

Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities

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Abstract. An understanding of the indirect effects of fishing on predator-prey relationships is required for the development of valid multispecies yield models for reef fisheries and for determining the factors governing fish community structure at larger scales. We used an underwater visual census technique to examine the indirect effects of fishing on the biomass and diversity (species richness) of reef fishes in a series of ten traditional Fijian fishing grounds (*qoliqoli*) subject to a range of fishing intensities. All members of the families Chaetodontidae (butterflyfishes), Labridae (wrasses), Lutjanidae (snappers), Mullidae (goatfishes), Scaridae (parrotfishes) and the sub-family Epinephelinae (groupers and coral trout) which could be reliably identified were censused. Each species censused was assigned to one of three trophic groups: herbivore, invertebrate feeder or piscivore. The biomass of all piscivorous fishes and of large (> 30 cm) piscivorous fishes differed significantly between *qoliqoli* and was significantly correlated with fishing intensity. However, the biomass of piscivorous fishes was not correlated with the biomass or diversity of their potential prey (which were not targeted by the fishery). This suggested that the indirect effects of fishing did not have an important bearing on fish diversity or biomass and that predation by the target species did not play an important role in structuring these Fijian reef fish communities. The results contrast with those from a number of studies at smaller scales and provided further indications that the structure of reef fish communities is not governed by a single dominant process, but by a range of processes which operate on different scales in different circumstances.

Introduction

Studies of the processes which structure reef fish communities have primarily focused upon fluctuations in the numbers of young fishes settling on reefs (Doherty 1991). However, predation is recognised as a key structuring process in many aquatic ecosystems (Kerfoot and Sih 1987) and there is evidence to suggest that post-settlement processes such as predation are also significant determinants of structure in reef fish communities (Hixon 1991; Jones 1991). For example, many fishes on reefs consume other fishes, potential prey species have evolved morphological, chemical or behavioural prey defences and prey density may be correlated with refuge availability (Hixon 1991).

The lack of emphasis on predation as a structuring process in reef fish communities may be due to the apparent intractability of its study (Hixon 1991; Caley 1993). Any experiment investigating the influence of predators on community structure requires the effective and unconfounded manipulation of predator density (Hixon 1991), yet attempts to manipulate predator density have often been hampered by difficulties with removing piscivores, preventing the immigration of new piscivores or by experimental artifacts (Lassig, 1982; Stimson et al. 1982; Thresher 1983; Doherty and Sale 1985; Sphigel and Fishelson 1991). In studies where predation has been shown to have an important structuring role, the investigators have tended to focus on small site-attached species on artificial or small patch reefs (Caley 1993; Hixon and Beets 1993; Carr and Hixon 1995). This focus has facilitated the application of effective experimental designs to field situations but has reduced the emphasis on the effects of predation at larger scales.

An understanding of the indirect effects of fishing on predator-prey relationships is a fundamental prerequisite for the development of valid multispecies yield models. Jones (1982), Grigg et al. (1984) and Munro and Williams (1985) have suggested that a fishing strategy which selectively targets predatory fishes may lead to increases in the production or biomass of their prey. At present, the

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evidence for compensatory increases in the abundance of prey fishes in response to the removal of their predators is equivocal and, if there are increases in prey production, they are not expected to compensate for the long-term losses in yields which result from removing predators (Jennings and Lock 1996). However, some significant relationships between predator abundance and prey species richness have been reported from carefully controlled small-scale studies where predator populations have been convincingly manipulated (Caley 1993; Hixon and Beets 1993; Carr and Hixon 1995). The apparent dominance of small fast growing species from low trophic levels in intensively fished areas has been cited as evidence for tight predator prey coupling, but changes in catch composition may result from fishing activities altering the fished habitat, from fishers shifting their attention to the only remaining resources or from fishers reducing the amount of catch discarded. These factors can rarely be treated explicitly in fishery studies (e.g. Jennings and Lock 1996, Jennings and Polunin 1996a).

Decreases in the abundance and size of piscivorous species are widely recognised as the most readily detectable effects of fishing pressure in multispecies fisheries (Russ 1991; Jennings and Lock 1996). These species are highest in the food chain, often have high catchability, and are typically favoured for consumption or sale. Bohnsack (1982) and Russ (1985) have recognised the potential value of fisheries as a means of manipulating predator densities and have compared prey populations on fished and unfished reefs. In the present study we use a fishery independent assessment technique to examine the indirect effects of fishing on the structure, biomass and diversity of fish communities in a series of Fijian fishing grounds. These traditional reef fishing grounds (*qoliqoli*) are protected by customary marine tenure agreements (Iwakiri 1983; Jennings and Polunin 1996c) and are fished solely by the inhabitants of specific villages (Jennings and Polunin 1995a, b). Considerable variations in the length of reef front and the size of human populations with fishing rights in different *qoliqoli* result in their being subject to a range of fishing intensities. Consequently, the *qoliqoli* provide an opportunity for large-scale studies of the indirect effects of fishing. Furthermore, studies of indirect fishing effects in these *qoliqoli* are unlikely to be confounded by damage to the fished habitat and interannual changes in fishing intensity because habitat-destructive fishing gears are rarely used and differences in fishing effort between *qoliqoli* are likely to be maintained from year to year because human population size is relatively stable and fishes are the most important source of dietary protein (Jennings and Polunin 1995a).

Methods

Study areas

The study was conducted within ten fishing grounds (*qoliqoli*) on the western coast of Kadavu Island (Fig. 1). The boundaries of each *qoliqoli* enclose an area of reef on which the inhabitants of specific villages have exclusive rights to fish (Table 1).

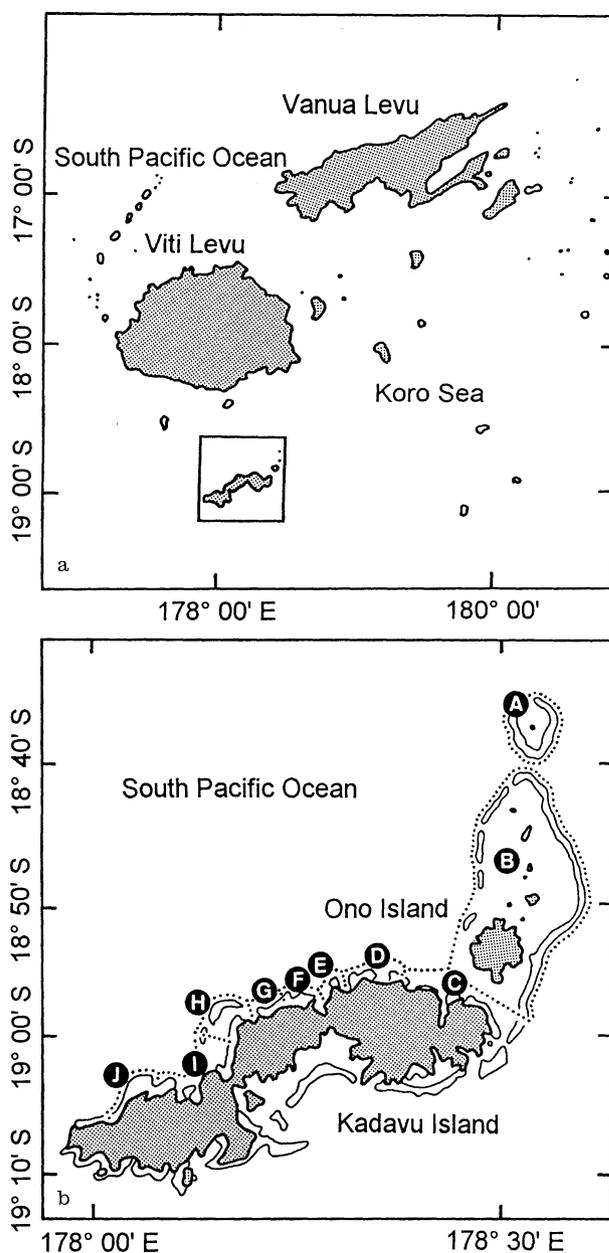


Fig. 1. a General location of Kadavu Island, and b the ten *qoliqoli* selected for study. Land is shaded, unbroken lines indicate major reef areas, broken lines indicate *qoliqoli* boundaries and *qoliqoli* codes follow Table 1

Census of the fish community

Quantitative estimates of the abundance and size of target-fishes in the ten *qoliqoli* were made using an underwater visual census (uvc) point count technique based on that developed by Samoily and Carlos (1992). We selected a point count technique because net movements of target fishes along the reef front (frequently a response to the prevailing current) would not bias abundance estimates as they would if transect techniques were used (Watson et al. 1995). Validation of the uvc point count methodology, and the benefits and disadvantages of the technique, were discussed by Samoily (1992), Samoily and Carlos (1992) and Jennings and Polunin (1995c).

All members of the families Chaetodontidae (butterflyfishes), Labridae (wrasses), Lutjanidae (snappers), Mullidae (goatfishes), Scaridae (parrotfishes) and the sub-family Epinephelinae (groupers

Table 1. Fishing intensity indices and associated data for the ten *qoliqoli*. *Qoliqoli* codes correspond with those used on Figs. 1 and 2

<i>Qoliqoli</i> code	<i>Qoliqoli</i>	Villages with fishing rights	Population ^a	Reef front ^b (km)	Fishing intensity index (population km reef front ⁻¹)
A	Natusara ^c	Dravuni	52 ^d	12.8	4.1
B	Ko Ono ^e	Buliya, Dravuni, Manuku, Naqara, Narikoso, Vabea, Waisomo	546 ^d (4)	29.2	18.7
C	Cokovata (Lomanikoro, Nakasaleka and Nakaugasele)	Kavala, Lawaki, Lomanikoro, Matasawalevu, Nakaugasele, Nakoro, Nakoronawa, Namatiu, Nukuvou, Rarama, Solotavui, Tiliva, Vacaleya	1314 (49)	7.2	182.5
D	Yale	Gasele, Levuka, Naioti, Nauciwai, Rakiraki,	382	4.6	83.0
E	Namoce	Daku	58	1.9	28.0
F ^f	Naqolotini Naocovonu	Naivakarauniniu, Vunisei Tavuki	102	1.8	56.7
G	Suesue	Naikorokoro	63	0.7	90.0
H	Drue	Drue, Navuatu	213 (5)	8.5	25.1
I ^g	Namuana and Boutalevu Tavuki	Namuana, Vunisea Baidamudamu, Natumua, Nukunuku, Solodamu, Tavuki	921 (21)	3.8	242.6
J	Yawe	Korovou, Nalotu, Naqalotu, Tawava, Watokalau, Yakita	667 (2)	5.7	117.0

^a The population indicates the total number of people with fishing rights in the *qoliqoli*. The number of non-indigenous Fijians in the total population is given in parentheses. Population data from Anon. (1988)

^b Reef front is defined as the length of well developed coral reef front, with no signs of siltation and with unobstructed frontage to the open ocean. Reef front with a west facing aspect in Natusara, Ko Ono and Cokovata can only be fished approximately 25% of the time that west facing reefs can be (due to prevailing trade winds) and thus only 25% of the total length of west facing reef front is included in these figures

^c This *qoliqoli* was referred to as Ko Ono Two by Jennings and Polunin (1995 a,b,c, 1996)

^d Villagers in Dravuni may fish in Natusara and Ko Ono. The actual population of Dravuni is 104. For the purposes of calculating a fishing intensity index, 50% of this population has been assigned to Natusara and 50% to Ko Ono

^e This *qoliqoli* was referred to as Ko Ono One by Jennings and Polunin (1995 a,b,c, 1996)

^f This area consists of two separate *qoliqoli*. The fishing rights holders in Naocovonu are from Tavuki Village in southern Kadavu but they permit the villagers of Naivakarauniniu and Vunisei to treat this *qoliqoli* as their own

^g This area consists of two separate *qoliqoli* which are both subject to high fishing pressure and which were treated together

and coral trout) which could be reliably identified were selected for study. Lethrinidae (emperors) are of key importance in the fishery (Jennings and Polunin 1995a) but were not included because the census methodology is inappropriate for these species (Jennings and Polunin 1995c). Abundance estimates of the target species were made at seven replicate sites in each *qoliqoli*. The sites were selected by dividing all areas of reef front (well-developed reef front sloping directly to a depth of at least 10 m, openly exposed to the open ocean, with low siltation rates and estimated mean coral cover in excess of 25%: as confirmed by direct underwater observation) in each *qoliqoli* into 100 m sections (on aerial photographs from the Australian Aerial Mapping 1994 survey conducted on behalf of the Land and Survey Department, Government of Fiji) and randomly selecting seven of these sites. At each site, the abundance and size of target fishes > 8 cm fork length was estimated within 12 adjacent census areas of 7 m radius by counting each fish and making an estimate of its length to the nearest 1 cm. The 12 areas were censused in a random sequence and each census area was centred on the 6 m depth contour (on the reef slope). Boundaries of each census area were estimated from as far above or to one side of the census area as the prevailing visibility permitted and counts of the most wary fishes began immediately. Species in each census area were recorded sequentially, the most active species being recorded first. When a count for one species was complete, all further movements of that species in or out of the census area were disregarded. The time required to complete a count was not standardised since this was dependent on the number and diversity of fish in the census area and

the complexity of habitat to be searched. In practice, counts took 6–13 minutes. Following the count, the diameter of the census area was measured twice (once parallel with, and once perpendicular to, the reef slope) to determine the accuracy with which the dimensions of the census area had been estimated. In addition, the depth at the centre of the census area was recorded to confirm that the area was centred on the 6 m depth contour. All counts were conducted by the same observer (SJ), during daylight hours, from September 1995 to January 1996.

Accuracy of fish length estimation was maintained by practising with objects of known length at intervals throughout the study period (57 lengths of plastic 2.0 cm diameter white plastic tube cut to lengths from 8 to 65 cm in 1 cm increments and threaded onto a 1.0 cm diameter rope in a haphazard sequence) and assessed using methods based on Polunin and Roberts (1993).

Description of habitat

The habitat was described within the perimeter of each replicate count. When a count was complete, the percentage cover (based on plan view) of massive coral, branching coral, rock, rubble and sand was estimated by eye, the minimum and maximum depths in the census area were recorded and the topographic complexity of the substrate was described using the six point scale of Polunin and Roberts (1993).

Estimation of fishing intensity

An index of fishing intensity in each *qoliqoli* was calculated by dividing the length of well-developed reef front in the *qoliqoli* by the number of people with fishing rights. The length of reef front was measured from aerial photographs (Australian Aerial Mapping 1994) and charts, and confirmed by direct underwater observation. Population data were obtained from Anon (1988).

Data analysis

Estimates of fish length were converted to mass using published length: weight relationships (Wright and Richards 1985; Kulbicki et al. 1993; Smith and Dalzell 1993). When a weight: length relationship for a given species was not available we used the relationship for a species with similar morphology, usually from the same genus. Each was assigned to one of three trophic groups: herbivore, invertebrate feeder or piscivore. For the purposes of this study, invertebrate feeders were defined as species which eat invertebrates but never eat fishes whereas piscivores were defined as species which consume fishes but may also eat invertebrates. Species were assigned to trophic groups on the basis of dietary studies conducted by Hiatt and Strasburg (1960), Sano et al. (1984), Parrish (1987), Myers (1989), Blaber et al. (1990) and Randall et al. (1990).

The relationships between habitats at the sites were explored by subjecting the site means of the replicate-specific habitat data to an agglomerative hierarchical clustering procedure using the average linkage method (Sokal and Michener 1958). Analysis of similarities (Clarke and Green 1988), was used to test for significant differences in the structure of habitats among *qoliqoli* subject to different fishing intensities.

The significance of differences in the biomass of families and trophic groups between all *qoliqoli* was assessed using analysis of variance (ANOVA) and the significance of differences between specific *qoliqoli* assessed using Tukey's test (Day and Quinn 1989). Biomass data required $\log_e(x + 1)$ transformation before analysis but original biomass data are presented for descriptive purposes because the data were normally distributed within sites and individual *qoliqoli*. Species richness was adopted as a measure of diversity.

Results

Tests of the accuracy of length estimation indicated that all estimates of length were within $\pm 11.4\%$ of the actual length and that the mean error associated with estimation was $\pm 4.0\%$ for actual lengths of 8–65 cm ($n = 171$). Estimated lengths were not consistently shorter or longer than actual lengths and no corrections were applied. The estimated positions of points on the census area boundary were consistently within ± 0.6 m of their correct position as determined following deployment of the measuring line. Records of fish which had been wrongly assigned to a position inside or outside the census boundary were excluded from, or included in, the data set at the time of the count. This was a relatively simple operation as there were few borderline decisions in each count (typically < 12).

One hundred and forty four species were censused: 30 chaetodontids, 20 epinephelids, 52 labrids, 14 lutjanids, 10 mullids and 18 scarids (Table 2). Chaetodontidae accounted for 6.5% of the total biomass of fishes censused, Epinephelinae 9.0%, Labridae 13.3%, Lutjanidae 19.5%, Mullidae 5.0% and Scaridae 46.7%. Three epinephelid, seven labrid, one lutjanid and one scarid species which

were encountered could not be identified and were not included in the analyses. In addition, it was often difficult to distinguish 8–15 cm individuals of *Scarus chameleon*, *S. globiceps*, *S. psittacus*, *S. schlegeli* and *S. spinus*. Fishes of these species were allocated to species categories in direct proportion to the abundance of larger and identifiable initial phase and terminal phase *Scarus* at each site.

The intensity of fishing, as measured by the fishing intensity index (Table 1), varied by a factor of 60 between the least and most intensively fished *qoliqoli*. The distribution of fishing intensity indices (Table 1) in relation to the geographic location of *qoliqoli* (Fig. 1) indicated that *qoliqoli* with similar fishing intensity were not grouped in a single region of Kadavu. Sites did not cluster into *qoliqoli* specific or fishing intensity specific groups on the basis of their habitat characteristics (Fig. 2). Analysis of similarities indicated that there were no significant

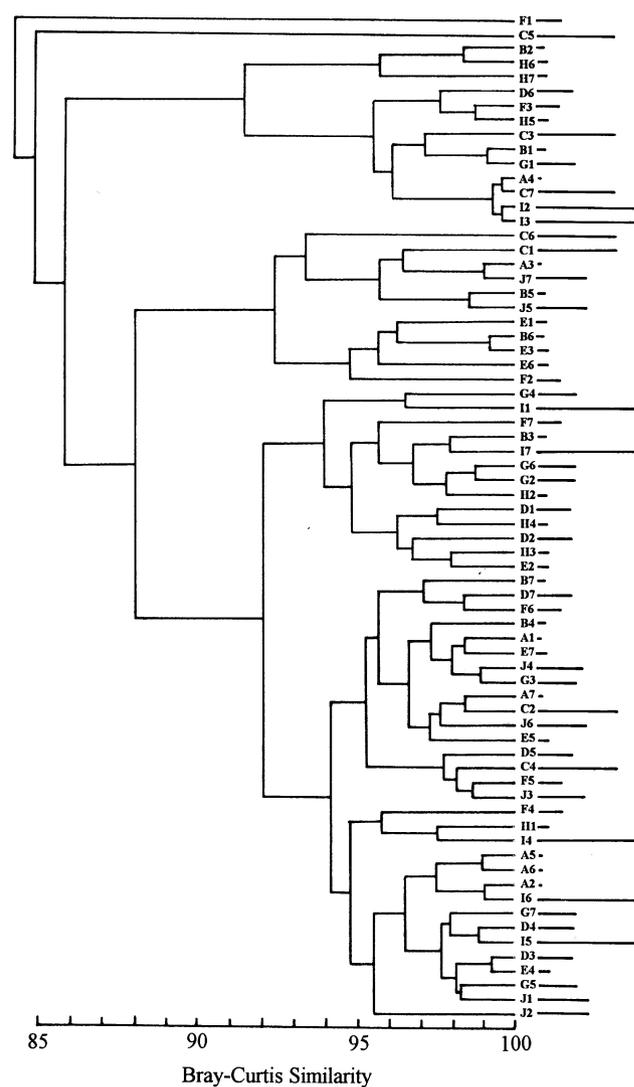


Fig. 2. A dendrogram showing the groupings of census sites formed by hierarchical classification analysis of habitat variables. *Qoliqoli* codes (letters) follow Table 1 and Fig. 1 and numeric codes indicate replicate site number. The length of the bar to the left of each site code is proportional to the fishing intensity at that site

Table 2. Fishes included in the census, their roles in the fishery, maximum lengths (L_{max} , from Myers 1989; Randall et al. 1990), the trophic groups to which they were assigned, their biomass as a percentage of total family biomass and the percentage of the seventy census sites at which they were recorded. Role codes: PT primary target species, ST secondary target species, BY by-catch species which are rarely targeted directly and NC species which are not caught. Trophic group codes: hb herbivore, iv invertebrate feeder and pi piscivore

Species and Authority	Role	L_{max}	Trophic group	Biomass (% total)	Ubiquity (% sites)
Chaetodontidae					
<i>Chaetodon auriga</i> Forsskål, 1775	BY	20	iv	4.8	68.6
<i>C. baronessa</i> Cuvier, 1831	NC	15	iv	2.6	95.7
<i>C. bennetti</i> Cuvier, 1831	NC	18	iv	0.9	51.4
<i>C. citrinellus</i> Cuvier, 1831	NC	11	iv	2.6	72.9
<i>C. ephippium</i> Cuvier, 1831	BY	23	iv	6.6	80.0
<i>C. flavirostris</i> Günther, 1873	NC	20	iv	0.3	15.7
<i>C. kleinii</i> Bloch, 1790	NC	13	iv	1.5	38.6
<i>C. lineolatus</i> Cuvier, 1831	BY	30	iv	2.1	30.0
<i>C. lunula</i> (Lacepède, 1803)	NC	20	iv	1.0	24.3
<i>C. melannotus</i> Bloch & Schneider, 1801	NC	15	iv	4.7	78.6
<i>C. mertensii</i> Cuvier, 1831	NC	13	iv	0.5	78.6
<i>C. ornatissimus</i> Cuvier, 1831	NC	19	iv	1.2	24.2
<i>C. pelewensis</i> Kner, 1868	NC	13	iv	6.5	100.0
<i>C. plebius</i> Cuvier, 1831	NC	13	iv	7.3	65.7
<i>C. rafflesi</i> Bennett, 1830	NC	15	iv	4.9	81.4
<i>C. reticulatus</i> Cuvier, 1831	NC	16	iv	2.6	61.4
<i>C. semeion</i> Bleeker, 1855	BY	23	iv	0.1	2.9
<i>C. trifascialis</i> Quoy & Gaimard, 1824	NC	18	iv	2.7	64.3
<i>C. trifasciatus</i> Park, 1797	NC	15	iv	10.0	98.6
<i>C. ulietensis</i> Cuvier, 1831	NC	15	iv	3.7	74.3
<i>C. unimaculatus</i> Bloch, 1787	BY	20	iv	4.7	90.0
<i>C. vagabundus</i> Linnaeus, 1758	NC	18	iv	4.2	88.6
<i>Forcipiger flavissimus</i> Jordan & McGregor, 1898	NC	22	iv	5.8	80.0
<i>F. longirostris</i> (Broussonet, 1782)	NC	22	iv	3.6	52.9
<i>Hemitaurichthys polylepis</i> (Bleeker, 1857)	NC	18	iv	0.4	8.6
<i>Heniochus acuminatus</i> (Linnaeus, 1758)	BY	25	iv	1.5	25.7
<i>H. chrysostomus</i> Cuvier, 1831	NC	16	iv	2.7	78.6
<i>H. monocerus</i> Cuvier, 1831	BY	23	iv	1.8	25.7
<i>H. singularis</i> Smith & Radcliffe, 1911	BY	23	iv	5.2	51.4
<i>H. varius</i> (Cuvier, 1829)	NC	18	iv	3.5	78.6
Epinephelinae					
<i>Anyperodon leucogrammicus</i> (Valenciennes, 1828)	ST	52	pi	0.8	4.3
<i>Cephalopholis argus</i> Bloch & Schneider, 1801	PT	40	pi	20.2	68.6
<i>C. leopardus</i> (Lacepède, 1801)	ST	20	pi	0.1	5.7
<i>C. miniata</i> (Forsskål, 1775)	PT	41	pi	0.3	1.4
<i>C. urodeta</i> (Forster, 1801)	ST	27	pi	14.0	95.7
<i>Epinephelus caeruleopunctatus</i> (Bloch, 1790)	PT	76	pi	0.1	1.4
<i>E. fasciatus</i> (Forsskål, 1775)	ST	40	pi	0.4	7.1
<i>E. fuscoguttatus</i> (Forsskål, 1775)	PT	90	pi	3.4	11.4
<i>E. hexagonatus</i> (Forster, 1801)	ST	32	pi	0.2	4.3
<i>E. howlandi</i> (Günther, 1873)	PT	45	pi	0.3	4.3
<i>E. macrospilos</i> (Bleeker, 1855)	PT	43	pi	0.2	2.9
<i>E. maculatus</i> (Bloch, 1790)	PT	50	pi	0.3	4.3
<i>E. merra</i> Bloch, 1793	PT	28	pi	2.3	44.3
<i>E. polyphkadion</i> (Bleeker, 1849)	PT	61	pi	18.6	67.1
<i>E. tauvina</i> (Forsskål, 1775)	PT	70	pi	1.9	14.3
<i>Gracila albomarginata</i> Fowler & Bean, 1930	ST	40	pi	0.3	1.4
<i>Plectropomus areolatus</i> (Rüppell, 1830)	PT	70	pi	1.8	7.1
<i>P. laevis</i> (Lacepède, 1802)	PT	100	pi	17.1	42.9
<i>P. leopardus</i> (Lacepède, 1802)	PT	75	pi	5.3	32.9
<i>Variola louti</i> (Forsskål, 1775)	PT	100	pi	12.5	58.6
Labridae					
<i>Anampses caeruleopunctatus</i> Rüppell, 1829	ST	42	iv	1.9	52.9
<i>A. geographicus</i> Valenciennes, 1840	BY	24	iv	0.1	8.6
<i>A. meleagrides</i> Valenciennes, 1840	BY	21	iv	0.1	10.0
<i>A. neoguinaicus</i> Bleeker, 1878	NC	17	iv	2.6	88.6
<i>A. twistii</i> Bleeker, 1856	NC	18	iv	1.6	77.1
<i>Bodianus anthioides</i> (Bennett, 1830)	BY	21	iv	0.1	1.4
<i>B. axillaris</i> (Bennett, 1831)	BY	20	iv	2.9	90.0
<i>B. diana</i> (Lacepède, 1801)	BY	25	iv	0.3	12.9
<i>B. loxozonus</i> (Snyder, 1908)	ST	40	iv	1.5	41.4

Table 2. (continued)

Species and Authority	Role	L _{max}	Trophic group	Biomass (% total)	Ubiquity (% sites)
<i>B. mesothorax</i> (Bloch & Schneider, 1801)	ST	20	iv	2.3	82.9
<i>Cheilinus chlorourus</i> (Bloch, 1791)	ST	36	iv	0.2	14.3
<i>C. digrammus</i> (Lacepède, 1801)	ST	30	pi	7.9	92.9
<i>C. fasciatus</i> (Bloch, 1791)	ST	36	iv	1.0	14.3
<i>C. trilobatus</i> Lacepède, 1801	ST	40	pi	13.2	92.8
<i>C. oxycephalus</i> Bleeker, 1853	BY	17	iv	0.4	44.3
<i>C. unifasciatus</i> Streets, 1877	ST	46	pi	1.3	45.7
<i>Choerodon jordani</i> (Snyder, 1908)	NC	17	iv	0.1	1.4
<i>Cirrhilabrus punctatus</i> Randall & Kuitert, 1989	NC	13	iv	2.3	32.9
<i>Coris aygula</i> Lacepède, 1801	ST	70	iv	2.0	40.0
<i>C. dorsomaculata</i> Fowler, 1908	BY	20	iv	0.2	34.3
<i>C. gaimard</i> (Quoy & Gaimard, 1824)	ST	40	iv	1.3	34.3
<i>C. shroederi</i> (Bleeker, 1858)	BY	17	iv	0.1	1.4
<i>Epibulis insidiator</i> (Pallas, 1770)	ST	35	pi	7.5	75.7
<i>Gomphosus varius</i> Lacepède, 1801	BY	22	pi	9.3	95.7
<i>Halichoeres biocellatus</i> Schultz, 1960	NC	12	iv	0.2	34.3
<i>H. hortulanus</i> (Lacepède, 1801)	BY	27	iv	7.1	97.1
<i>H. margaritaceus</i> (Valenciennes, 1839)	BY	13	iv	0.2	20.0
<i>H. marginatus</i> Rüppell, 1835	NC	17	iv	0.8	48.6
<i>H. nebulosus</i> (Valenciennes, 1839)	NC	12	iv	0.1	4.3
<i>H. ornatissimus</i> (Garrett, 1863)	NC	15	iv	0.8	62.9
<i>H. prosopion</i> (Bleeker, 1853)	NC	13	iv	0.3	30.0
<i>H. trimaculatus</i> (Quoy & Gaimard, 1834)	BY	20	iv	0.1	14.3
<i>Hemigymmus fasciatus</i> (Bloch, 1792)	ST	50	iv	7.9	78.6
<i>H. melapterus</i> (Bloch, 1791)	ST	60	iv	3.6	41.4
<i>Hologymnosus doliatus</i> (Lacepède, 1801)	ST	50	pi	1.9	14.3
<i>Labrichthys unilineatus</i> (Guichenot, 1847)	NC	18	iv	0.4	77.1
<i>Labropsis australis</i> Randall, 1981	NC	12	iv	0.3	74.3
<i>L. xanthonata</i> Randall, 1981	NC	13	iv	0.1	65.7
<i>Macropharyngodon meleagris</i> (Valenciennes, 1839)	NC	15	iv	0.1	11.4
<i>M. negrosensis</i> Herre, 1932	NC	13	iv	0.1	1.4
<i>Novaculichthys taeniourus</i> (Lacepède, 1801)	BY	30	iv	0.2	7.1
<i>Pseudocheilinus octotaenia</i> Jenkins, 1900	NC	14	iv	0.3	60.0
<i>Stethojulis bandanensis</i> (Bleeker, 1851)	NC	13	iv	0.8	75.7
<i>S. strigiventer</i> (Bennett, 1832)	NC	15	iv	0.1	8.6
<i>S. trilineata</i> (Bloch & Schneider, 1801)	NC	15	iv	0.3	20.0
<i>Thalassoma amblycephalum</i> (Bleeker, 1856)	NC	16	iv	0.8	62.8
<i>T. hardwicke</i> (Bennett, 1828)	NC	18	pi	7.3	100.0
<i>T. janseni</i> (Bleeker, 1856)	NC	20	pi	0.9	72.9
<i>T. lunare</i> (Linnaeus, 1758)	BY	25	pi	1.2	51.4
<i>T. lutescens</i> (Lay & Bennett, 1839)	BY	25	iv	4.0	97.1
<i>T. purpureum</i> (Forsskal, 1775)	BY	43	pi	0.1	2.9
<i>T. quinquevittatum</i> (Lay & Bennett, 1839)	NC	17	pi	0.6	30.0
Lutjanidae					
<i>Aphareus furca</i> (Lacepède, 1802)	ST	40	pi	2.5	38.6
<i>Aprion virescens</i> Valenciennes, 1830	PT	100	pi	3.8	8.6
<i>Lutjanus argentimaculatus</i> (Forsskal, 1775)	PT	100	pi	0.7	5.7
<i>L. biguttatus</i> (Valenciennes, 1830)	ST	25	pi	0.6	4.3
<i>L. bohar</i> (Forsskal, 1775)	PT	100	pi	28.5	92.9
<i>L. fulviflamma</i> (Forsskal, 1775)	PT	35	pi	11.5	54.3
<i>L. fulvus</i> (Schneider, 1801)	PT	40	pi	3.4	41.4
<i>L. gibbus</i> (Forsskal, 1775)	PT	50	pi	28.3	92.9
<i>L. kasmira</i> (Forsskal, 1775)	PT	35	pi	4.2	54.3
<i>L. monostigma</i> (Cuvier, 1828)	PT	50	pi	4.4	40.0
<i>L. rivulatus</i> (Cuvier, 1828)	PT	65	pi	0.2	1.4
<i>L. semicinctus</i> Quoy & Gaimard, 1824	PT	35	pi	2.5	44.3
<i>Macolor macularis</i> Fowler, 1931	ST	55	iv	8.1	72.9
<i>M. niger</i> (Forsskal, 1775)	ST	55	iv	1.1	35.7
Mullidae					
<i>Mulloides flavolineatus</i> (Lacepède, 1801)	ST	40	iv	1.5	21.4
<i>M. vanicolensis</i> (Valenciennes, 1831)	ST	38	iv	8.3	41.4
<i>Parupeneus barberinoides</i> (Lacepède, 1801)	BY	25	iv	1.4	14.3
<i>P. barberinus</i> (Lacepède, 1801)	ST	50	iv	5.0	37.1
<i>P. bifasciatus</i> (Lacepède, 1801)	BY	35	iv	43.1	97.1
<i>P. ciliatus</i> (Lacepède, 1801)	ST	38	iv	8.9	42.9

Table 2. (continued)

Species and Authority	Role	L _{max}	Trophic group	Biomass (% total)	Ubiquity (% sites)
<i>P. cyclostomus</i> (Lacepède, 1801)	ST	50	pi	10.5	61.4
<i>P. indicus</i> (Shaw, 1803)	ST	35	iv	0.1	1.4
<i>P. multifasciatus</i> (Quoy & Gaimard, 1825)	BY	30	iv	19.6	100.0
<i>P. pleurostigma</i> (Bennett, 1830)	BY	33	iv	1.5	37.1
Scaridae					
<i>Cetoscarus bicolor</i> (Rüppell, 1829)	PT	80	hb	3.9	80.0
<i>Chlorurus bleekeri</i> (de Beaufort, 1940)	ST	33	hb	0.6	27.1
<i>C. microrhinos</i> (Bleeker, 1854)	ST	70	hb	8.2	87.1
<i>C. sordidus</i> (Forsskal, 1775)	ST	40	hb	19.9	100.0
<i>Hipposcarus longiceps</i> (Valenciennes, 1840)	ST	44	hb	2.7	42.8
<i>Scarus altipinnis</i> (Steindachner, 1879)	PT	60	hb	9.6	91.4
<i>S. chameleon</i> (Choat & Randall, 1986)	ST	31	hb	1.7	61.4
<i>S. dimidiatus</i> Bleeker, 1859	ST	31	hb	1.5	40.0
<i>S. forsteni</i> (Bleeker, 1861)	ST	55	hb	2.0	54.2
<i>S. frenatus</i> Lacepède, 1802	ST	47	hb	4.6	68.6
<i>S. ghobban</i> Forsskal, 1775	PT	75	hb	0.5	14.3
<i>S. glabiceps</i> Valenciennes, 1840	ST	30	hb	9.3	94.3
<i>S. niger</i> Forsskal, 1775	ST	35	hb	11.3	97.1
<i>S. oviceps</i> Valenciennes, 1840	ST	32	hb	2.4	60.0
<i>S. psittacus</i> Forsskal, 1775	ST	30	hb	4.2	90.0
<i>S. rubroviolaceus</i> Bleeker, 1847	PT	70	hb	2.4	48.6
<i>S. schlegeli</i> (Bleeker, 1861)	ST	38	hb	11.2	91.4
<i>S. spinus</i> (Kner, 1868)	ST	32	hb	3.9	92.9

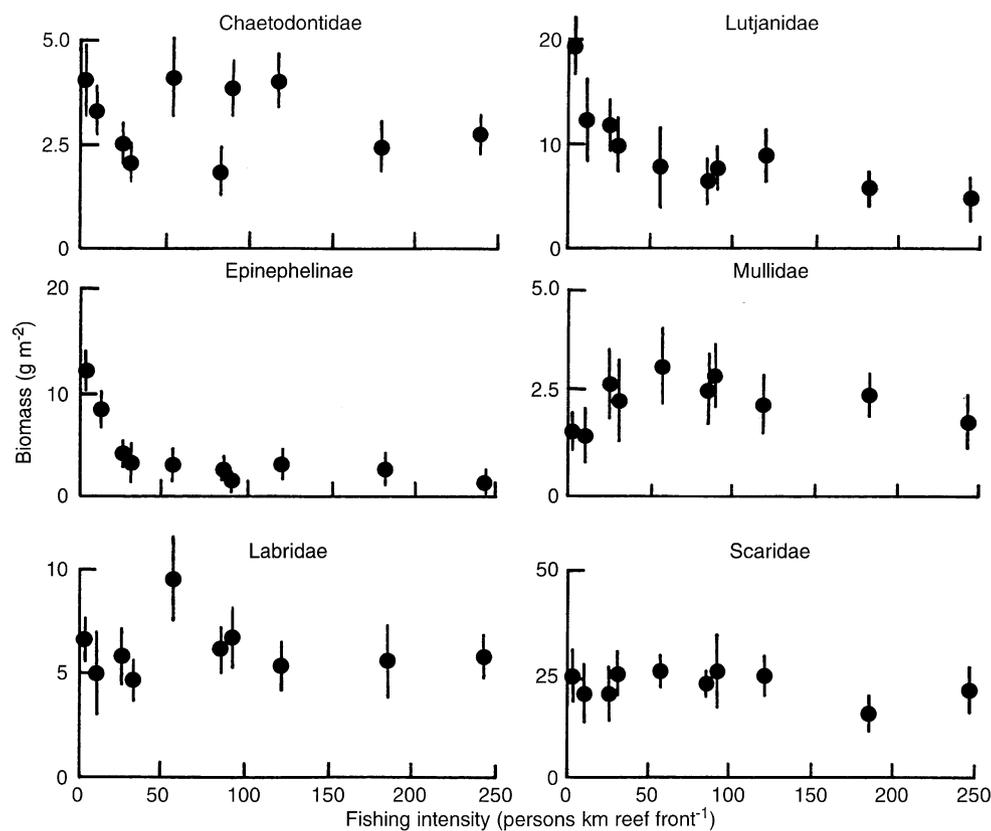


Fig. 3. Relationships between the biomass (mean \pm 95% CL, $n = 7$) of fishes in six families and fishing intensity in the ten *qoliqoli*

differences in the selected habitat characteristics between the ten *qoliqoli* ($P < 0.05$).

Within the *qoliqoli* subject to a range of fishing intensities there were significant differences in the total biomass of fishes in all the target families except Scaridae (Fig. 3,

ANOVA $P < 0.05$ in all cases). For Epinephelinae and Lutjanidae, the two families which include most of the primary target species in the fishery (Table 2), biomass was significantly higher in the less intensively fished *qoliqoli* (Tukey, $P < 0.05$). The biomass of all invertebrate

feeding fishes (Table 2) did not change significantly with increasing fishing intensity (Fig. 4a), but the biomass of all piscivorous fishes (Table 2, Fig. 4b) and large (> 30 cm) piscivorous fishes (Fig. 4c) differed significantly between *qoliqoli* (ANOVA, $P < 0.0001$ in both cases) and was significantly correlated with fishing intensity ($P < 0.05$). The biomass of all herbivorous and invertebrate feeding fishes < 15 cm (Table 2, Fig. 5a) and the biomass of herbivorous and invertebrate feeding fishes < 15 cm which were not fished (Fig. 5b) did not differ significantly between *qoliqoli* ($P > 0.05$). The biomass of all herbivorous and invertebrate feeding fishes < 15 cm, of species which may be targeted by the fishery, did differ significantly between *qoliqoli* (ANOVA, $P < 0.05$) but there was no indication of a consistent relationship with fishing intensity (Fig. 5c).

The within-family diversity of fishes in each of the six families studied differed significantly between *qoliqoli* (Fig. 6, ANOVA $P < 0.05$ in all cases). The diversity of Epinephelinae was significantly higher in the two least

intensively fished *qoliqoli* than in the *qoliqoli* fished most intensively (Tukey, $P < 0.05$). However, within other families, there was no indication of a consistent relationship between diversity and fishing intensity. The diversity of all herbivorous and invertebrate feeding fishes which were not targeted by the fishery (Fig. 7a), the diversity of all herbivorous and invertebrate feeding fishes < 15 cm (Fig. 7b) and the diversity of all herbivorous and invertebrate feeding fishes < 15 cm, of species which were not targeted by the fishery (Fig. 7c), did differ significantly between sites (ANOVA, $P < 0.05$ in each case) but there was no indication of a consistent relationship with fishing intensity.

The biomass of piscivorous fishes > 30 cm, and the biomass of their potential herbivorous and invertebrate feeding prey < 15 cm (Fig. 8a), was not significantly correlated ($P > 0.1$). Similarly, there was no significant correlation between the biomass of these predatory fishes and the diversity of their potential herbivorous and invertebrate feeding prey (Fig. 8b, $P > 0.1$).

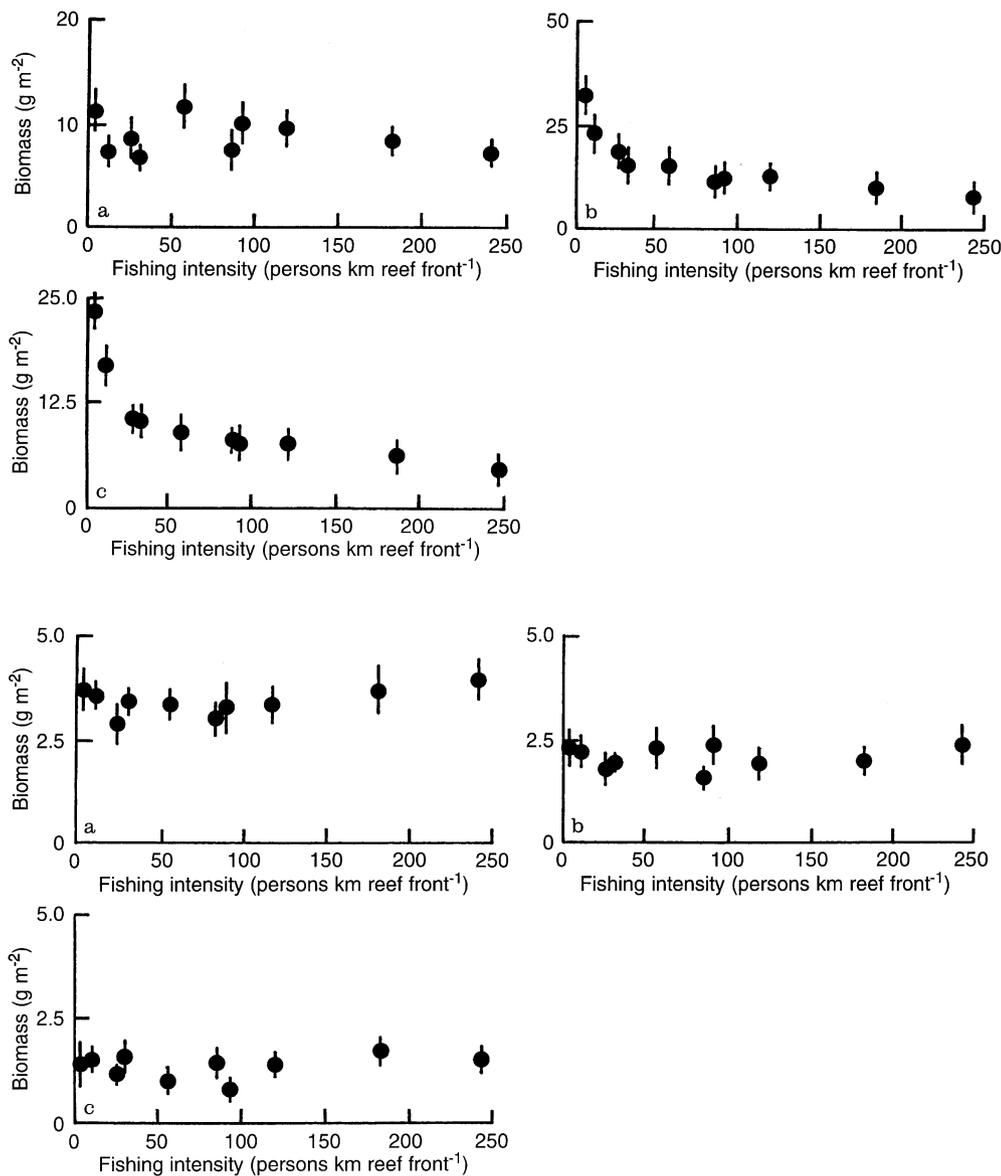


Fig. 4a-c. Relationships between the biomass (mean \pm 95% CL, $n = 7$) of **a** invertebrate feeding fishes (code 'iv' in Table 2); **b** piscivorous fishes (code 'pi') and **c** piscivorous fishes (code 'pi') > 30 cm and fishing intensity in the ten *qoliqoli*

Fig. 5a-c. Relationships between the biomass (mean \pm 95% CL, $n = 7$) of **a** herbivorous and invertebrate feeding fishes (codes 'iv' and 'hb' Table 2) < 15 cm; **b** herbivorous and invertebrate feeding fishes (codes 'iv' and 'hb') < 15 cm which are not caught by any fishing method in use within the *qoliqoli* (code 'NC') and **c** herbivorous and invertebrate feeding fishes (codes 'iv' and 'hb') < 15 cm which may be caught (codes 'PT', 'ST' and 'BY'), and fishing intensity in the ten *qoliqoli*

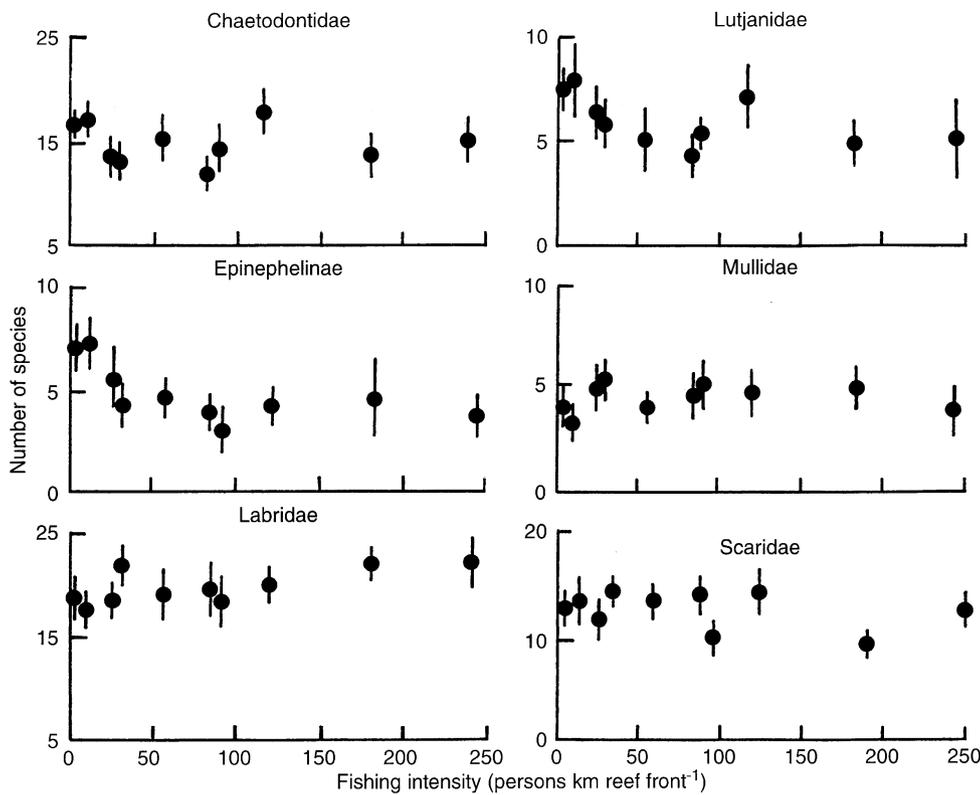


Fig. 6. Relationships between the number of species recorded in each *qoliqoli* (mean \pm 95% CL, $n = 7$) and fishing intensity

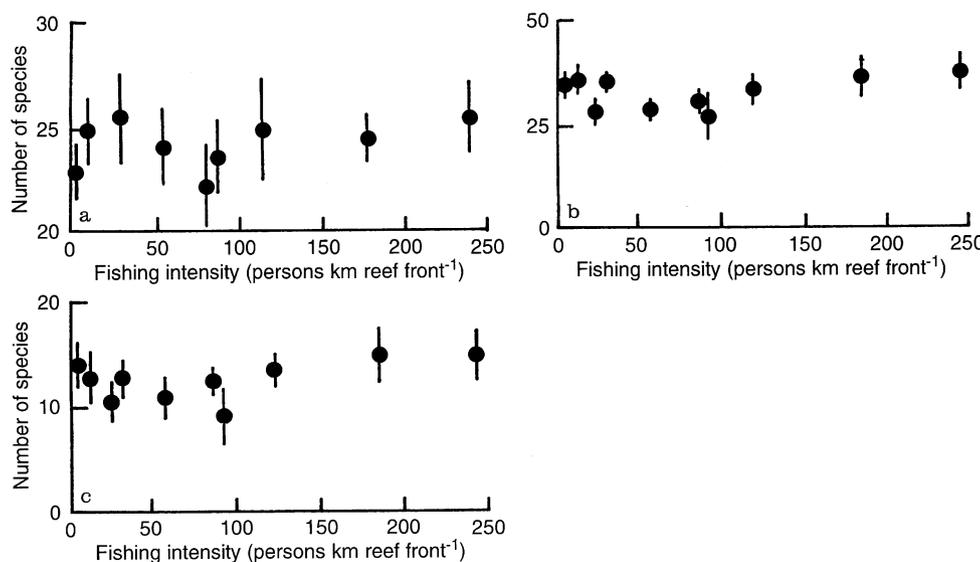


Fig. 7a-c. Relationships between the number of species (mean \pm 95% CL, $n = 7$) of **a** herbivorous and invertebrate feeding fishes (codes 'hb' and 'iv' Table 2) which are not caught by any fishing method in use within the *qoliqoli* (code 'NC'); **b** herbivorous and invertebrate feeding fishes (codes 'hb' and 'iv') < 15 cm which are not caught by any fishing method in use within the *qoliqoli* (code 'NC') and **c** herbivorous and invertebrate feeding fishes (codes 'hb' and 'iv') < 15 cm which may be caught (codes 'PT', 'ST' and 'BY'), and fishing intensity in the ten *qoliqoli*

Discussion

Characteristics of the reef habitat and the geographical location of the *qoliqoli* could have a marked influence on the structure of fish communities (e.g. Williams 1991). However, there was no evidence for gross differences in the reef habitats between *qoliqoli* and there was no consistent relationship between *qoliqoli* location and the fishing intensity index. We suggest that fishing is responsible for the significant differences in the biomass of piscivorous fishes between *qoliqoli* which were observed. This suggestion is in accordance with other studies of the effects of fishing on reef fish communities (Samoilys 1988; Russ and

Alcala 1989; Russ 1991; Grigg 1994; McClanahan 1994; Watson and Ormond 1994; Jennings et al. 1995, 1996; Jennings and Lock 1996; Jennings and Polunin 1996b) and provides further support for the suggestion that fishes from higher trophic levels are good indicators of fishing pressure (Russ 1991). The curvilinear relationship between biomass and fishing intensity is in accordance with that described for other series of fishing grounds in Fiji (Jennings and Polunin 1996b) and the Seychelles (Jennings et al. 1995). The management implications of this relationship are discussed by Jennings and Polunin (1995b, 1996b).

Whilst the negative relationship between the biomass of the target piscivorous fishes and fishing intensity was

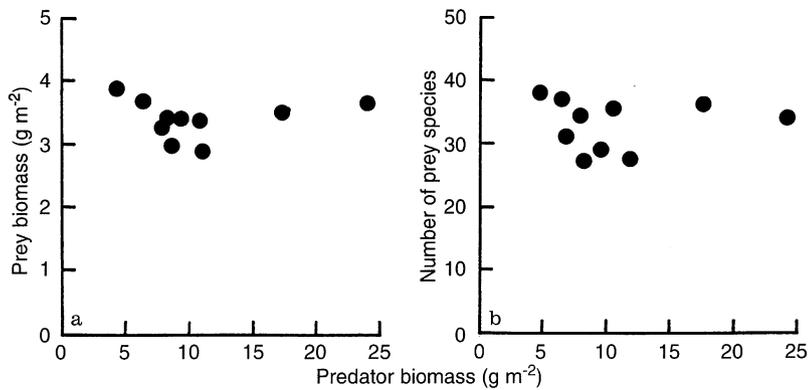


Fig. 8a, b. Relationships between the mean biomass of piscivorous fishes (code 'pi' Table 2) > 30 cm and **a** the biomass of herbivorous and invertebrate feeding fishes (codes 'hb' and 'iv') < 15 cm which are their potential prey; **b** the diversity of herbivorous and invertebrate feeding fishes (codes 'hb' and 'iv') < 15 cm which are their potential prey

significant, there was no evidence for a corresponding increase in the diversity or biomass of potential prey species. This pattern suggests that the indirect effects of fishing did not have an important bearing on fish diversity or biomass in these Fijian *qoliqoli* and that fishing strategies which selectively target these piscivorous fishes will not lead to increases in the biomass or diversity of their potential prey.

There is, however, a possibility that predator-prey relationships are an important structuring force in these Fijian reef fish communities but that the design of this study would not have allowed us to detect such effects. Thus, the decrease in the biomass of epinephelinid and lutjanid fishes in response to fishing may not have been indicative of changes in the biomass of those carangid, lethrinid or muraenid fishes which could not be censused effectively. Previous census work with lethrinid fishes in Fiji suggests that their relative biomass decreases in response to fishing pressure (Jennings and Polunin 1996b), but no such work has been conducted with muraenids. The effects of carangids are liable to be of more concern because they are recognised as roving fishes with high fish consumption rates (Sudekum et al. 1991, Carr and Hixon 1995). Our attempts to count carangids in Fiji have been unsuccessful, as they are rarely encountered, even on exposed outer reef slopes. It remains a possibility that the predation rates of these fishes, which would be expected to range widely between *qoliqoli* subject to different fishing intensities, may lead to a relatively high and consistent predation rates across all *qoliqoli*.

A second potential problem with our approach is that fishes we have classified as piscivores may only eat those fishes which we have classified as prey on an occasional basis. Most existing studies of reef fish diets have been based on examination of the stomach contents of a few individuals (e.g. Hiatt and Strasburg 1960; Vivien 1973; Sano et al. 1984; Parrish 1987; Blaber et al. 1990) and there are few quantitative studies of food consumption rates and feeding strategies of piscivores (De Crosta 1984; Sweatman 1984; Sudekum et al. 1991). The examinations of stomach contents do suggest that the species we treat as potential prey would be consumed, but if studies of predator-prey relationships on reefs are to progress then there is an urgent requirement for further study of feeding strategies and food consumption rates in reef fishes.

Whilst predation is clearly the key process by which energy is transferred within the reef ecosystem (Parrish et al. 1985; 1986), its role in structuring fish communities does not appear to be uniformly strong. Diversity and biomass of prey do not consistently change in response to changes in predator populations, contrary to the predictions of existing models of community structure and in accordance with the suggestion that the effects of individual predators may be limited by the complexity and dynamism of trophic interactions within the reef ecosystem (Hixon 1991; Ebeling and Hixon 1991). The results of the present study suggest that predation by target species does not play an important role in determining the large-scale structure of Fijian reef fish communities. If this suggestion is true, then multispecies fishery yield models which assume tight predator-prey coupling would not provide an appropriate means by which to determine yield from these fisheries. It is notable that the studies of Bohnsack (1982) in Florida, Russ (1985) in the Philippines and Jennings et al. (1995) in the Seychelles also provided good evidence for differences in the biomass of fished predators between fished and unfished sites, but also failed to detect changes in the structure of non-target fish communities. Their results contrast with those from a number of sound experimental studies at smaller scales (Caley 1993, Hixon and Beets 1993, Carr and Hixon 1995) which suggest that predation can determine the abundance and diversity of reef fishes. Such apparently contradictory evidence provides further indication that the structure of reef fish communities is rarely governed by a single dominant process, but by a range of processes such as recruitment variability, predation, competition, physical disturbance and oceanographic conditions, which operate on different scales in different circumstances. On Fijian reefs at the time of this study, the biomass of target piscivorous fishes did not appear to determine the diversity or biomass of prey fish communities.

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