newly opened, preferred habitat on the main reef more effectively than other piscivores. It seems unlikely that the magnitude or success of migrations by synodontids would have increased without a reduction in resident piscivores. In fact, synodontids on the removal reefs began to increase approximately when removal of predators began, and synodontids never showed a clear increasing trend on control reefs. As newly arrived synodontids were repeatedly removed from experimental reefs by spearfishing, space was reopened for additional synodontids to move from the reef periphery and occupy the main reef. Feeding and migratory

behaviors consistent with this hypothesis have been observed in the Western Pacific (Hiatt and Strasburg, 1960), the Caribbean (Piaastro, 1973), the island of Hawaii (Hobson, 1974), and the Great Barrier Reef (Sweatman, 1984; Leis and Carson-Ewart, 1998), and appear to be characteristic of synodontids. Piaastro (1973) found that a local *Synodus* species had a large home range but did not defend territories. Sweatman (1984) similarly observed that harassment by other reef fishes (including cirrhitids and other piscivores) confined synodontids to areas of low prey density.

5. Summary

In the present experiment, in spite of more than 3 years of substantial fishing pressure on patch reef piscivores, we could not maintain a noticeably reduced population of synodontids or most other “resident” piscivorous species on those reefs. Patch reef piscivores in this study appeared to be rather resilient to local fishing pressure, at least over a time scale of a few years. Part of this resilience results from immigration from surrounding habitat with no fishing pressure. Patch reefs in our study were apparently not as isolated with regard to fish movement as we initially assumed. Other more recent work (e.g. Frederick, 1997) has similarly found reef fish mobility in patchy reef habitats to be much greater than generally assumed. Our results further support the idea that occupying an established position on a reef provides a piscivore a competitive advantage for concealment and/or feeding, as implied by the rapid replacement by colonizers or settlers following experimental removal of established residents.

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