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Effects of intense fishing pressure on an assemblage of coral reef fishes

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ABSTRACT: Fishing is the most important exploitative activity on coral reefs. Despite this, there are few direct tests, utilizing manipulative or natural experiments, of the impact of fishing on coral reef fish assemblages. This paper documents a natural experiment in the central Philippines: a dramatic increase in fishing pressure within a 750 m long marine reserve, previously protected from fishing for 10 yr (1974 to 1984). In 1983, the site had a significantly higher abundance of fishes, particularly those considered to be favoured targets of fishermen (e.g. serranids, lutjanids, lethrinids), than similar sites which were fished. Abundances were estimated by visual census within the reserve and at 3 control sites. In early 1984, protective management broke down and fishing by up to 100 municipal fisherman began, using traps, hand-lines, gill-nets, spears and occasionally more destructive, non-selective fishing methods, such as explosives and drive nets. The reserve and control sites were recensused after 18 mo of fishing in the Sumilon Island reserve. There were decreases in abundance of favoured targets of fishermen and a significant change in community structure – including significant decreases in both species richness and density – of the coral reef fish assemblage inside the reserve but not at the 3 control sites. Species which contributed most to the change in community structure were not favoured targets and had not constituted a large proportion of yield in previous years. Significant decreases in abundance of small, schooling planktivores and benthic feeding chaetodontids, and significant increases in abundance of small labrids and large scarids, were related largely to the effectiveness of explosives and drive nets against planktivores and herbivores and degradation of the shallow benthic habitat caused by both these methods. Thus, the intense fishing pressure had both direct and indirect effects and a far wider impact on the fish assemblage than the predicted significant decreases in abundance of target species.

INTRODUCTION

Fishes are an important resource on coral reefs, particularly in the developing world. Smith (1978) estimated the fisheries potential of coral reefs world-wide at 6×10^6 tonne yr^{-1}, a figure which contrasts with the actual yield from tropical reef areas in 1983 (0.48×10^6 tonne; Longhurst & Pauly 1987). The importance of coral reef fisheries may be less in the absolute magnitude of the catch than in their contribution to the catch of fishermen on low incomes and with few alternative opportunities for employment. For example, ca 10 to 15 % of the total fish yield in the Philippines is taken from coral reefs (Carpenter 1977, Murdy & Ferraris 1980). Over 50 % of this yield is taken by subsistence and artisanal fishermen (Smith et al. 1980).

Knowledge of the impact of fishing on communities of coral reef fishes is limited. It has been shown that overall catch rates decline in heavily exploited areas (Munro 1983, Koslow et al. 1988), that selective fishing reduces the relative abundance of large predatory fishes (Bohnsack 1982, Munro 1983, Russ 1985, Koslow et al. 1988) and that destructive fishing techniques, such as use of explosives or drive nets, can lead to serious and extensive destruction of coral reef habitat (Gomez et al. 1981, 1987, Alcala & Gomez 1987). Despite the fact that fishing is the most important human exploitative activity on coral reefs, few detailed studies exist, utilizing manipulative or natural experiments, on the effects of fishing on communities of coral reef fishes.

In a broader context, coral reefs are excellent microcosms to address questions of the effect of fishing on multispecies stocks. Effects of exploitation of marine communities and management of multispecies fisheries are the subjects of a large literature (e.g. May et al. 1979, Beddington & May 1982, Larkin 1982, 1984, Beddington 1984, Gulland & Garcia 1984) with a great deal of interest directed to effects of fishing on and management of tropical multispecies stocks (e.g. Pauly

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& Murphy 1982). Larkin (1982) drew attention to the need for more research to be directed toward understanding the mechanisms which determine the species composition of tropical, multispecies stocks subjected to varying levels of fishing. Several authors have advocated the need for an empirical, experimental approach to such questions (Larkin 1982, Sainsbury 1982, Walters 1984). Larkin (1982) identified a specific need for experiments in which sites are subjected to different levels of fishing pressure (including unfished controls) and in which the communities of fishes are sampled by a method independent of the fishery. Several studies have compared patterns of abundance and species richness of assemblages of coral reef fishes at sites subjected to different levels of fishing pressure (e.g. Bohnsack 1982, Munro 1983, Russ 1985) and some studies have made such comparisons at sites where fishing pressure has changed through time (e.g. Koslow et al. 1988).

This paper describes a natural experiment which led to a dramatic increase in fishing pressure in a small marine reserve in the central Philippines. The reserve had been previously protected from fishing for 10 yr (1974 to 1984) and visual, quantitative estimates of abundance of ca 100 species of coral reef fishes were available before (1983) and after (1985) an 18 mo period of intense fishing in the reserve, and at 3 control sites where fishing pressure changed little, if at all. The data are used to address 2 questions: (1) What are the effects of intense fishing on assemblages of coral reef fishes? (2) What are the best indicators of intense fishing pressure on assemblages of coral reef fishes?

MATERIALS AND METHODS

Study sites. The study was carried out on sections of fringing reef slope at 2 sites at each of 2 islands in the central Visayas region of the Philippines. The islands were Sumilon Island, southeast of Cebu (9°21′ N, 123°23′ E) and Apo Island, southeast of Negros (9°4′ N, 123°16′ E). Sumilon Island is a coralline island of 23 ha, surrounded by a fringing coral reef of 50 ha to the 40 m isobath. Apo Island is a mainland island of 70 ha surrounded by 156 ha of fringing coral reef to the 60 m isobath.

The 2 sites at Sumilon Island were the reserve, a 750 m section of reef slope on the western side of the island, and the non-reserve to the north and east of the island. The reef slopes at these sites differed in both angle of slope and in dominant type of substratum. The reef crest in the reserve is at a depth of 2 to 3 m at mean tidal level. The reef crest and slope within the reserve are mostly consolidated limestone with a relatively high cover of hard and soft corals. The angle (to the horizontal) of the slope is ca 45 to 55° to a depth of 9 m, and it then drops away at an angle of 70 to 90° between 9 and 14 m depth. Large, overhanging ledges ingressing into the slope for distances of 1 to 4 m are common at depths of 9 to 14 m (Russ in press).

The non-reserve site at Sumilon Island has a reef 'crest' at a depth of 5 to 7 m and this crest and the reef slope were covered with sand and only a moderate cover of living coral. The angle of the slope was generally shallow (40 to 45°) to 14 m and, since the substratum was sandy, there were very few ledges in the sections censused.

The 2 sites at Apo Island were the reserve, a 600 m section of reef slope on the southeastern side of the island, and a section of the non-reserve on the western side of the island. The reef crest within the reserve is at a depth of 6 to 7 m. The reef crest and slope consisted of consolidated limestone with a high cover of living corals. The angle of the slope is ca 50 to 60° to a depth of 14 m. Overhanging ledges occur at depths of 9 to 14 m but these are smaller and less numerous than those on the slope of the Sumilon Island reserve.

The non-reserve site at Apo Island has a reef crest at a depth of 5 to 7 m and a reef slope with an angle of 35 to 40° to 14 m. The crest and slope were consolidated limestone overlying a base of volcanic rock. There was a high percentage cover of corals, particularly soft corals. There are very few ledges and very little sand at this site.

The Sumilon Island reserve was protected from all forms of exploitation from 1974 until May 1984 (Alcala 1981, 1988). The reserve was established under an agreement between Silliman University and the local council of Oslob, Cebu. The reserve was made a national fish sanctuary in 1980. A caretaker-fisherman employed by the University resided on the island from 1976 until November 1984. His task was to maintain protective management of the reserve and to record fish yields taken by ca 100 municipal (subsistence and artisanal) fishermen who fished the non-reserve portion of the island (Alcala 1981, 1988). These fishermen were from the mainland (Cebu Island) ca 5 km away. They used hand-paddled canoes to travel to Sumilon Island and used traditional fishing methods – bamboo traps, hook and line, gill net and spears (Alcala 1981, 1988, Alcala & Russ in press). The few violations of the protective management of the reserve during the period to May 1984 have been documented by White (1984).

In May 1984 protective management of the reserve on Sumilon Island broke down, resulting in intensive fishing inside the reserve by ca 100 municipal fishermen. There was no increase in the overall number of fishermen fishing the reefs (Alcala 1988) but in addition to the traditional methods of fishing, 2 other methods

were used occasionally – muro-ami (drive net) and dynamite fishing. Both methods are very effective and particularly destructive to the benthic habitat (Carpenter & Alcala 1977, Alcala & Gomez 1987). At least 2 occurrences of both dynamite and muro-ami fishing in the reserve were reported prior to November 1984. The caretaker was transferred from Sumilon Island at this time and the subsequent frequency of use of dynamite and muro-ami fishing is unknown. There was clear evidence that muro-ami fishing had occurred in the reserve just prior to December 1985. Remnants of scarelines used in the drive-net fishing were observed in the reserve by one of the authors (G.R.R.).

The Apo Island reserve was protected from fishing in 1982 but enforcement of protection up to the time of the census in 1983 was not strict. Enforcement did improve between 1983 and 1985. The non-reserve area of Apo Island is known to be subject to intense subsistence fishing (Alcala & Luchavez 1981).

Methods. Quantitative estimates of abundance of coral reef fishes were made at the 4 sites using a visual census technique. Censuses were made in December 1983 (after almost 10 yr of protection within the Sumilon Island reserve) and again in December 1985 (ca 18 mo after fishing violations in Sumilon Island reserve began).

A total of 102 species of coral reef fishes belonging to 18 families were chosen for study and censused simultaneously using a combination of 2 modified techniques of visual census developed by the Great Barrier Reef Marine Park Authority (GBRMPA) in Australia. The first technique was developed to detect differences in assemblages of coral reef fishes at different sites to provide baseline data for zoning, management and monitoring of coral reefs. The abundance of large numbers of numerically dominant and visually obvious species of fishes is assessed by placing species into abundance categories on a logarithmic scale. This visual census technique has been applied successfully to reefs of the Great Barrier Reef (e.g. Williams 1982, 1986, Russ 1984a, b). The second technique, requiring actual counts of individuals, was developed to determine the standing crop of species known to be highly favoured targets of fishermen, e.g. serranids. The abundances of 'visually obvious' species within a census area were estimated cumulatively on a $\log_4$ abundance scale from 0 to 8 (Table 1). The abundances of 'target' species within a census area were determined by counting each individual and making an estimate of its total length. Total length estimates of serranids were made to within ± 2 cm whilst individuals of all other 'target' species were placed into size categories in intervals of 5 cm. Juveniles (less than 2 to 10 cm, depending on the species) were not counted. An estimate of the wet weight of individual serranids was made by using published length-weight relationships of species similar to those encountered in this study. This combined visual census technique has been applied successfully to reefs in the Philippines (Russ 1985).

Table 1. Logarithmic abundance categories used in estimates of abundance of numerically dominant species of fishes

$\log_4$ abundance category	Number of fishes
1	1
2	2–4
3	5–16
4	17–64
5	65–256
6	257–1024
7	1025–4096
8	4097–16384

Species from the following families were censused using abundance category data: Pomacentridae (15 spp.), Anthiidae (2 spp.), Caesionidae (5 spp.), Acanthuridae (9 spp.), Scaridae (9 spp.), Labridae (8 spp.), Chaetodontidae (14 spp.), Nemipteridae (1 sp.) and Zanclidae (1 sp.). Counts of individuals were made for species in the following families: Serranidae (8 spp.), Lutjanidae (7 spp.), Lethrinidae (4 spp.), Carangidae (all species combined), Scombridae (1 sp.), Haemulidae (1 sp.), Siganidae (3 spp.), Kyphosidae (1 sp.), Mullidae (3 spp.) and some larger Acanthuridae (9 spp.).

An individual census area was demarcated by laying out a 50 m tape on and parallel to the reef crest, defined as the point where the reef flat began to slope downward sharply, generally at an angle of more than 45°. A single observer (G.R.R.) would begin 5 m from the end of the tape and swim (using SCUBA) down the reef slope to a depth of 14 m. The abundances of all species were estimated or counted within 5 m either side of and above the observer and recorded onto prepared census sheets of waterproof paper. At a depth of 14 m the diver turned and swam at this depth for ca 10 m along the reef slope, parallel to and in the direction in which the tape was laid. The observer then swam up the slope, again recording abundance of fishes as before until reaching the tape. This procedure of swimming down and back up the reef slope, recording abundance cumulatively, was repeated along the entire length of the tape so that an area was censused 50 m in length and with a width equal to the distance from the position of the tape on the reef crest to a depth of 14 m. Four to 6 measurements were made of the distance from the tape down the reef slope to a depth of 14 m, making sure that the tape followed the contour of the slope. The average of these measurements was used as the best

estimate of width of a census area. The average width of all censuses was ca 17.5 m so that the average area censused was ca 875 m^2. A census took ca 40 to 50 min. Six replicate, non-overlapping censuses were made once at each site in December 1983 and December 1985. The only exception to this was the 5 replicates taken at the Apo Island non-reserve site in 1983.

The 47 censuses, including the 80 most abundant species in the study, were subjected to an agglomerative, hierarchical classification (Williams 1971) using Bray-Curtis similarity coefficients (Bray & Curtis 1957) and Burr's incremental sum of squares sorting strategy (Burr 1970). The analysis was run using the SAHN program in CSIRO's TAXON package (Williams & Lance 1977). The Cramer value was used as a diagnostic to estimate the relative contribution of each species to the discrimination of particular groups produced by the classification (Lance & Williams 1977). Mann-Whitney U tests were used to test the significance of change in abundance between 1983 and 1985 of particular species at each site.

Comparisons of species richness and abundance between 1983 and 1985 are presented graphically for each site. In all graphical presentations the mid-point of an abundance category was used as the best estimate of abundance except in the 2 highest log abundance categories (Categories 7 and 8) in which the minimum of the category range was used. The latter procedure eliminated excessively large estimates of numbers caused by the very large range within Abundance Categories 7 and 8 (Table 1). The procedure in no way biases between time comparisons. The aim of this study was to establish if significant changes in abundance of particular species occurred at the Sumilon Island reserve between 1983 and 1985 in response to a dramatic increase in fishing pressure. The 3 additional sites (Sumilon Island non-reserve, Apo Island reserve, Apo Island non-reserve) were used as 'controls' in the study to monitor natural levels of change at sites not subject to change in fishing pressure. For these reasons analyses were restricted to comparisons between 1983 and 1985 for either species richness or

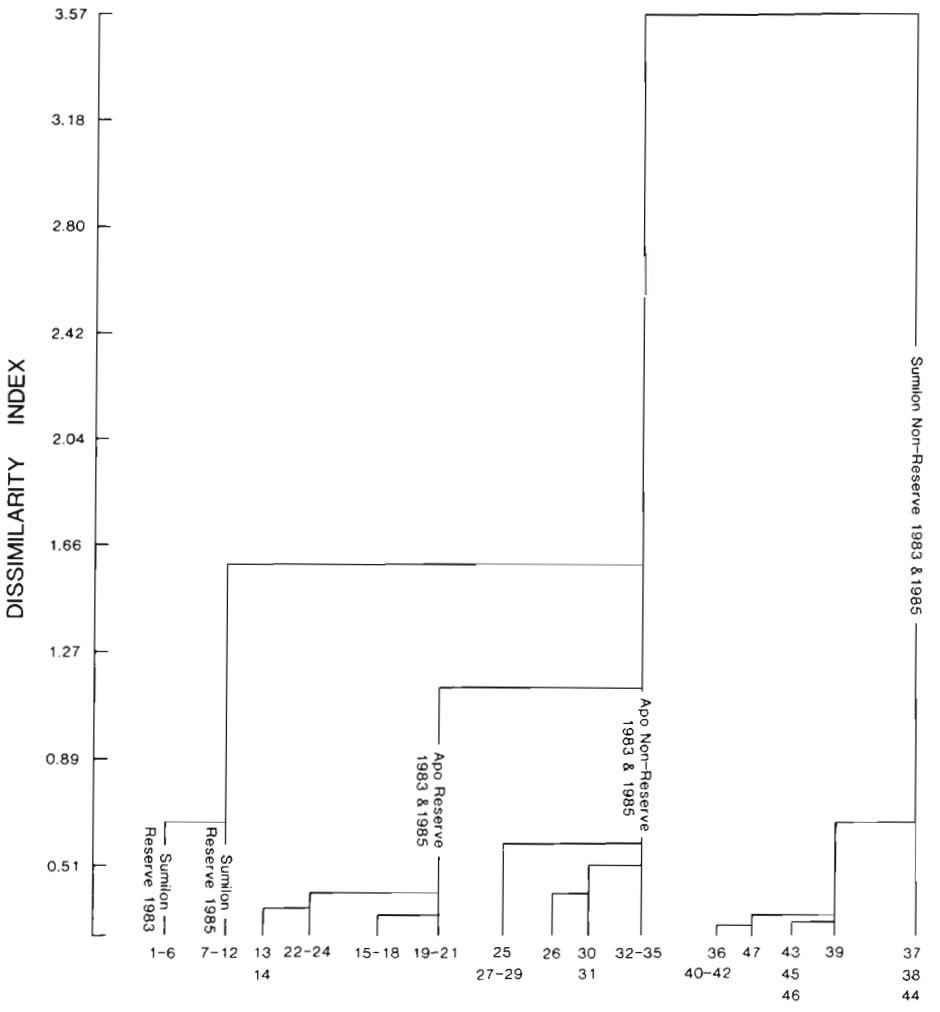

Fig. 1 Dendrogram from the classification analysis of 47 censuses. The censuses were Sumilon reserve 1983 (1 to 6), Sumilon reserve 1985 (7 to 12), Apo reserve 1983 (13 to 18), Apo reserve 1985 (19 to 24), Apo non-reserve 1983 (25 to 29), Apo non-reserve 1985 (30 to 35), Sumilon non-reserve 1983 (36 to 41), Sumilon non-reserve 1985 (42 to 47)

abundance at each site separately, using either Student's *t*-tests (for comparison of numbers of species or actual abundances) or Mann-Whitney U tests (for comparison of abundance category data).

RESULTS

The dendrogram resulting from the classification analysis shows that all 6 replicate censuses in the Sumilon Island reserve in 1983 split from all 6 replicates in this reserve in 1985 at a level of dissimilarity of 0.60 (Fig. 1). At this level of dissimilarity, all of the 1983 and 1985 censuses were still fused for each of the 3 control sites (Sumilon Island non-reserve, Apo Island reserve, Apo Island non-reserve). The test of Sandland & Young (1979) indicated that there was a significant change in community structure of the assemblage of coral reef fishes between 1983 and 1985 in the Sumilon Island reserve but not at the 3 control sites.

Fig. 2 shows the mean number of species and mean number of individuals per unit area for 1983 (pre-fishing in the Sumilon Island reserve) and 1985 (post-fishing in the reserve) at the Sumilon Island reserve and at 3 control sites where fishing pressure changed little, if at all. There was a significant reduction in species richness between 1983 and 1985 at the Sumilon Island reserve ($t_{10} = 4.24$, $p < 0.01$). No significant changes in species richness were detected at any of the 3 control sites (Fig. 2). There was a significant reduction in density of fishes between 1983 and 1985 at the Sumilon Island reserve (Mann Whitney $U_{6,6} = 33$, $p < 0.05$). No significant changes in density were detected at any of the 3 control sites (Fig. 2).

Comparisons of species richness and of density of fishes between 1983 and 1985 at the Sumilon Island reserve are shown at the level of family or major trophic group in Tables 2 and 3. Fishing pressure resulted in significant decreases in the species richness of large piscivores (serranids, lutjanids, lethrinids and carangids), lutjanids plus lethrinids, labrids (particularly *Cheilinus* and *Hemigymnus*) and chaetodontids (Table 2; Fig. 3). There were no significant differences in species richness between 1983 and 1985 for planktivorous pomacentrids, caesionids, anthiids, scarids, acanthurids or serranids. The results from the Sumilon Island reserve are compared with those from Apo Island reserve, the control site which is most similar to the Sumilon Island reserve in terms of both habitat and community structure. There were significant decreases in species richness of planktivorous pomacentrids and labrids and a significant increase in the species richness of large piscivores at this control site. These changes presumably reflect natural variability in such assemblages, although the significant increase in species richness of large piscivores may be related to effects of protective management in the Apo Island reserve.

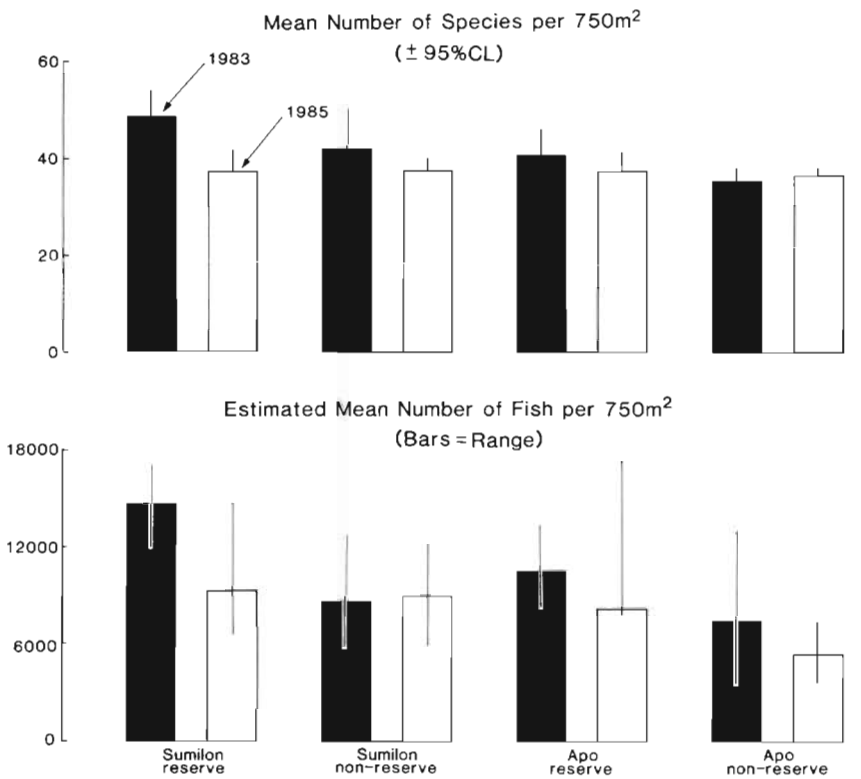

Fig. 2. Mean number of species and mean number of individuals per 750 m² for 1983 (pre-fishing in the Sumilon Island reserve) and 1985 (post-fishing in the reserve) at the Sumilon Island reserve and at 3 control sites where fishing pressure changed little, if at all. There was a significant decrease in both species richness and density of fishes in the Sumilon Island reserve but not at the control sites

Table 2. Mean number of species per 750 m^2 (95 % confidence limits in brackets) of families or major trophic groups at the Sumilon Island reserve and the Apo Island reserve in 1983 (pre-fishing at Sumilon) and 1985 (post-fishing at Sumilon). Trophic categories: P, planktivore; H, herbivore; D, detritivore; I, invertebrate feeder (non-coral); C, coral feeder; F, fish feeder. Results of 2-tailed *t*-tests (with 10 degrees of freedom) comparing species richness between 1983 and 1985 are shown under p. *** $p<0.001$; ** $p<0.01$; * $p<0.05$; ns: not significant. The probability of obtaining at least one Type 1 error amongst pairwise comparisons at each site is 0.55

Category	Sumilon Reserve			Apo Reserve		
	1983	1985	p	1983	1985	p
TOTAL	48.6 (5.5)	37.3 (4.0)	*	40.7 (5.1)	37.3 (3.8)	ns
Pomacentridae (P)	8.5 (0.5)	9.2 (0.7)	ns	9.6 (0.5)	8.3 (0.9)	*
Caesionidae (P)	2.3 (1.1)	1.8 (0.9)	ns	1.7 (0.8)	1.8 (0.8)	ns
Anthiinae (P)	1.6 (0)	1.4 (0)	ns	1.7 (0)	1.5 (0)	ns
Scaridae (H)	5.4 (0.7)	4.7 (0.6)	ns	5.1 (0.6)	4.8 (1.3)	ns
Acanthuridae (H, P, D)	6.9 (1.4)	7.1 (1.3)	ns	6.4 (1.5)	6.3 (0.6)	ns
Labridae (I)	5.4 (0.4)	4.3 (1.0)	*	4.8 (0.4)	3.3 (1.2)	*
Chaetodontidae (C, I)	8.8 (0.5)	3.5 (0.7)	***	5.3 (0.7)	4.5 (1.1)	ns
Large piscivores (F)	5.3 (1.7)	1.8 (1.0)	***	0.6 (0.7)	1.7 (0.3)	**
Serranidae (F)	1.6 (1.1)	0.9 (0.6)	ns	0.1 (0.4)	0.4 (0.4)	ns
Lutjanidae + Lethrinidae (I, F)	3.0 (1.0)	0.4 (0.4)	**	0.4 (0.8)	0.9 (0.3)	ns

Table 3. Mean number of individuals per 750 m^2 (range or 95 % confidence limits in brackets) of families or major trophic groups at the Sumilon Island reserve and the Apo Island reserve in 1983 (pre-fishing at Sumilon) and 1985 (post-fishing at Sumilon). Trophic categories: P, planktivore; H, herbivore; D, detritivore; I, invertebrate feeder (non-coral); C, coral feeder; F, fish feeder. Results of 2-tailed Mann-Whitney U tests (n = 6 per cell) comparing density between 1983 and 1985 are shown under p. ** $p<0.01$; * $p<0.05$; ns: not significant. The probability of obtaining at least one Type 1 error amongst pairwise comparisons at each site is 0.60

Category	Sumilon Reserve			Apo Reserve		
	1983	1985	p	1983	1985	p
TOTAL	14596 (11900–16900)	9332 (6600–14700)	*	10452 (8300–13300)	8142 (7900–17300)	ns
Pomacentridae (P)	8386 (5965–9155)	3855 (3749–4757)	*	6310 (3137–9942)	4616 (3530–6793)	ns
Caesionidae (P)	1579 (830–2490)	566 (112–830)	*	910 (544–1450)	949 (493–1775)	ns
Anthiinae (P)	4045 (3837–4149)	3092 (1165–3585)	ns	2327 (1007–4354)	1220 (985–1579)	ns
Scaridae (H)	41 (16–77)	116 (66–181)	**	60 (16–150)	37 (10–59)	ns
Acanthuridae (H, P, D)	197 (121–274)	178 (95–275)	ns	76 (30–115)	71 (24–139)	ns
Labridae (I)	47 (19–118)	148 (66–238)	**	312 (22–557)	34 (5–131)	*
Chaetodontidae (C, I)	44.8 (34–67)	9.5 (5.6–12.6)	**	67.6 (45.1–153)	74.7 (37.7–143)	ns
Large piscivores (F)	13.5 (5.3)	3.4 (2.3)	**	1.1 (1.6)	2.3 (1.6)	ns
Serranidae (F)	3.9 (2.8)	2.1 (1.4)	ns	0.2 (0.4)	0.4 (0.4)	ns
Lutjanidae + Lethrinidae (I, F)	7.5 (4.8)	0.5 (0.6)	**	1.0 (1.7)	1.5 (1.6)	ns
Carangidae + Scombridae (F)	2.2 (1.9)	0.8 (0.9)	ns	0	0.4 (0.4)	ns

Density of fishes was a far more useful indicator of the effects of fishing than species richness (Table 3). Fishing pressure resulted in significant decreases in density of large piscivores, lutjanids plus lethrinids (Fig 4), caesionids, planktivorous pomacentrids and chaetodontids (Table 3; Fig 3). In addition, serranids (Fig. 5) and carangids plus scombrids (Fig. 4) declined sharply in density, but not significantly so. The standing crop of serranids decreased significantly between 1983 and 1985 at Sumilon Island reserve ($t_{10} = 2.58$, $p < 0.05$; Fig. 5). Mean standing crop of serranids in 1983 was 2.52 kg 750m^{-2} (95 % CL = 0.78) and in 1985 was 1.28 kg 750m^{-2} (95 % CL = 0.94).

In addition to decreases in density of many groups of fishes inside the Sumilon Island reserve between 1983 and 1985, 2 groups did not change significantly in density (acanthurids, anthiids) and 2 groups increased in density significantly (scarids, labrids) (Table 3). The significant increase in density of adult scarids over the 18 mo period on the shallow reef slope cannot be due to any effects of fishing enhancing subsequent larval recruitment. The individuals were too large to have been derived from larval settlement and subsequent growth in such a short period. Thus the significant increase in density of adult scarids was likely to be due to fishing techni-

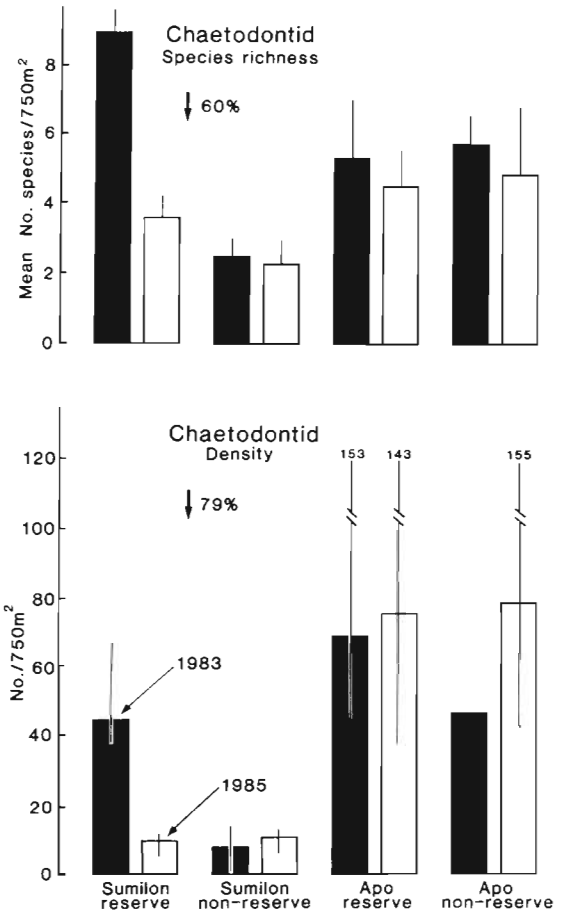

Fig. 3. Mean number of species and mean number of individuals per 750 m^2 of chaetodontids for 1983 (pre-fishing in the Sumilon Island reserve) and 1985 (post-fishing in the reserve) at Sumilon Island reserve and at 3 control sites where fishing changed little, if at all. Species richness and density of chaetodontids decreased significantly in the Sumilon Island reserve (by 60 % and 79 % respectively) but not at the control sites. Error bars are 95 % confidence limits for species richness and range for density

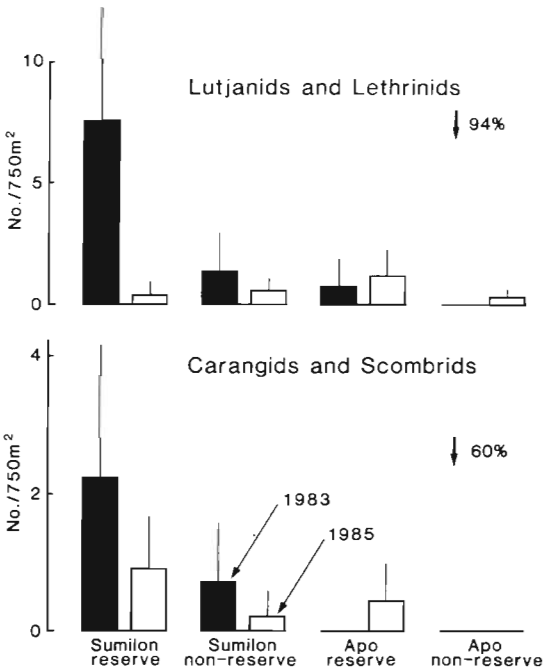

Fig. 4. Mean densities of lutjanids plus lethrinids and carangids plus scombrids (numbers per 750 m^2) for 1983 (pre-fishing in the Sumilon Island reserve) and 1985 (post-fishing in the reserve) at Sumilon Island reserve and at 3 control sites where fishing pressure changed little, if at all. Densities of lutjanids plus lethrinids decreased significantly in the Sumilon Island reserve (by 94 %). Densities of carangids plus scombrids decreased by 60 % but this result was not statistically significant because of the very large variances in density between replicate censuses. Densities of both groups did not change significantly at the control sites. Error bars are 95 % confidence limits

ques such as drive nets forcing these large herbivores to migrate from their favoured habitat (the shallow reef flat; Russ in press) to the reef slope where the visual censuses were made. The significant increase in density of labrids was due to a large recruitment of *Cirrhilabrus* sp., *Thalassoma lunare* and *T. hardwicki*, possibly in response to an increase in amount of rubble habitat.

In contrast to the large number of significant changes in density of fishes at the Sumilon Island reserve (Table 3), only one group of fishes showed a significant change in density at the Apo Island reserve control site (Table 3). Labrids decreased significantly in density between 1983 and 1985. This was caused mainly by the disappearance of large numbers of *Thalassoma lunare* and *T. hardwicki*.

Fig. 6 shows the percentage composition of the community at the level of family for the Sumilon Island reserve and the Apo Island reserve in 1983 (pre-fishing at Sumilon) and 1985 (post-fishing at Sumilon). The distribution of individuals within families did not differ significantly between 1983 and 1985 at either site (Kolmogorov-Smirnov tests, $p > 0.05$). At the Sumilon Island reserve the major changes between 1983 and 1985 were a sharp drop in the proportion of planktivorous pomacentrids and caesionids and a sharp increase in the proportion of labrids (Fig. 6). The sharp increase in the proportion of labrids was due largely to a significant increase in density of the planktivorous *Cirrhilabrus* sp. (Table 4). In 1983 anthiids were most abundant on the deeper slope (Russ in press) where they were less vulnerable to explosives and drive nets. Thus, their absolute abundance did not change significantly (Table 3) but their relative abundance increased (Fig. 6). The only large changes in the distribution of individuals amongst families at Apo Island reserve between 1983 and 1985 were a decline in the proportion of anthiids and a sharp increase in the pro-

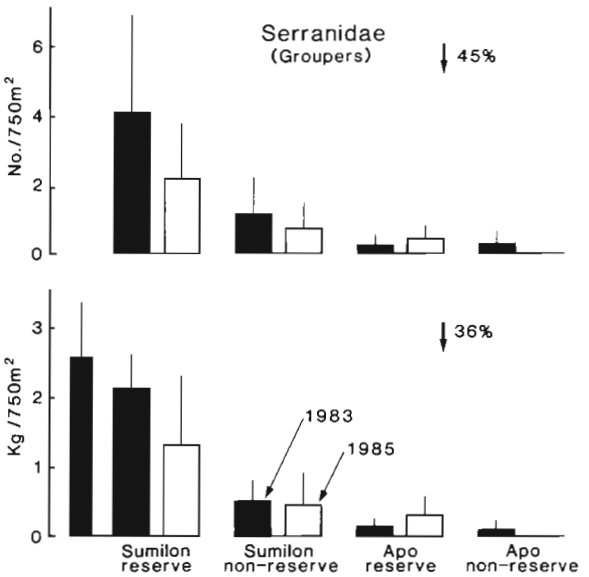

Fig. 5. Mean density and standing crop of serranids for 1983 (pre-fishing in the Sumilon Island reserve) and 1985 (post-fishing in the reserve) at Sumilon Island reserve and at 3 control sites where fishing pressure changed little, if at all. There was a 45 % decrease in density and a 36 % decrease in standing crop of serranids in the Sumilon Island reserve but these results were not statistically significant because of very large variances between replicate censuses. However, standing crop did decrease significantly between 1983 and 1985 at Sumilon Island reserve (by 49 %) if one individual *Epinephelus fuscoguttatus*, estimated to weigh 3.7 kg, was included in the 1983 data set (narrow bar at left of lower histogram). Error bars are 95 % confidence limits

portion of labrids (Fig. 6). Both communities were dominated numerically by planktivores (pomacentrids, anthiids and caesionids) and Fig. 6 indicates that the community composition at the family level at Sumilon Island reserve was surprisingly stable in the face of 18 mo of intensive fishing.

At the level of species, however, there was a significant change in community structure at the Sumilon Island reserve between 1983 and 1985. Table 4 summarizes information on changes in density of the 25 species which contributed most to this significant change in community structure (Fig. 1). Table 4 indicates clearly that the density of most of these species changed significantly between 1983 and 1985 at the Sumilon Island reserve but not at Apo Island reserve. The 25 species in Table 4 are from 7 families (labrids, pomacentrids, scarids, chaetodontids, lutjanids, acanthurids and siganids) which constituted less than 19 % of the total fish yield from Sumilon Island in 1983/84. That the significant change in community structure was accounted for substantially by species constituting a small percentage of the yield in previous years suggests at least 2 things. Firstly, that the intensive fishing following breakdown of the Sumilon Island reserve was far less selective than that of the usual fishing techniques or levels of fishing. Secondly, that some of the fishing techniques used were particularly destructive to the habitat (explosives, drive nets) and many of the changes in the community were induced by habitat destruction.

The significant increases in density of *Cirrhilabrus* sp., *Thalassoma lunare* and *T. hardwicki* and the significant decreases in density of 6 species of chaetodontid (Table 4) are likely to be related directly to habitat modification. Drive-net fishing and explosives are known to be able to reduce live coral cover. Live coral cover of Sumilon Island reserve was reduced from 50 to 25 % on the shallow reef slope and from 30 to 10 % on the reef flat between 1983 and 1985 (A. T. White pers. comm.). There was clear evidence that drive-net fishing had contributed substantially to these decreases (remnants of scarelines were found amongst the coral). The decrease in live coral cover was associated with an increase in the amount of coral rubble on both the shallow reef slope and reef flat (G.R.R. pers. obs.). The increase in density of *Cirrhilabrus* and *Thalassoma* spp. may have been related to the increase in abundance of coral rubble, and the decreases in species richness and density of chaetodontids is very likely to be due to the reduction in live coral cover since many of the species of chaetodontids in Table 4 are obligate coral feeders (Russ in press).

Five of the species which decreased significantly in density in the Sumilon Island reserve from 1983 to 1985 were planktivorous pomacentrids (species of *Chromis*, *Amblyglyphidodon* and *Pomacentrus* in Table 4). All of these species were very abundant in the water column on the crest and shallow reef slope in 1983 (Russ in press) and would have been particularly susceptible to dynamite fishing.

Three of 5 species of large herbivore (*Scarus dimidiatus*, *S. bleekeri* and *Naso lituratus*) in Table 4 increased significantly in density from 1983 to 1985. All 3 species had peak densities on the reef flat in 1983 (Russ in press) and it is likely that drive-net fishing forced them from their favoured habitat to the reef slope where the censuses were made. A fourth species of large herbivore in Table 4 *(Scarus gibbus)* had a peak density on the crest and shallow reef slope in 1983 (Russ in press) and decreased significantly in density between 1983 and 1985 (Table 4). *Siganus punctatissimus* declined significantly in density between 1983 and 1985. Of the 2 species of detritivore, *Ctenochaetus tomienensis* declined significantly in abundance but *C. binotatus* did not (Table 4).

Three species in Table 4 known to be favoured targets of fishermen decreased significantly in density in the Sumilon Island reserve between 1983 and 1985

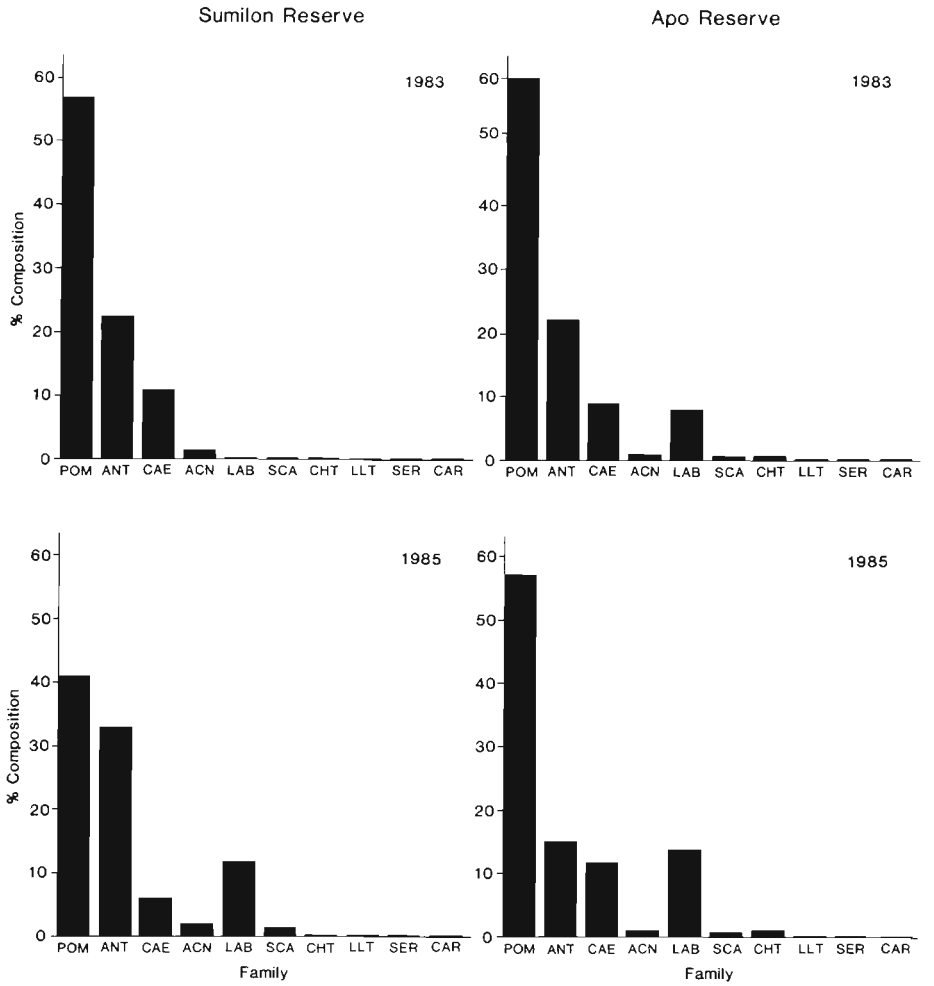

Fig. 6. Percentage composition of the community of coral reef fishes at family level for 1983 (pre-fishing in the Sumilon Island reserve) and 1985 (post-fishing in the reserve) at the Sumilon Island reserve and at Apo Island reserve, a control site where fishing pressure changed little, if at all. The distribution of individuals within families did not differ significantly between 1983 and 1985 at either site (Kolmogorov-Smirnov tests, $p > 0.05$). POM: Pomacentridae; ANT: Anthiidae; CAE: Caesionidae; ACN: Acanthuridae; LAB: Labridae; SCA: Scaridae; CHT: Chaetodontidae; LLT: Lutjanidae plus Lethrinidae; SER: Serranidae; CAR: Carangidae

(*Lutjanus decussatus, Hemigymnus melapterus* and *Cheilinus diagramma*).

Table 5 summarizes information on changes in density of species within 7 families which constituted 77 % of the total yield of fishes from Sumilon Island in 1983/84. One family (the Caesionidae) constituted 65 % of the total yield from the island in 1983/84. All of the species in Table 5 displayed large decreases in density at the Sumilon Island reserve between 1983 and 1985. Only one of the 12 species showed a large decline in abundance at the control site at Apo Island reserve (Table 5). Six of the 12 species in Table 5 decreased significantly in abundance at the Sumilon Island reserve between 1983 and 1985. The power of the significance tests in Table 5, comparing densities in 1983 and 1985, was very low (1-tailed Mann Whitney U tests with $n = 6$ in each cell) and thus there was a strong likelihood of Type 2 error in the tests. This is particularly true for the 6 species in Table 5 which decreased in density at Sumilon Island reserve between 1983 and 1985 but for which the statistical test indicated that the decrease was not significant.

DISCUSSION

Few detailed studies are available which address the following 2 important questions: (1) What are the effects of various fishing techniques (selective versus non-selective, destructive to the habitat or not) on assemblages of coral reef fishes? (2) What are the best indicators of the effects of these differing fishing techniques on assemblages of coral reef fishes?

The answers to these questions depend clearly on the level of fishing intensity, the selective nature of the fishing, and destructiveness of the techniques to the benthic habitat. It is frequently suggested that the most likely detectable effects of light to moderate selective fishing pressure on coral reefs would be a reduction in the average size of individuals of target species (e.g. Craik 1981) and reduction in abundance of the larger carnivorous and piscivorous species such as serranids, lutjanids and lethrinids because these are the most highly favoured 'targets' of fishermen (e.g. Bohnsack 1982, Randall 1982, Munro 1983, Russ 1985, Koslow et al. 1988). A readily detectable effect of such fishing is also likely to be a reduction in the abundance of elas-

Table 4. List of the 25 taxa of fishes accounting for most of the variability attributable to effects of fishing at the Sumilon Island reserve. The Cramer Value varies from 0 to 1 and indicates the relative contribution of a taxon to the discrimination between fish communities in the Sumilon Island reserve in 1983 (pre-fishing) and 1985 (post-fishing). Mean number of individuals per 750 m^2 (range in brackets) are shown for Sumilon Island reserve and Apo Island reserve in 1983 and 1985. Results of 2-tailed Mann-Whitney U tests (n = 6 per cell) comparing density between 1983 and 1985 are shown under p. Arrow indicates direction of change. ** $p<0.01$; * $p<0.05$; ns: not significant. The probability of obtaining at least one Type 1 error amongst pairwise comparisons at each site is 1.25

Taxon	Cramer value	Sumilon Reserve 1983	Sumilon Reserve 1985	p	Apo Reserve 1983	Apo Reserve 1985	p
Cirrhilabrus sp.	0.9206	5.8 (0–40)	941 (640–4100)	**↑	530 (160–1025)	1085 (640–4097)	ns
Chromis viridis	0.8701	622 (640–1025)	98 (40–160)	↓**	292 (40–1025)	68 (0–160)	ns
Amblyglyphidodon leucogaster	0.8701	622 (640–1025)	98 (40–160)	↓**	598 (640–1025)	493 (–)	ns
Lutjanus decussatus	0.8701	1.9 (1–3)	0.11 (0–1)	↓**	0.4 (0–3)	0	ns
Chaetodon trifasciatus	0.8628	5.3 (3–10)	0.35 (0–3)	↓**	0.9 (0–3)	0	ns
Scarus dimidiatus	0.8452	5.0 (1–10)	28 (–)	**↑	12.5 (1–40)	4.5 (1–10)	ns
Pomacentrus moluccensis	0.8452	778 (640–1025)	448 (–)	↓**	585 (160–1025)	431 (160–640)	ns
Thalassoma hardwicki	0.8340	7.2 (1–40)	56 (40–160)	**↑	0.9 (0–3)	0.13 (0–1)	ns
T. lunare	0.8165	16.2 (10–40)	84 (40–160)	**↑	302 (10–640)	28 (3–160)	↓*
Chaetodon baronessa	0.8083	7.1 (3–10)	1.6 (1–3)	↓**	0.3 (0–1)	0	ns
Chromis ternatensis	0.8018	2903 (1025–4097)	672 (640–1025)	↓**	1578 (640–4097)	1134 (640–4097)	ns
Chaetodon lunula	0.7839	6.2 (3–10)	1.2 (0–10)	↓**	1 (0–3)	2.1 (0–10)	ns
C. kleini	0.7809	8.1 (–)	1.4 (0–3)	↓**	51 (40–160)	62 (60–140)	ns
Scarus bleekeri	0.7428	15.3 (3–40)	70 (40–160)	*↑	16.4 (3–40)	17.2 (1–40)	ns
Chaetodon melannotus	0.7423	5.3 (3–10)	0.9 (0–3)	↓*	1.3 (0–3)	0	ns
Scarus gibbus	0.7303	2 (0–3)	0.2 (0–1)	↓*	1.7 (1–3)	2.1 (1–3)	ns
Amblyglyphidodon curacao	0.7071	675 (640–1025)	280 (160–640)	↓*	708 (640–1025)	468 (160–1025)	ns
Ctenochaetus tomienensis	0.7001	97 (40–160)	24.5 (10–40)	↓*	0.4 (0–3)	0.4 (0–3)	ns
C. binotatus	0.6767	16.2 (10–40)	21.0 (10–40)	ns	25.5 (10–40)	27 (10–40)	ns
Siganus punctatissimus	0.6767	1.4 (0–3)	0	↓*	0	0	–
Hemigymnus melapterus	0.6767	4.1 (1–10)	0.5 (0–3)	↓*	2 (0–10)	1.4 (0–3)	ns
Chaetodon speculum	0.6767	1.8 (0–3)	0.2 (0–1)	↓*	2.6 (–)	2.1 (1–3)	ns
C. ulietensis	0.6767	1.4 (0–3)	0	ns	1 (0–3)	1.2 (0–3)	ns
Cheilinus diagramma	0.6761	10.3 (3–40)	1.5 (0–3)	↓*	2.9 (1–10)	2.3 (1–10)	ns
Naso lituratus	0.6708	0.1 (0–1)	1.0 (0–3)	*↑	0.4 (0–1)	0.9 (0–2)	ns

Table 5. List of Cramer Values and mean number of individuals per 750 m^2 (range in brackets) for 12 species of fishes within 7 families which constituted 77 % of the total yield of fishes from Sumilon Island in 1983/84. The Cramer Value varies from 0 to 1 and indicates the relative contribution of a taxon to the discrimination between fish communities in the Sumilon Island reserve in 1983 (pre-fishing) and 1985 (post-fishing). Densities are shown for Sumilon Island reserve and Apo Island reserve in 1983 and 1985. Results of 1-tailed Mann-Whitney U tests (n = 6 per cell) comparing density between 1983 and 1985 are shown under p. One-tailed tests were applied under the expectation that target species such as these would not be expected to increase in density following an increase in fishing pressure at Sumilon Island reserve. ** $p<0.01$; * $p<0.05$; ns: not significant. The probability of obtaining at least one Type 1 error amongst pairwise comparisons at each site is 0.60

Taxon	Cramer Value	Sumilon Reserve 1983	Sumilon Reserve 1985	p	Apo Reserve 1983	Apo Reserve 1985	p
Lutjanus decussatus	0.8701	1.9 (1–3)	0.1 (0–1)	**	0.4 (0–3)	0	ns
Siganus punctatissimus	0.6767	1.4 (0–3)	0	*	0	0	ns
Hemigymnus melapterus	0.6767	4.1 (1–10)	0.5 (0–3)	*	2.0 (0–10)	1.9 (1–3)	ns
Cheilinus diagramma	0.6761	10.3 (3–40)	1.5 (0–3)	*	2.9 (1–10)	3.1 (1–10)	ns
Monotaxis grandoculis	0.6547	1.1 (0–3)	0	*	0	0	ns
Lutjanus bohar	0.5488	0.7 (0–2)	0	ns	0	0	ns
Lethrinus spp.	0.5345	0.7 (0–2)	0	ns	0	0.1 (0–1)	ns
Pterocaesio diagrammus	0.4853	364 (0–1025)	19 (0–160)	ns	34 (0–160)	103 (0–640)	ns
P. pisang	0.4369	830 (1025)	463 (0–1025)	*	762 (640–1025)	641 (640–1025)	ns
Macolor niger	0.4121	2.0 (0–6)	0.7 (0–4)	ns	0.7 (0–4)	1.3 (0–5)	ns
Cephalopholis sexmaculatus	0.3293	2.8 (2–6)	1.8 (0–5)	ns	0.2 (0–1)	0.1 (0–1)	ns
Carangidae	0.3244	2.2 (0–5)	0.8 (0–3)	ns	0	0.4 (0–1)	ns

mobranchs which, if not targeted by fishermen, are still captured and killed frequently by them (Munro & Williams 1985). Intense fishing pressure, involving use of both selective and non-selective fishing techniques and sometimes techniques which can be destructive to the benthic habitat, frequently is predicted to have significant effects on the abundance of a broad spectrum of species, often resulting in major shifts in community and trophic structure (e.g. Munro et al. 1987, Koslow et al. 1988). Few studies have documented such effects in detail.

Munro (1983) compared the heavily fished reefs of the Port Royal Cays in Jamaica with the relatively lightly fished, offshore Pedro Bank. He demonstrated that intensive fishing by traps led to substantial reductions in size structure, total biomass and total catch of reef fishes and suggested that fishing on the north Jamaican coast may have been so intensive as to reduce recruitment to the area. Bohnsack (1982) compared patterns of abundance of species of reef fishes on a coral reef subjected to heavy spearfishing pressure with 2 reefs protected from such fishing for 20 yr. He showed that the abundance and size of large predatory fishes was much lower on the fished reef but that abundance patterns of the reef fish assemblages as a whole did not differ significantly between reefs. In a similar study Russ (1985) compared a site protected from fishing in the Philippines for 10 yr with 2 similar sites open to intensive fishing. There were significantly higher densities of large predatory fishes at the protected site, along with higher overall abundance and species richness of the reef fish assemblage. Nevertheless, such differences could not be attributed unequivocally to the effects of protection from fishing. Koslow et al. (1988) did make relatively direct measures of the impact of trap fishing on assemblages of coral reef fishes at the same locations as those studied earlier by Munro (1983). Koslow et al. (1988) showed that fishing over a 15 yr period had substantial effects on the abundance of large predatory and herbivorous fishes and led to major shifts in catch composition and, by inference, community structure.

The present study made use of a 'natural' experiment to provide evidence of 4 effects of intense fishing (involving a combination of techniques with varying degrees of selectivity and destructiveness to the benthic habitat) upon an assemblage of coral reef fishes. The data provide direct evidence of the reliability of certain variates as indicators of such fishing pressure. The 4 effects which, when combined, resulted in a significant change in community structure, were:

(1) *Direct effects* of intense fishing on *abundance* of fishes. These effects involved removal of fishes normally targeted by fishermen (by both selective and non-selective methods) and also removal of many species not normally targeted by fishermen (by non-selective methods).

(2) *Indirect effects* of intense fishing on *abundance* of fishes. These effects involved destructive fishing techniques modifying the benthic substratum and thus affecting abundance of fishes indirectly.

(3) *Direct effects* of intense fishing on *distribution* of fishes. The study provided indirect evidence that drive-net fishing ('muro-ami' and 'Kayakas'; Carpenter & Alcala 1977, Gomez et al. 1987) forced large, herbivorous species from their normal habitat (the reef flat) to the shallow reef slope.

(4) *Direct and indirect effects* on *species richness* of assemblages of reef fishes.

These effects are not mutually exclusive and in this study it was sometimes difficult to partition the contribution of each to the significant change in community structure.

The most marked direct effects of intense fishing on abundance involved the significant decreases in density of planktivorous pomacentrids and caesionids (Table 3; Fig. 6). The caesionids have been a major target species in the reef fishery at Sumilon Island since at least 1974 (Alcala 1981) but planktivorous pomacentrids have never been targeted by fishermen. Caesionids consituted 65 % of the total yield from Sumilon Island in 1983/84, most of which were captured in traps (Alcala & Russ in press). Both groups occurred in large schools in shallow water near the crest in the Sumilon Island reserve (Russ in press) and are known to be highly vulnerable to both drive-net fishing and explosives (Carpenter & Alcala 1977; Russ pers. obs.). Another major source of mortality of caesionids between 1983 and 1985 was traps set in the reserve. The decrease in density of caesionids of 64 % in the Sumilon Island reserve (Table 3) contributed substantially to a significant decrease (of 54 %) in the total yield of reef fishes from the island between 1983/84 and 1985/86 (Alcala & Russ in press).

On the basis of data collected at Sumilon and Apo Islands in 1983, Russ (1985) did make inferences about the most useful indicators of fishing pressure on assemblages of coral reef fishes. The abundance of large carnivorous and piscivorous species (e.g. serranids, lutjanids, lethrinids, carangids) was suggested as a variate likely to decrease in response to an increase in fishing pressure. Such a prediction was consistent with those made from studies of coral reefs (e.g. Bohnsack 1982, Randall 1982, Munro et al. 1987, Koslow et al. 1988) and other tropical ecosystems (e.g. Jones 1982, Beddington 1984, Gulland & Garcia 1984). In this study large piscivores did decrease significantly in density in response to fishing pressure (Table 3). Serranids declined in density in response to fishing

pressure but not significantly so (Fig. 5). The lack of a significant decline was most likely due to the fact that the most abundant serranid in the Sumilon Island reserve *(Cephalopholis sexmaculatus)* was a secretive species characteristic of ledge and cave communities at depths greater than 10 m (Russ in press). Fishing by hook and line and by spear (these 2 gears accounted for 36 % of the total catch in 1983/84) clearly were not as effective against this species as predicted (Russ 1985). The most noticeable reduction in density of target species was a 94 % decline of lutjanids plus lethrinids (Fig. 4). A 60 % reduction in density of carangids and scombrids was also recorded (Fig. 4), along with significant decreases in density of large labrids (*Hemigymnus melapterus* and *Cheilinus diagramma*). Thus, the abundances of large carnivorous species commonly targeted by fishermen provided very good indices of the effect of fishing on this assemblage of coral reef fishes. This result is consistent with the results of the study of Bohnsack (1982) in Florida and the long-term study of Koslow et al. (1988) in the Caribbean.

A common theme in the literature on responses of communities of fishes to removal of top predators is the likelihood of changes in the overall abundance and relative abundances of prey (e.g. Beddington & May 1982, Beddington 1984, Koslow et al. 1988). Depletion of top predators resulting in an increase in the abundance of prey has been well-documented in closed systems such as tropical lakes (Jones 1982) but has not been demonstrated unequivocally on coral reefs. At least 2 attributes of assemblages of coral reef fishes suggest that removal of a species of top predator is unlikely to lead to a spectacular increase in abundance of its prey. Firstly, there are many species of carnivorous fishes on coral reefs, many of which are generalists and highly opportunistic in their feeding habits. Any increase in abundance of a species of prey following removal of one of its predators is likely to lead to functional responses of other predators which may switch their attention to the abundant prey item. Secondly, although post-settlement predation may have an important effect on population density of coral reef fishes, current ideas on what determines abundance suggest that larval supply (recruitment) is more likely to be the ultimate control on abundance of populations than is predation (see review by Doherty & Williams 1988). Since recruitment of coral reef fishes is highly variable in space and time, any response of a population of prey to depletion of one of its predators may be very difficult to detect. Depletion of a large number of carnivorous species may not necessarily lead to detectable increases in abundance of prey. Russ (1985), in a correlative study, showed that a site with the highest density of carnivorous and piscivorous fishes was also the site of highest density of small prey (pomacentrids, anthiids) suggesting that some factor other than post-settlement predation was controlling the abundance of the prey.

The indirect effects on abundance of fishes (i.e. the effects of habitat damage) in this study appear to have been particularly important. Fishing with drive nets and explosives was very destructive to the benthic habitat, reducing live coral cover substantially in the shallow portions of the Sumilon Island reserve between 1983 and 1985 (White pers. comm., Russ pers. obs.). Abundance and diversity of live coral cover can be positively correlated with biomass of coral reef fishes (Carpenter et al. 1981). It is very likely that the reduction in live coral cover was largely responsible for the significant decrease in density of chaetodontids, most of which are obligate coral feeders, although it is impossible to differentiate between the effects of direct removal and those of habitat modification. Similar spectacular reductions in both abundance and species richness of obligate coral feeding chaetodontids following rapid reduction in live coral cover have been recorded by Bell & Galzin (1984) and Williams (1986). The increase in abundance of coral rubble in the shallow portions of the Sumilon Island reserve between 1983 and 1985 could have contributed to the successful recruitment of labrids such as *Cirrhilabrus* and *Thalassoma* but experimental evidence to support this contention is lacking. A factor potentially confounding the effects of fishing on the benthic habitat in Sumilon Island reserve between 1983 and 1985 was the presence of a typhoon in the area in September 1984 (White pers. comm). However, reports suggested that damage to the benthic habitat in the reserve was slight. Furthermore, any damage attributable to the typhoon should have been detected at control sites, particularly the non-reserve site at Sumilon Island. This was not the case. It is unlikely that such an effect was large relative to the extremely destructive effects of explosives (Alcala & Gomez 1987) and drive-net fishing (Carpenter & Alcala 1977, Gomez et al. 1987).

The destruction of habitat by fishing techniques has been at least partially implicated in massive changes in community structure of communities of fishes on soft substrata in the tropics. A decrease in structural heterogeneity of the substratum (reduction in abundance of benthic invertebrates, particularly sponges) may have been partially involved in the shift in community dominance from species of *Lutjanus* and *Lethrinus* to species of *Nemipterus* and *Saurida* on the North West shelf of Australia in response to trawl fishing (Sainsbury 1988). Larkin (1982), discussing the detailed study of Pauly (1979) which documented changes in community structure of benthic fishes in the Gulf of Thailand in response to trawl fishing, suggested that disruption of the benthic habitat could have contri-

buted to a significant decline in abundance of leiognathids.

An unexpected result of the intense fishing pressure in the Sumilon Island reserve was the apparent direct effect of fishing on the distribution of large herbivores. A detailed study of the pattern of zonation of reef fishes in the Sumilon Island reserve in 1983 (Russ in press) demonstrated that herbivores, particularly scarids, occurred in significantly higher density on the reef flat than the reef crest or slope. Censuses carried out from the reef crest to 14 m on the reef slope in 1983 and 1985 demonstrated a significant increase in density of adult scarids (Table 3). This was associated with a significant decline in density of scarids on the reef flat (Russ unpubl.). The most parsimonius explanation for these results would appear to be that intense fishing, particularly with drive-nets, forced adult scarids from their preferred habitat (the reef flat) to the shallow reef slope. This could have resulted from the direct effects of fishing or from habitat destruction by the fishing methods or both. It should be noted that in addition to the change in pattern of zonation, there was an overall decrease in total abundance of scarids (i.e. on reef flat, reef crest and reef slope combined). It is interesting to note that the data in Table 3 on changes in density of herbivores and large piscivores in response to fishing pressure appears to fit the expected pattern under the 'predator removal' hypothesis discussed earlier, i.e. removal of predators should lead to increase in abundance of fishes lower in the trophic chain. Detailed information on the distribution and abundance of herbivores before and after fishing has demonstrated that such an explanation, despite the attractiveness of its simplicity, is incorrect.

The various direct and indirect effects of intense fishing pressure on the abundance and distribution of fishes in the Sumilon Island reserve combined to affect patterns of species richness. The significant decline in overall species richness in Sumilon Island reserve between 1983 and 1985 provides excellent evidence of the intensity of the fishing pressure. The significant decrease in species richness of large piscivores, including lutjanids and lethrinids (Table 2) was almost certainly the result of direct removal of fish by fishermen. The significant decrease in species richness of chaetodontids was most likely the result of destructive fishing techniques reducing cover of live coral. In general, species richness was much less sensitive as an indicator of fishing pressure than abundance, as predicted by Russ (1985). This is demonstrated by the lower proportion of significant changes in species richness than abundance at Sumilon Island (compare columns headed p in Tables 2 and 3). White (1987) did, however, report a significant increase in species richness and abundance of fishes in the Apo Island reserve between 1985 and 1986, a period representing the 4th year of protection from fishing.

In summary, the intense fishing pressure in the Sumilon Island reserve had a much broader impact on the assemblage of reef fishes than predicted by Russ (1985). The main target species (e.g. caesionids, large piscivores) did decline significantly in density and thus were the best indicators of fishing pressure on the assemblages, as expected. The significant decline in density of caesionids contributed substantially to the significant decline in yield to fishermen from Sumilon Island between 1983 and 1985 (Alcala & Russ in press). The intense, non-selective fishing led also to significant decreases in density of species not normally targeted by fishermen (e.g. planktivorous pomacentrids). Some of these decreases were likely to be related directly to habitat destruction by some of the fishing techniques (e.g. the decrease in density of chaetodontids).

Future studies of the effects of fishing on assemblages of coral reef fishes should consider closely the nature and functioning of these communities. Two points of particular importance are how we think about the trophic structure of communities of coral reef fishes and the factors which ultimately control abundance of populations. Traditionally, coral reefs have been viewed as closed ecosystems in nutrient-poor waters, relying heavily on tight nutrient recycling to maintain productivity, with benthic production being the basis for secondary production of fishes (Odum & Odum 1955). In such systems secondary production of fishes may well be quite limited and removal of a significant biomass of fish quite disruptive to the ecosystem. A large proportion of coral reefs worldwide are in fact close to land masses and are likely to be subject to large input of organic matter and nutrients. This contention is supported by circumstantial evidence that communities of coral reef fishes are dominated both numerically and in terms of biomass by planktivores (Williams & Hatcher 1983, Russ 1984c; Fig. 6). Many of these planktivores are most abundant on windward sides of reefs and evidence now suggests that this substantial biomass of fishes may be heavily dependent on inputs of plankton impinging onto reefs from outside (Hamner et al. 1988). The 'classic' food chain thought to be the major basis of secondary production of coral reef fishes (benthic algae → herbivores → primary and secondary carnivores) may not apply strictly to a large number of coral reefs worldwide. This will have to be taken into account in future models of the effect of fishing pressure on the multispecies stocks of coral reef fishes.

The second point of importance which will have to be considered in future models of the effects of fishing on assemblages of coral reef fishes relates to the factors which ultimately control abundance of populations. Assemblages of reef fishes were traditionally viewed as

equilibrial, resource-limited systems with strong mean interaction strengths between species, the most important of which were competition and predation (see review by Sale 1980). Doherty & Williams (1988) have argued convincingly that environmental factors affecting recruitment are more likely to control abundance of populations of coral reef fishes than either predation or competition, although renewed interest is being shown in the role of post-recruitment processes (Jones 1987), particularly predation (e.g. Shulman 1985, Shulman & Ogden 1987, Warner & Hughes 1989). Emphases on competition and predation form the basis of the development of models for management of multispecies fisheries in other ecosystems (e.g. May et al. 1979, Beddington 1984), although they have been questioned in the context of development of multispecies models for management purposes (e.g. Larkin 1982, Sainsbury 1982). Development of more realistic models of the effects of fishing on assemblages of coral reef fishes will occur if such assemblages are viewed as more open, non-resource limited, non-equilibrial systems not necessarily characterized by strong interactions between species but influenced strongly by variability in recruitment.

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