



Scale-dependant control of motile epifaunal community structure along a coral reef fishing gradient

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Abstract

Large-scale fishing is mostly conducted using towed gears that reduce the biomass and diversity of benthic invertebrates. However, it is impossible to differentiate between the physical disturbance effect of towed gears from the effect of fish predator removal upon benthic invertebrate communities. Here we explore the impact of fish removal alone on the community structure of small motile coral reef invertebrates (epifauna) along a subsistence fishing intensity gradient in the Lau group, Fiji. We deployed settlement plates at three areas in each of six fishing grounds and examined the density and class richness of the motile epifaunal communities and the associated algal communities in relation to the structure of fish and benthic communities. Motile epifaunal density was unrelated to fishing intensity. However, at smaller inter-area scale (0.5–10 km) motile epifaunal density was negatively related to plate algal biomass, whereas at the larger inter-fishing-ground scale (4–180 km) motile epifaunal density was positively related to the rugosity (substrate complexity) of the surrounding benthos. The class richness and diversity (Margalef's d) of motile epifaunal communities were negatively related to fishing intensity, but unrelated to grazing intensity, rugosity or algal biomass at either scale. Benthic community structure varied significantly with fishing intensity; hard-coral cover was lower and turf-algal cover was higher at high fishing pressure. The variation in benthic community structure was associated with variation in fish community structure, which in turn varied with fishing intensity. Motile epifaunal community structure upon plates was linked to the structure of the surrounding benthic community, but was not directly linked to the plate algal community. We suggest the decline in richness of the motile epifauna community along the fishing gradient is attributable to either to exploiter-mediated coexistence or the reduction in 'habitat quality' of the

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surrounding benthos. At the large spatial scale substrate complexity is the key determinant of motile epifaunal density, suggesting predation by fishes plays an important structuring role at this scale. Assuming that rugosity is inversely related to predation risk then this study represents the first evidence for spatial-dependence on the top-down (predation) vs. bottom-up (algal biomass) control of community structure. We argue fisheries exploitation, in the absence of a physical disturbance can negatively influence motile epifaunal community structure at large spatial scales.

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1. Introduction

Habitat destructive fishing gears such as bottom trawls modify benthic habitats and reduce the biomass and diversity of invertebrate communities affecting secondary production at large spatial scales (Kaiser, 1998; Collie et al., 2000; Kaiser et al., 2000; Jennings et al., 2001a). However, towed fishing gears have two inseparable impacts on benthic invertebrate community structure: the physical disturbance effect of towed gears and the removal of predatory target and nontarget fishes. The physical disturbance of towed gear results in direct mortality or reduced survivorship of benthic invertebrates (Kaiser and Spencer, 1995; Collie et al., 1997). Fishes can potentially influence benthic invertebrate community structure via predation pressure (Whitman and Sebens, 1992; Greenstreet et al., 1997). Exploitation-mediated changes in fish community structure have also been inferred to result in variation in the taxonomic composition of temperate soft-bottom invertebrates (Frid et al., 1999). Fishing is known to reduce the biomass of predatory fishes (Russ and Alcala, 1989; Jennings et al., 1995; Jennings and Polunin, 1995a,b, 1996, 1997); however, an unresolved issue is whether fish removal alone can influence benthic invertebrate communities, in the absence of the physical disturbance effect of fishing gears.

In hard substrate systems, such as coral reefs and kelp beds, fishes exert predatory control on large motile invertebrates (>0.5 mm), such as urchins, molluscs and lobsters, and smaller motile invertebrates (<0.5 mm) (McClanahan, 1994, 1995; McClanahan and Sala, 1997; Sala et al., 1998; Steneck, 1998; Tegner and Dayton, 2000). The exploitation and depletion of predatory fishes at the top of food webs has led to the proliferation of large grazing invertebrates, such as urchins, which have in turn altered algal abundance or community structure at lower trophic levels. The indirect ecological interaction between predators and the base of the food web via key intermediary species is known as a trophic cascade (Kitchell and Carpenter, 1993; Pinnegar et al., 2000). While the role of large motile invertebrates as cascade intermediaries has been well documented, the potential ecosystem role of small motile invertebrates (<0.5 cm) remains largely unexplored in hard substrate systems, such as coral reefs.

Grazing motile epifauna potentially has an ecosystem role on coral reefs because they consume 1% of daily epilithic algal standing crop and between 19% and 31% of daily net areal production (Klumpp et al., 1988; Klumpp and Polunin, 1989; Polunin and Klumpp, 1992) and can have substantial impacts on algal biomass in areas protected from larger

herbivores (Brawley and Adey, 1981). Hypotheses on the control of motile epifaunal density include both top-down and bottom-up possibilities. Top-down hypotheses highlight the importance of fish predation and the availability of refugia from predation in structuring motile epifaunal communities (Vadas, 1985; Carpenter, 1986). There are generally greater densities of motile epifauna in refugia and examples of refugia include the high local algal biomass of damselfish territories and areas where fish foraging is limited, such as wave swept areas or small crevices (Bailey-Brock et al., 1980; Lobel, 1980; Carpenter, 1986; Klumpp et al., 1988; Klumpp and Polunin, 1990). The bottom-up argument stems from the observation that little energy, typically 10–20% of algal biomass, is transferred up through a typical herbivore food web, suggesting there is little scope for herbivore (e.g. motile epifaunal) control of algal populations (Vadas, 1985). This hypothesis is supported by the positive relationship between algal biomass and the density of epifaunal groups, e.g. amphipods, copepods, molluscs and polychaetes, which suggests algal biomass determines epifaunal density (Bailey-Brock et al., 1980; Klumpp et al., 1988). Experimental increases in algal cover have led to 10-fold increases in motile epifauna, and polychaete abundance was approximately eight times higher in algal-dominated areas compared to nearshore areas lacking algae (Bailey-Brock et al., 1980). Further evidence for bottom-up algal control is evinced by declines in motile epifaunal abundance as algal density decreases in the austral summer (Klumpp et al., 1987). The prevailing view is that motile epifaunal density is determined by algal biomass at relatively small scales (< 3 km), however, it is not known whether this is true at larger spatial scales.

Scale is a pertinent issue in ecology because the knowledge gained about key structuring processes at one scale cannot necessarily be used to understand or predict patterns at another scale (Levin, 1992; Willis and Whittaker, 2002). The top-down role of fish predation in structuring coral reef fish communities appears to be scale-dependent. At small spatial scales (10–100 m) fish predators strongly influence the structure of prey fish communities (Caley, 1993; Hixon, 1993; Caley and St. John, 1996; Beukers and Jones, 1998), but at large spatial scales (0.1–5 km) no influence of aggregate predator depletion upon the structure of prey fish assemblages has been detected (Jennings and Polunin, 1997). In contrast to predation, fish–algal interactions do not appear to vary with scale in hard substrate systems. The pattern of fish–algal associations at large spatial scales is consistent with the small-scale response of fishes to experimental manipulation of algal communities (Williams and Polunin, 2001; Levin and Hay, 2002; Williams et al., 2002).

Few shelf areas remain where fish are exploited without substantial disturbance to benthic habitats by mobile benthic fishing gears (Watling and Norse, 1998). One such area is Fiji, where reef fish are routinely exploited by nondestructive fishing gears, such as spears and hook and line methods (Jennings and Polunin, 1995b). Fiji offers an almost unique opportunity to study fishing effects at large spatial scales because mapped marine tenure systems exist where residents have sole long-term access to defined fishing grounds (Jennings et al., 2001b). The variation in human population size and coral reef area among fishing grounds has been successfully used to provide a spatial gradient of fishing intensity and successful testing of fishing effects hypotheses (Jennings and Polunin, 1995a,b,c, 1997).

Given the potentially important grazing role of motile epifauna and the role of fish predation in structuring motile epifaunal communities, it is plausible that (a) they form an

intermediary role in a trophic cascade, and (b) fishing could disrupt this linkage between fish communities and benthic community structure by changing the motile epifaunal community structure. Here we examine whether community structure of motile epifauna associated with algal communities varies along a fishing intensity gradient consisting of six fishing grounds (islands) in the Lau Island group, Fiji. We also examine variation in fish and benthic communities along the fishing intensity gradient to determine correlates of motile epifaunal community structure. Epifaunal community structure can either be sampled directly from benthic substrata or by sampling the community which develops on settlement plates (Vadas, 1985; Carpenter, 1986; Klumpp et al., 1988). The large spatial scale of this study (0.5–180 km) and small-scale habitat heterogeneity restricted our study to sampling epifaunal communities that had been left to develop on coral settlement plates for six months. First, we expect increased density of motile epifauna at high fishing intensity due to the reduction in predatory fishes. Second, we expect motile epifaunal density to be linked to either the algal biomass on settlement plates or reef substrate complexity (rugosity), or a combination of both. In this case, we assume that rugosity is an indirect measure of epifaunal shelter or refugia availability. There is the possibility that the sign of the correlation varies with spatial scale, with one variable explaining density at smaller scale and the other variable explaining most of the variation at a larger scale. Third, we expect motile epifaunal diversity to decline along the fishing intensity gradient, as has been found with other benthic disturbances, such as trawling and pollution (e.g. Warwick and Clarke, 1994, 1995; Schratzberger and Warwick, 1998).

2. Methods

2.1. Study location and fishing intensity in Fiji

The Lau Island group in the eastern division of Fiji is relatively isolated and only subject to subsistence levels of agriculture and fisheries (Fig. 1). Each island in this study constituted a single discrete fishing ground (*qoliqoli*), where the exclusive fishing rights of each island's inhabitants extend from the shoreline to approximately 200 m beyond the outer reef. Fishing grounds were chosen based on the similarity of outer reef architecture. Fish and benthic surveys were conducted on shallow (7 m chart datum) leeward (western) outer reefs during three cruises (Apr–May 1999, Sept–Nov 1999, Feb–Mar 2000) at six fishing grounds (Table 1). The barrier reef front of each fishing ground was divided into areas, each 400 m in length, on the appropriate marine chart. Fishing grounds of various sizes were sampled in a proportional manner by randomly selecting one third of all available areas (between 3 and 8). Three areas were surveyed at the smallest fishing grounds while eight areas were sampled at the largest fishing ground (Table 1). Sample areas within each fishing ground were relocated using geographical positioning system, however, we did not attempt to exactly relocate each replicate site among sampling dates; consequently, variation at site level among sampling dates is a combination of both seasonal and sample location variance.

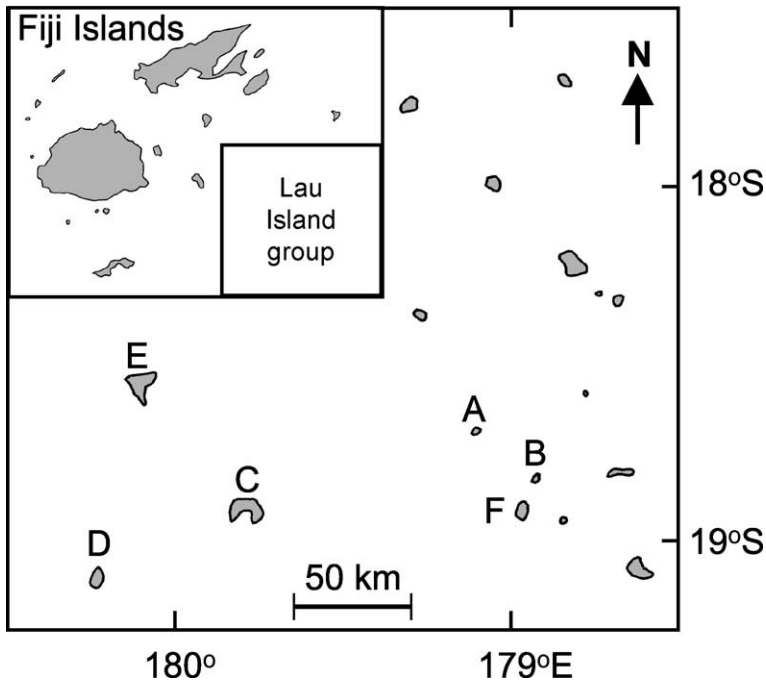


Fig. 1. The fishing grounds (islands) selected for study labelled in alphabetical order of fishing intensity (see Table 1). Inset shows the location of the Lau islands within Fiji.

A fishing intensity index for each fishing ground was obtained by dividing the human population (Anonymous, 1998) by the length of barrier reef front measured from aerial photographs (scale = 1:50,000; Australian Aerial Mapping 1994, available from the Department of Land and Surveys, Suva, Fiji). Two fishing grounds, Vuaqava and Tavunasici, were uninhabited and the effective human population sizes were calculated from the average number of visiting fishers from the tenure-holding village and the estimated number of fishing visits per year. The fishing intensity index is strongly

Table 1

Survey details including names of fishing grounds, number of areas surveyed, number of areas from which coral plates were recovered, number of plates recovered, human population size, coral reef front length and fishing intensity index

Island code	Fishing ground	Number of areas surveyed	Number of areas from which plates were recovered	Total number of plates recovered (coral, ceramic)	Human population	Reef front (km)	Fishing intensity (population km reef front ⁻¹)
A	Tavunasici	3	3	15, 22	20	7.6	2.6
B	Vuaqava	3	3	13, 19	100	15.1	6.6
C	Totoya	5	3	13, 18	806	44.7	18.0
D	Matuku	6	3	12, 21	854	35.0	24.4
E	Moala	8	1	8, 20	1596	60.9	26.2
F	Kabara	5	2	5, 11	1012	23.4	43.3

positively correlated with the actual fishing activity and fish yield (Jennings and Polunin, 1995c).

2.2. Fish census

Fish density was estimated using SCUBA underwater visual census (UVC) of 7-m radius point counts. A total of 182 diurnally active reef associated species from 18 families were censused (Appendix 1). Fishes of >8-cm fork length were censused using six replicate point counts (~ 154 m²) haphazardly distributed within each area (Fig. 2) (as described by Jennings and Polunin, 1995b, 1997; Samoilys and Carlos, 2000). Point counts have similar power to transect methods at the level of replication used here (Samoilys and Carlos, 2000). The boundary of the point count was first estimated and noted relative to reef landmarks, and the radius was confirmed using a tape measure on completion of each count. The surveyor (NKD) was trained in underwater estimation of a 7-m point count radius distance and radius estimates were accurate to within ± 5 cm. Individual fish were counted and fork length estimated to the nearest 1 cm. The surveyor was trained in fish size estimation to a resolution of 1 cm using objects of fixed sizes presented at 3-and 7-m distance underwater (Bell et al., 1985; Darwall and Dulvy, 1996). Fish size estimation was found to be accurate to within ± 0.7 cm at both distances. Underwater visibility was >20 m throughout the study and all surveys were conducted in daylight at least 1 h after sunrise and 1 h before sunset. Mobile species were censused first followed by territorial and cryptic species. Individual fish entering the point count during the survey were not recorded. Count time was not standardised because this was dependent on fish abundance, diversity and habitat complexity. The mean count time was 9.5 min (range 4–16).

Estimates of fish length were converted to biomass using species-specific length–weight conversions (Wright and Richards, 1985; Letourneur et al., 1998). If a length–weight relationship was not available, the relationship for a species of similar morphology in the same genus was used. Densities from point counts were expressed as g m⁻², which is equivalent to kg km⁻².

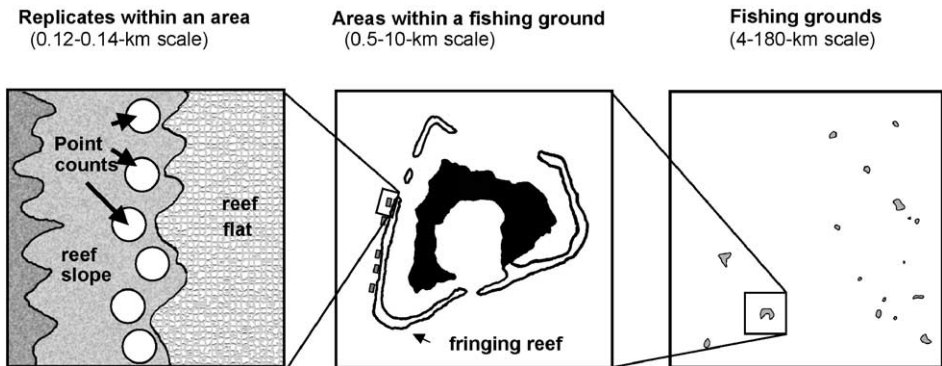


Fig. 2. Hierarchical sampling design and the spatial scale of sampling in the Lau Islands, Fiji.

2.3. Benthic community structure

Digital video footage was recorded at 70 positions haphazardly distributed in a zigzag manner either side of the 7-m-depth contour, centred on and largely within each UVC replicate. Each position was approximately 65 ± 1.6 (mean \pm SE) cm apart. The camera was kept at a fixed distance (26 cm) above the substrate using a spacing rod which provided a 22.5×22.5 cm (~ 500 cm²) quadrat. Video tapes were replayed on a television screen overlaid with one of five randomly chosen transparent acetate sheets containing 20 randomly located 1-cm-diameter circles (Williams et al., 2002). The number of circles occupied by each benthic category was recorded and raised to a percentage. Aggregate categories recorded in this analysis included: ascidians, 'bare' substrate (i.e. imperceptible algal biomass), blue-green algae, crustose coralline algae, coralline lethal orange disease (CLOD), hard coral, macroalgae >5 cm in height, *Palythoa* spp., soft coral, sponges and filamentous turf algae <5 cm in height. Analysis began with the first video frame of each UVC site, and the tape was advanced and randomly paused at the next or next-but-one frame until 30 frames had been analysed for each UVC site. The total area photographically sampled in each UVC site comprised 15 m², which was $\sim 10\%$ of the area of each UVC site.

Rugosity was measured by fitting a 3-m length of small-link chain to the reef surface perpendicular to the reef crest at the centre of the census area. The corresponding horizontal distance was measured by tape and the ratio of chain length/horizontal length calculated (McClanahan and Shafir, 1990). Low rugosity ratios correspond to low surface relief.

2.4. Settlement plates

Five coral plates (12 \times 12 cm) and 10 unglazed ceramic plates (15 \times 15 cm) were haphazardly placed on the reef surface approximately 30–50 cm apart along the 7-m-depth contour (McClanahan, 1997) in three areas, picked at random, in each of six fishing grounds during the first cruise and retrieved after 6 months. The coral plates were cut from cross-section slices of freshly harvested heads of the massive coral *Porites lutea* using a commercial rock-cutting saw (McClanahan, 1997). The square coral plates were approximately 1-cm thick with a mean surface area of 144.3 ± 2.9 cm² (mean \pm SE). On retrieval, the plates were bagged in situ using ziplock polythene bags and returned to the surface. On board, formalin was added to achieve a buffered concentration of approximately 5%, and each bag was sealed and returned to the laboratory in padded lightproof storage boxes. Motile epifauna were collected by washing each coral plate over 5- and 0.5-mm sieves using filtered seawater; the intermediate motile epifauna fraction was protein-stained using rose bengal and preserved in 70% ethanol. Care was taken to minimise the inclusion of motile epifauna from plate underside and edges in the study samples. Motile epifauna was then identified to varying levels of taxonomic resolution (suborder-class) and counted. No attempt was made to recover motile epifauna from ceramic plates.

The percent cover of filamentous turf algae <5 cm, crustose coralline algae and macroalgae on each plate was determined by superimposing an acetate sheet of 100 randomly placed circular points onto each settlement plate and counting the number of points occupied by each algal category. Algal biomass was estimated by sub-sampling

Table 2

The effects of sampling date, fishing intensity and their interaction on mean density (g m^{-2}) of (a) all censused fish and (b) fish trophic categories, fish families and percentage cover of benthic categories

(a) All fish (dependant variable)	Two-way GLM ANOVA			
	<i>F</i> value	<i>P</i> value		
Fishing intensity	10.4	<0.001 *		
Sampling date	2.0	0.14		
Interaction	1.3	0.23		
(b) Community (dependant variable)	Two-way GLM MANOVA		Two-way crossed ANOSIM	
	<i>F</i> value	<i>P</i> value	Global <i>R</i>	<i>P</i> value
<i>Fish trophic category</i>				
Fishing intensity	4.4	<0.0001 *	0.25	0.001 *
Sampling date	5.3	<0.0001 *	0.11	0.04 *
Interaction	1.2	0.08	–	–
<i>Fish family</i>				
Fishing intensity	4.0	<0.0001 *	0.15	0.001 *
Sampling date	4.3	<0.0001 *	0.07	0.043 *
Interaction	1.0	0.35		
<i>Benthic category</i>				
Fishing intensity	11.4	<0.0001 *	0.64	0.001 *
Sampling date	4.4	<0.0001 *	0.2	0.001 *
Interaction	2.4	<0.0001 *	–	–

Significance at <0.05 is represented by an asterisk.

three randomly placed 1-cm^2 quadrats from each plate (N.V.C. Polunin, unpublished data). Each quadrat was excavated to a depth of approximately 3 mm, to include any endolithic algae, and the sample was decalcified with dilute HCL. The sample was filtered onto predried and preweighed filter papers and oven-dried at $60\text{ }^\circ\text{C}$ for 3 days until a constant weight was achieved (using a Shimadzu Libror AEX-200G balance). The average number of bite marks cm^{-1} was used as an indication of grazing pressure. The number of bite marks and excavations on each plate was counted along three transects randomly placed across the face of each coral plate. Transects were placed perpendicular to the plate edge. Parrotfish excavations on the plate edge were excluded as these often overlapped and were difficult to count accurately.

2.5. Analysis

The unbalanced sampling design required analysis using general linear models. Fish and motile epifaunal densities were $\log_{10}(x+1)$ transformed; benthic and plate algal percent cover data were arcsine transformed to achieve normality and homogeneity of variance. For the analysis of fishing effects, data were aggregated at the lowest hierarchical level of replication (sites), and then nested at successively larger spatial scales, i.e. UVC sites $<$ areas $<$ fishing grounds (Fig. 2). For analysis of spatial scale effects, data were

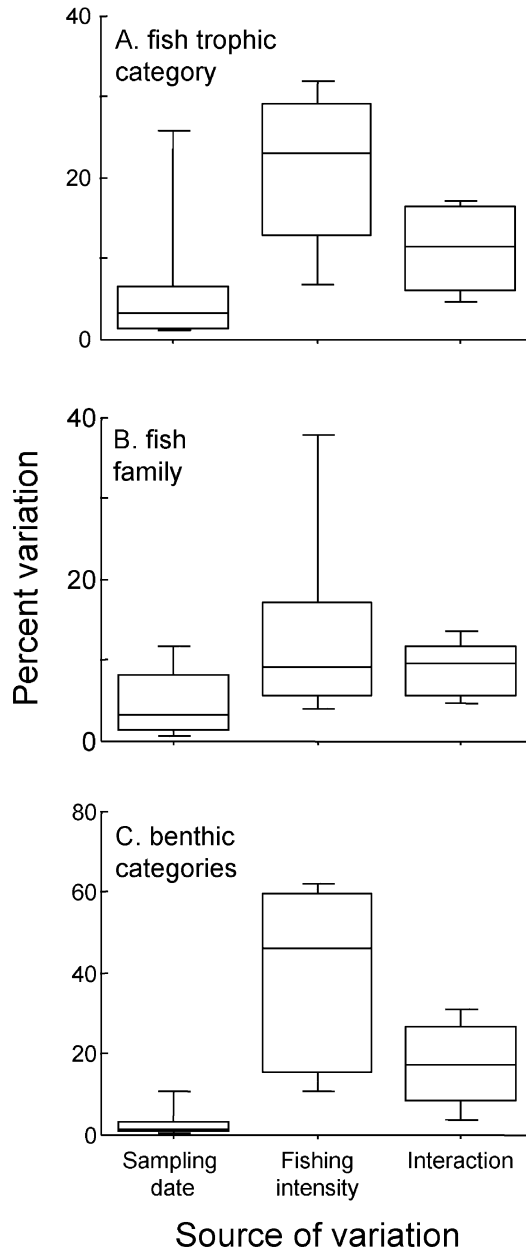


Fig. 3. Boxplots of the variation (%) explained by sampling date, fishing intensity and their interaction, for (A) fish trophic categories, (B) fish families and (C) benthic categories. The central line represents the median; the box represents the 50% interquartile range of observations and the whiskers represent the limit of observations ($1.5 \times$ interquartile range).

analysed at two levels; among areas (0.5–10 km) and among fishing grounds (4–180 km). Two-way parametric (MANOVA, Wilk's λ , as implemented by SAS, SAS Institute) and nonparametric randomisation (ANOSIM, as implemented by PRIMER version 5.2.2.) were used to explore the effects of fishing intensity and sampling date on fish trophic, fish family and benthic community structure. We used multidimensional scaling (MDS) and ANOSIM was applied to similarity matrices calculated using a Bray–Curtis similarity measure (Clarke and Warwick, 1994). This combined MANOVA/ANOSIM approach was chosen because although the data were parametric the number of areas sampled at each fishing ground was not uniform, and MANOVA is sensitive to unbalanced sampling designs (Johnson and Field, 1993). Plates were recovered from three areas at each fishing ground, with the exception of Moala where coral plates were recovered from only one area. Therefore, subsequent analyses of motile epifaunal density and richness were restricted to the remaining five fishing grounds. Cross-correlations of algal plate, motile epifauna plate, benthic and fish community structures were determined using the RELATE procedure of PRIMER (Clarke and Warwick, 1994).

3. Results

3.1. Fish density

Total fish density varied significantly with fishing intensity, but not with sampling date (Table 2a). The mean biomass of fish trophic categories and families varied significantly with both fishing intensity and sampling date, but the interaction was not significant (Fig. 3A,B; Table 2b). There were significantly lower densities of all trophic categories at more heavily fished grounds, apart from territorial omnivores, which exhibited a dome-shaped response, and omnivores which did not exhibit a response (Fig. 4; Table 3a). The effect of fishing intensity upon fish families was generally much weaker compared to trophic categories, however, there were significantly lower densities of the parrotfishes at more heavily fished grounds (Fig. 5; Table 3b). There was also significant variation in butterflyfish and goatfish densities among grounds, but these taxa did not decline along the fishing gradient as would have been expected.

3.2. Benthic community structure

The benthic community structure varied significantly with fishing intensity and among sampling dates, but the proportion of variance explained by fishing intensity was on average 10 times greater than that explained by sampling date (Fig. 3C; Table 2b). There was also a significant interaction between sampling date and fishing intensity, but this explained less than half of the variance of fishing intensity alone.

At more heavily fished grounds there was a significantly lower cover of hard corals and significantly greater cover of turf algae, coralline algae and blue-green algae (Fig. 6; Table 3c). There were also significant differences in the cover of macroalgae and sponges, but

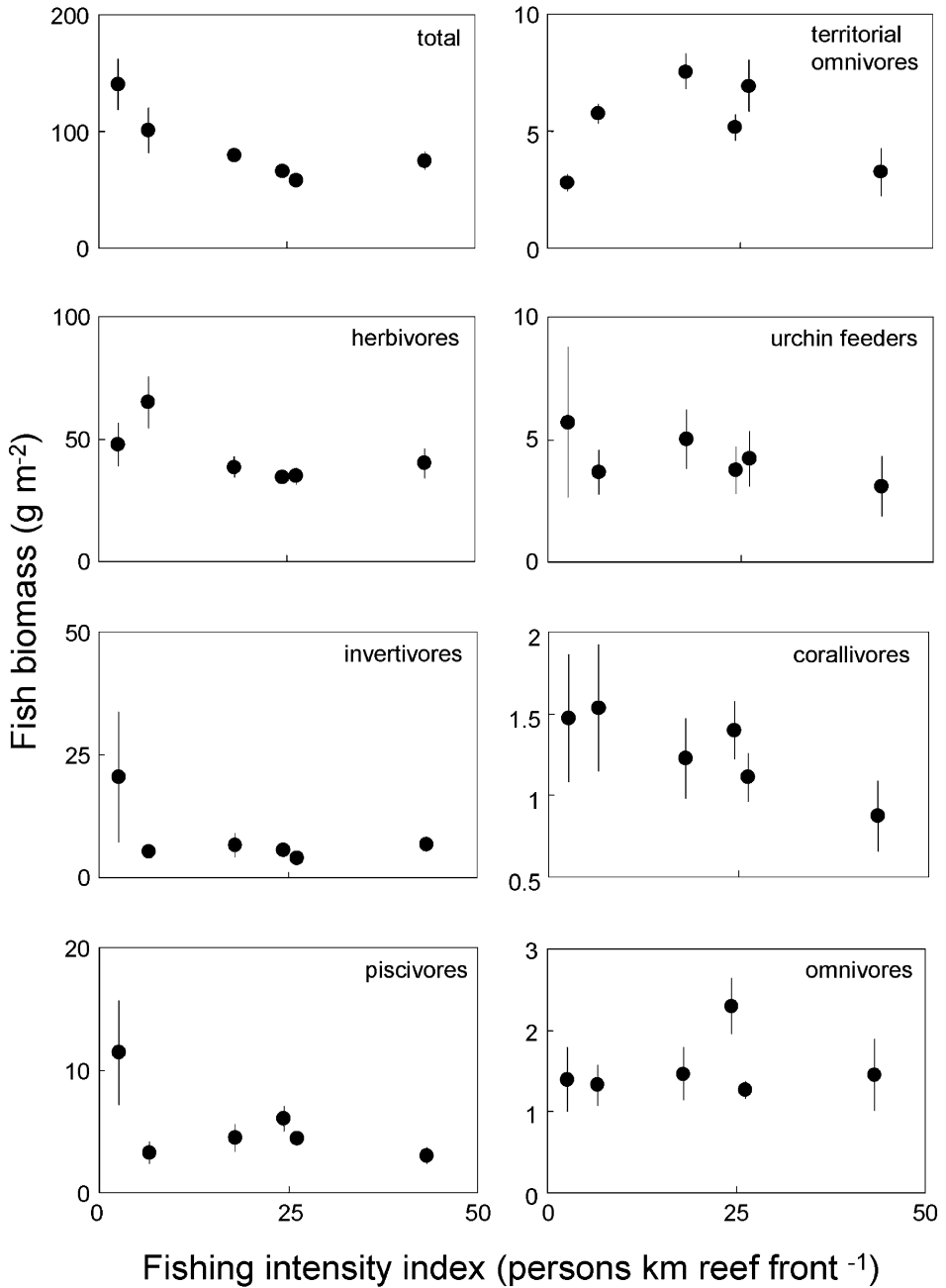


Fig. 4. Relationships between the total fish biomass, the biomass of fish trophic categories and fishing intensity in six fishing grounds (mean \pm standard error). Trophic categories are arrayed in descending order of biomass.

Table 3

The effects of sampling date, fishing intensity and their interaction on the mean density (g m^{-2}) of (a) each fish trophic category, (b) each fish family and (c) percent cover of each benthic category

Community (dependant variable)	Two-way GLM ANOVA		
	Sampling date	Fishing intensity	Interaction
	<i>F</i> value	<i>F</i> value	<i>F</i> value
<i>(a) Fish trophic categories</i>			
Corallivores	0.6	2.4* *	1.4
Herbivores	0.8	5.6* * *	0.6
Invertivores	6.7* *	3.5* *	1.1
Omnivores	1.3	3.3* *	1.7
Piscivores	2.4	9.8* * *	2.0 *
Planktivores	4.1 *	3.6* *	1.2
Territorial omnivores	34.9* * *	15.4* * *	1.1
<i>(b) Fish families</i>			
Surgeonfishes (Acanthuridae)	0.1	0.8	1.4
Triggerfishes (Balistidae)	0.01	0.6	1.0
Butterflyfishes (Chaetodontidae)	5.2* *	2.8 *	2.4 *
Porcupinefishes (Diodontidae)	0.6	0.5	0.9
Grunts (Haemulidae)	0.3	2.1	1.3
Chubs (Kyphosidae)	0.6	1.0	0.9
Wrasses (Labridae)	0.2	1.0	1.5
Emperors (Lethrinidae)	0.1	0.4	0.7
Snappers (Lutjanidae)	4.5 *	1.9	3.6* * *
Filefishes (Monacanthidae)	0.6	1.3	1.2
Goatfishes (Mullidae)	0.2	2.7 *	4.7* * *
Threadfin brems (Nemipteridae)	0.5	0.4	0.4
Boxfishes (Ostraciidae)	0.4	0.7	1.7
Parrotfishes (Scaridae)	0.2	2.8 *	2.6 *
Groupers (Serranidae)	1.0	1.4	1.6
Rabbitfishes (Siganidae)	0.4	2.0	1.5
Pufferfishes (Tetraodontidae)	0.2	0.5	1.0
<i>(c) Benthic categories</i>			
Ascidians	4.7 *	3.3 *	3.1* *
Bare substrate	0.7	1.2	1.4
Blue-green algae	0.01	3.9* *	2.1 *
Crustose coralline algae	2.0	5.0* * *	1.1
CLOD disease	0.7	1.7	1.3
Hard corals	3.4 *	31.2* * *	8.7* * *
Macroalgae	4.1 *	17.9* * *	3.0* *
<i>Palythoa</i> spp.	1.2	3.7* *	3.0* * *
Soft corals	3.7 *	21.0* * *	3.6* * *
Sponges	4.4 *	13.6* * *	3.9* * *
Turf algae	0.4	21.9* * *	7.8* * *

Note that territorial omnivores are solely composed of species from the fish family, Pomacentridae. Significance is represented by asterisks as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

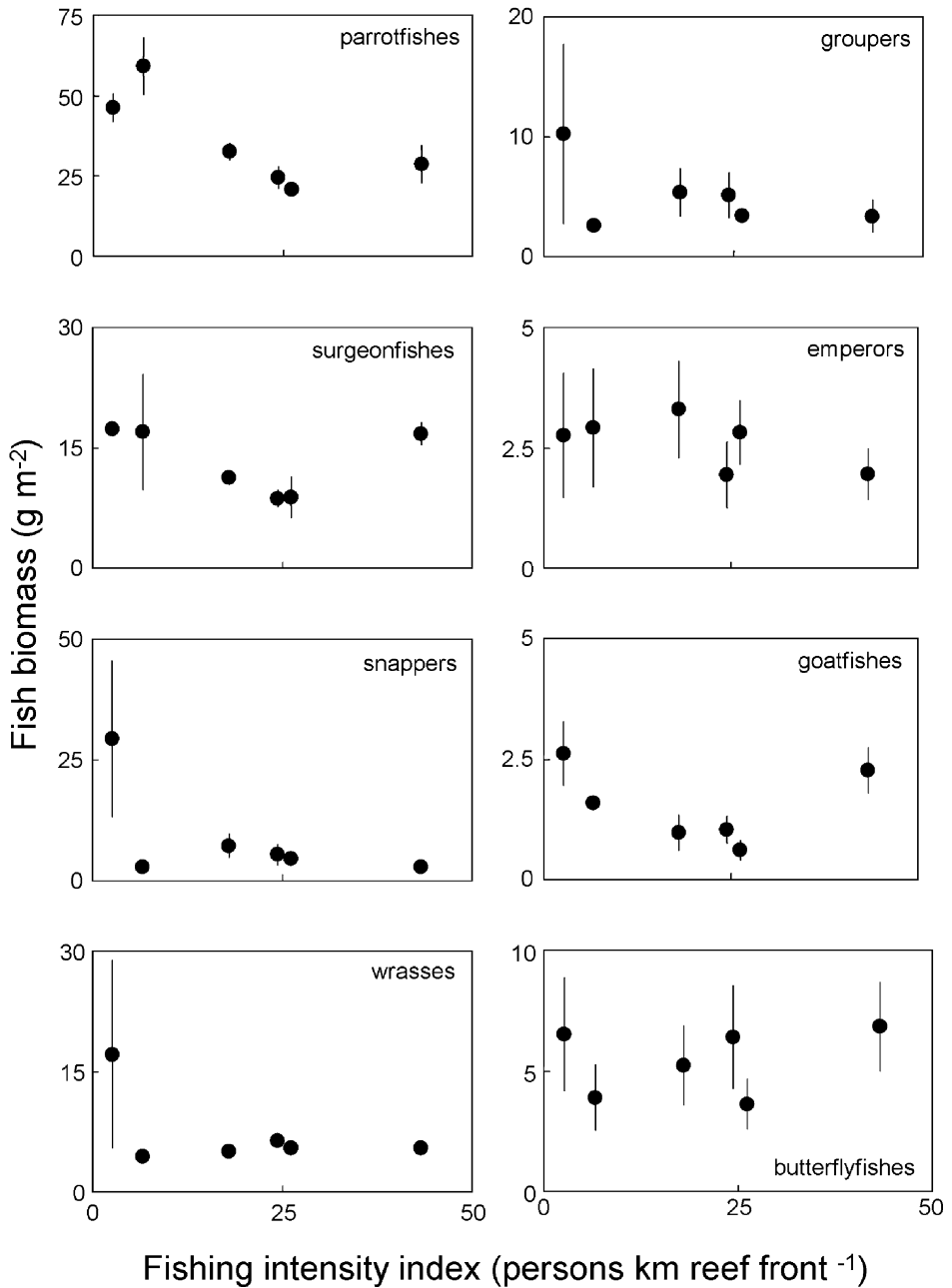


Fig. 5. Relationships between the biomass of fish families and fishing intensity in six fishing grounds (mean \pm standard error). Families are arrayed in descending order of biomass density.

these were not consistent with a linear fishing effect. There was no significant difference in either measure of rugosity or reef slope among fishing grounds.

3.3. Plate algal community structure

Turf algae (54%) and coralline algae (31%) dominated both the coral and ceramic plates. There was little 'bare' area (3%), and some fleshy macroalgae were present (11%, mainly *Padina* and *Lobophora* with some *Halimeda*) on the plates.

There was no significant difference in algal community structure between the different plate materials (coral vs. ceramic), but there was a significant difference among fishing

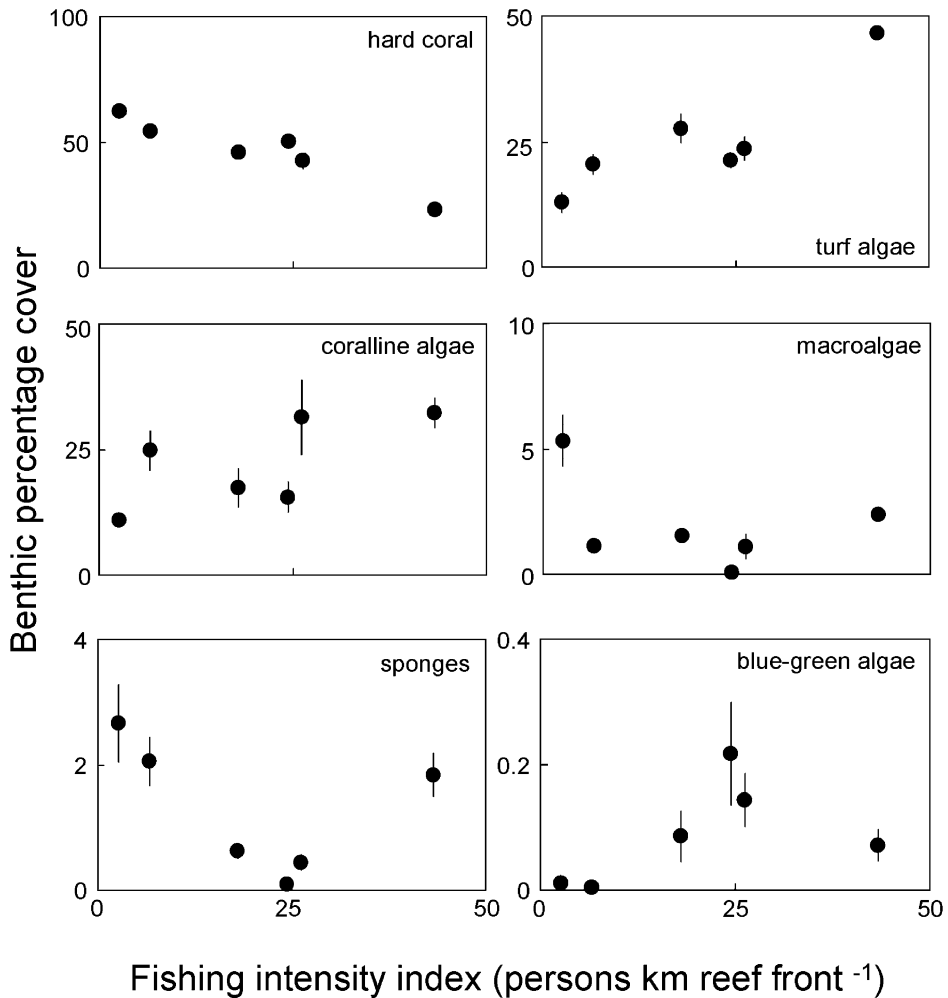


Fig. 6. Relationships between the percent reef cover of selected benthic categories and fishing intensity in six fishing grounds (mean \pm standard error).

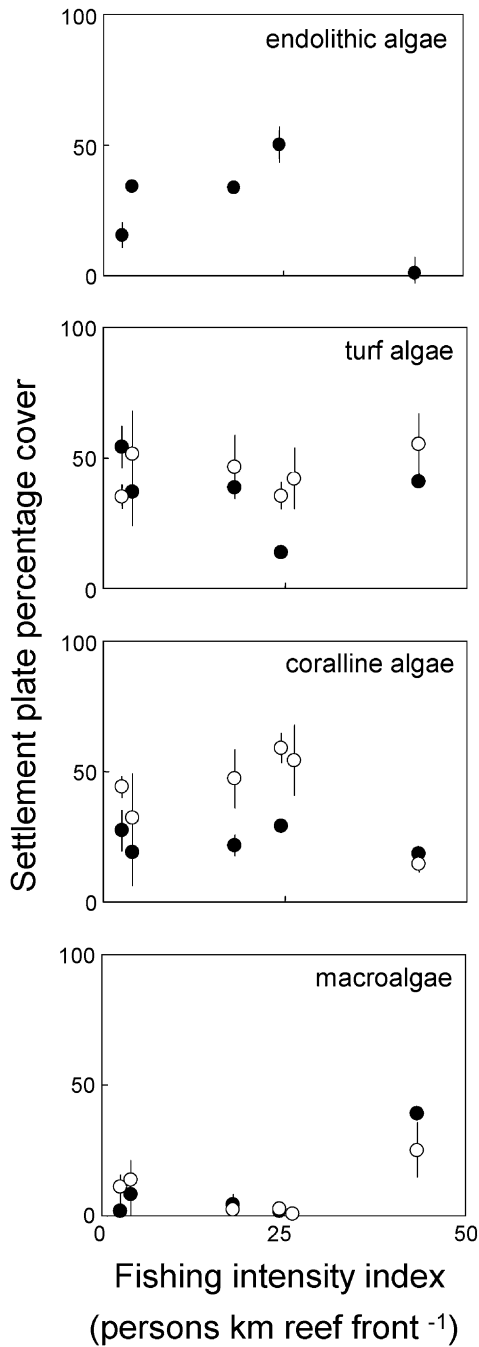


Fig. 7. Relationships between the percent cover of turf algae, coralline algae and macroalgae on settlement plates and fishing intensity in five fishing grounds (mean \pm standard error). (●) Coral plates; (○) ceramic plates. Note: endolithic algae was not observed on ceramic plates.

Table 4

The effect of fishing intensity on algal community metrics on settlement plates

Algal communities	One-way GLM ANOVA	
	F value	P value
Algal biomass (mg cm^{-2})	0.3	0.8
Bite marks (no. cm^{-1})	0.4	0.8
'Bare' (%)	0.6	0.7
Endolithic algae (%)	11.1	0.002**
Turf algae (%)	1.9	0.2
Crustose coralline algae (%)	0.6	0.7
Macroalgae (%)	19.5	<0.001***

Significance is represented by asterisks as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

grounds (two-way ANOSIM; plate material Global $r = 0.0$, $P = 0.5$, fishing intensity Global $r = 0.18$, $P = 0.026$). From here on, only the results from coral plates are considered. There was no consistent effect of fishing intensity on plate algal communities; endolithic

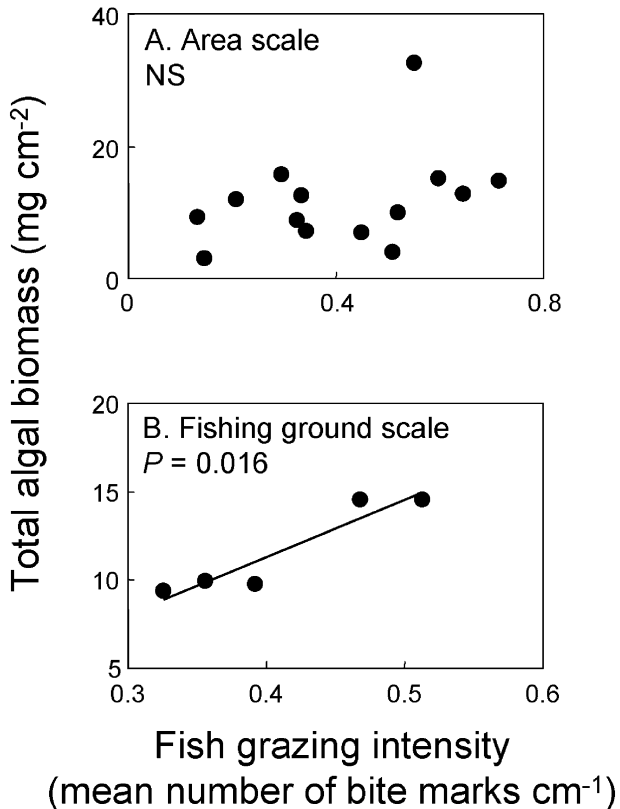


Fig. 8. Relationships between the total algal biomass and fish grazing intensity (A) across all 14 areas, and (B) at five fishing grounds. P values were derived from linear regression tests and NS means the test was not significant; see text for details.

Table 5

The mean density of each taxonomic class of motile epifauna (individuals per 100 cm²) at each fishing ground and the combined percent abundance of each class

Class	Fishing ground code (fishing pressure index, persons km reef front ⁻¹)					Percent abundance
	A (2.6)	B (6.6)	C (18)	D (24.4)	F (43.3)	
Malacostraca	64.2	175.3	107.5	91.5	73.9	54.1
Polychaeta	27.5	61.6	35.6	25.9	71.6	23.5
Copepoda	5.6	40.0	9.8	3.4	13.3	7.6
Gastropoda	10.1	16.9	5.3	9.3	11.1	5.6
Nematoda	2.4	8.0	7.0	9.2	6.8	3.5
Echinoidea	22.5	3.6	0.2	0.0	0.0	2.8
Stelleroidea	1.9	2.8	0.6	1.0	2.4	0.9
Bivalva	1.5	2.4	1.9	0.6	1.2	0.8
Turbellaria	4.2	2.1	0.8	0.3	0.0	0.8
Ostracoda	0.6	1.0	0.7	1.3	0.0	0.4
Holothuroidea	0.0	0.3	0.2	0.0	0.0	0.1

algal cover exhibited a dome-shaped response to fishing intensity; and turf algae and coralline algae did not differ among fishing grounds and macroalgal cover was greater only at the most heavily fished ground (Fig. 7; Table 4). There was no significant difference in algal biomass or the mean number of bite marks cm⁻¹ on plates among fishing grounds. Algal biomass was positively related to the mean number of bite marks cm⁻¹, but only at the largest scale (Fig. 8; $F_{1,3}=24.2$, $P=0.016$). There was no relationship between algal biomass and rugosity at either area or fishing-ground scale.

Table 6

The effect of fishing intensity on the density (individuals 100 cm⁻²) of motile epifaunal classes on settlement plates

Epifauna, taxonomic class	One-way GLM ANOVA	
	<i>F</i> value	<i>P</i> value
Malacostraca	1.7	0.2
Polychaeta	1.1	0.4
Copepoda	4.8	0.024 *
Gastropoda	3.8	0.046 *
Nematoda	0.7	0.6
Echinoidea	5.2	0.019 *
Stelleroidea	1.5	0.3
Bivalva	1.4	0.3
Turbellaria	4.3	0.03 *
Ostracoda	1.8	0.2
Holothuroidea	0.7	0.6
Total combined	2.1	0.2

Significance is represented by asterisks as follows: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

3.4. Plate motile epifauna community structure

The density of motile epifauna averaged 189 individuals 100 cm^{-2} and the most abundant classes were Malacostraca (54% of individuals), Polychaeta (23.5%), Copepoda (7.6%) and Gastropoda (5.6%) (Table 5). Several taxonomic classes exhibited significant differences in density among fishing grounds, but only Echinoidea and Turbellaria declined systematically with fishing intensity (Tables 5 and 6). Motile epifaunal density was negatively related to algal biomass at area scale, but unrelated at fishing-ground scale (Fig. 9A,B; area $R^2=0.33$, $F_{1,12}=7.25$, $P=0.02$; fishing ground $R^2=0$, $F_{1,12}=0$, $P=0.97$). Motile epifaunal density was weakly positively related to reef rugosity at area scale and strongly related to rugosity at fishing-ground scale (Fig. 9C,D; area scale $R^2=0.20$, $F_{1,12}=4.2$, $P=0.064$; fishing-ground scale quadratic regression $R^2=0.99$,

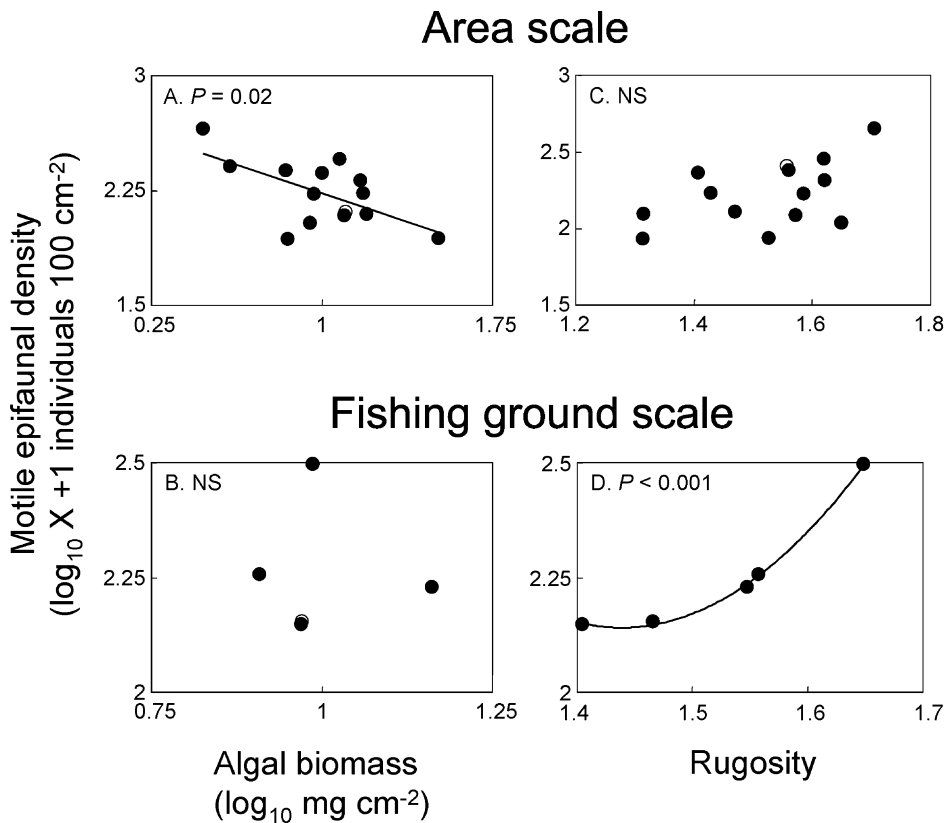


Fig. 9. Relationships between motile epifaunal density and the total algal biomass (A) across all 14 areas, and (B) at five islands (mean \pm standard error). Relationships between motile epifaunal density and rugosity (C) across all 14 areas, and (D) at five fishing grounds (mean \pm standard error). Hollow data points are used to highlight nearly overlapping points. P values are from linear regression tests, except for (D) where quadratic regression was used and NS means the test was not significant; see text for details.

$F_{2,3} = 724$, $P < 0.001$). When both explanatory variables are considered together, algal biomass explained more variation (77%) in motile epifaunal density than rugosity (33%) at the area scale (multiple regression, $R^2 = 0.40$, $F_{2,11} = 5.27$, $P = 0.025$). However, at fishing-ground scale, rugosity explained 99% of the variation in motile epifaunal density. There

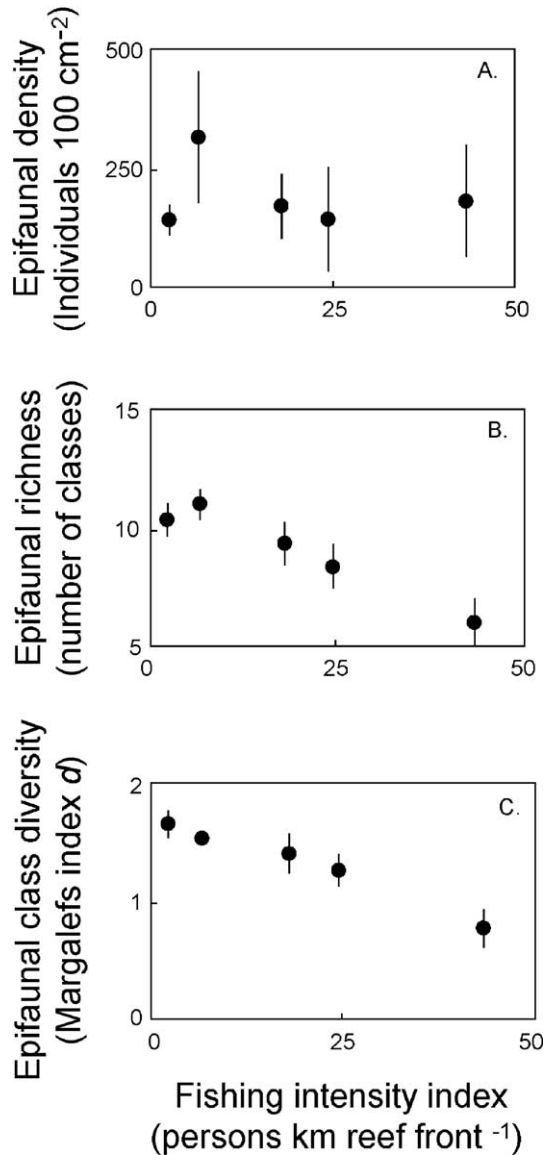


Fig. 10. Relationships between (A) density, (B) taxonomic class richness and (C) class diversity of motile epifauna and fishing intensity (persons km reef front⁻¹) at five fishing grounds (mean \pm standard error).

were no relationships between the density of motile epifauna and the fish grazing intensity on the coral plates at either area or fishing-ground scale.

Motile epifaunal density did not vary systematically along the fishing intensity gradient (Fig. 10A). However, the class richness and diversity of motile epifaunal communities were significantly lower at the more heavily fished grounds (Fig. 10B; richness, $F_{1,4} = 5.75$, $P = 0.011$; Fig. 10C; Margalef's d , $F_{1,4} = 8.09$, $P = 0.004$). The rare epifaunal classes (Echinoidea, Turbellaria, Ostracoda and Holothuroidea) were absent at

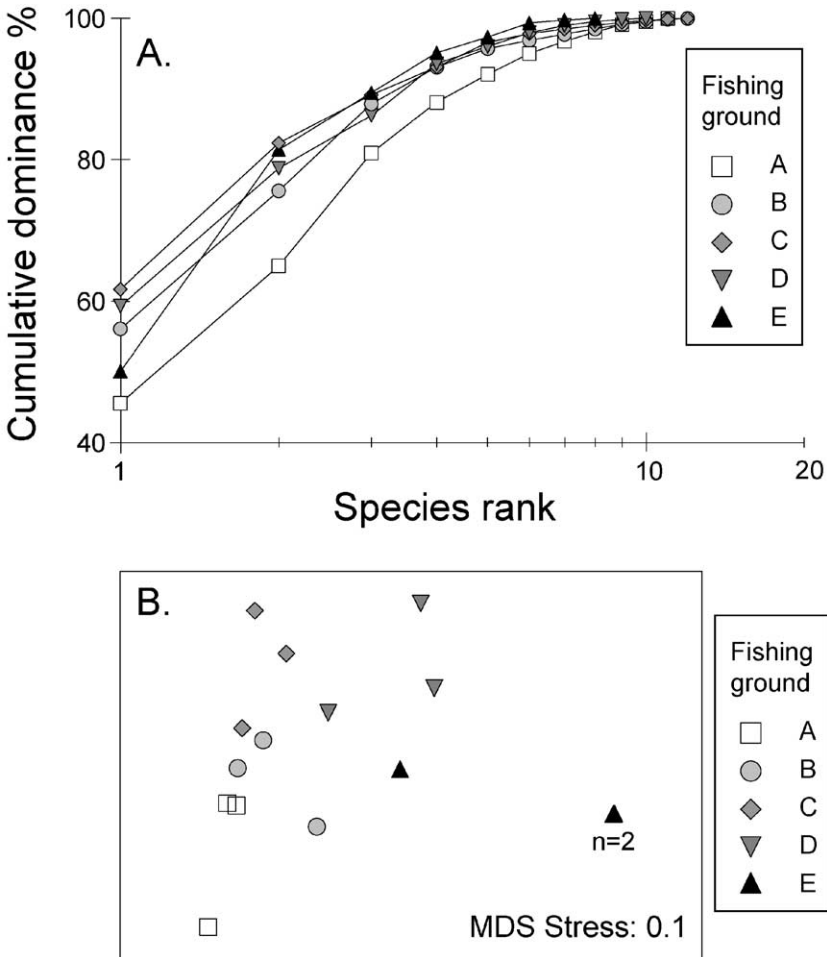


Fig. 11. (A) k -dominance curves for coral plate motile epifauna classes at five fishing grounds. (B) MDS ordination of the motile epifaunal communities at 15 plate sites at five fishing grounds. Areas are shaded from light to dark and labelled in alphabetical order corresponding to increasing fishing intensity (see Table 2). These analyses were based on the proportion of Annelida, Asteroidea, Bivalva, Caprillidea, Copepoda, Crinoidea, Cumacea, Decopoda, Echinoidea, Gammaridea, Gastropoda, Holothuroidea, Isopoda, Natantia, Nematoda, Nudibranchia, Ophiuroidea, Ostracoda, Platyhelminths, Polyplacophora, Pycnognida, Tanaidacea at each site.

the most heavily fished ground and only Polychaeta exhibited greater density at the most heavily fished ground (Table 5). This pattern was reflected in the k -dominance curves, with the curve representing the lightest fishing intensity lying below and to the right of the others, and the curves shifting upward and to the left with increasing fishing intensity, suggesting fewer classes contributed to dominance at higher fishing intensities (Fig. 11A). The MDS ordination indicated significant grouping of areas within fishing grounds, indicating a link between motile epifaunal community structure and fishing intensity (Fig. 11B; ANOSIM Global $r=0.527$, $P=0.001$). There were no relationships between class richness or diversity of motile epifauna and fish grazing intensity, algal biomass on coral plates or benthic rugosity at either area or fishing-ground scales.

3.5. Correlations among fish, benthic, plate algal and motile epifaunal communities

Motile-epifaunal community structure was strongly correlated with benthic community structure using cross-correlation of similarity matrices ($\rho=0.512$, $P=0.001$) and weakly correlated with plate algal community structure ($\rho=0.24$, $P=0.068$). Benthic community structure was significantly correlated with fish community structure (fish families, $\rho=0.388$, $P=0.002$; fish trophic categories, $\rho=0.245$, $P=0.047$). However, fish community structure, using either families or trophic categories, was not significantly correlated with either the algal communities or motile epifaunal communities on settlement plates.

4. Discussion

This study indicates fishing can influence the community structure of small motile epifauna, in the absence of physical disturbance. There were clear differences in the k -dominance of these epifaunal communities along the fishing intensity gradient, which was consistent with lower epifaunal class richness and diversity at grounds with higher fishing intensities. There was a clear multivariate link between fishing intensity and community structure of small epifaunal (Fig. 11B), but there was no clear effect of fishing on total epifaunal density (Fig. 10). However, epifaunal density was determined by a combination of settlement-plate algal biomass and coral reef rugosity. The relative importance of algal biomass and rugosity for structuring epifaunal density was scale-dependent; at smaller spatial scales (among areas, 0.5–10 km) algal biomass was more important, and at larger spatial scales (among fishing grounds, 4–180 km) rugosity was more important. To the best of our knowledge, this study constitutes the first evidence to suggest that the processes controlling community structure may vary with spatial scale.

The conclusions of this study are potentially limited by a number of factors; here we address each in turn. The settlement plates were deployed for a relatively short period of time, which raises the possibility that algal and epifaunal communities might not have stabilised, and therefore our findings may not be representative over longer time scales. However, this is unlikely to be important to our findings because

communities of small epifauna develop rapidly, and the time to reach short-term (weeks) stability in algal cover and diversity is approximately 100 days on coral settlement plates (Martin-Smith, 1994; McClanahan, 1997). Another limitation was that while there was a multivariate link between fish and other communities, it was not possible to determine the proximate links between benthic and plate community structures and particular fish trophic or family groupings. Most of the significant differences in fish community structure were heavily dependent on the high densities found in the least fished ground. In order to understand the proximate links between fish and benthic communities, we suggest greater replication at the fishing-ground scale is required. The recruitment of epifauna is often cited as having a major structuring role in benthic communities (e.g. Sutherland, 1981). The variance of fish and benthic communities associated with sampling date subsumes variation associated with both recruitment and sampling error. The variance attributable to sampling date of fish and benthic communities was minor compared to variance attributable to fishing intensity; we suggest that the recruitment of fish or benthos did not contribute significantly to their observed community structures over the duration of this study. This raises the possibility that recruitment may also be less important relative to fishing intensity for structuring coral reef epifaunal communities. However, we caution that direct measurement of the effects of fish benthic and epifaunal recruitment would be required to test this possibility. A key limitation of our study is that an experimental manipulation would be required to confirm the causal links among rugosity, predation risk and epifaunal density. However, there are two fundamental constraints to confirming causality at the large spatial scale studied here. First, manipulating small-scale factors requires caging of substrata; this would be expensive and logistically difficult to construct and maintain in the required hierarchical design at such large spatial scales (Vadas, 1985; Raffaelli and Moller, 2000). Second, large-scale influences, such as fishing and recruitment, cannot be manipulated experimentally; in this situation the only available test for causality is a comparative one, as was performed here (Petraitis and Latham, 1999). Finally, we only examined the role of fishing as a causal factor in determining fish and benthic community structures; we have not examined the importance of nutrient input or island-scale oceanographic factors, which may also have the capacity to influence coral reef communities.

4.1. Factors influencing motile epifaunal density

The density of motile epifauna is known to be a function of either substrate complexity (rugosity), algal biomass (habitat quality) and recruitment success (Bailey-Brock et al., 1980; Lobel, 1980; Vadas, 1985; Carpenter, 1986; Klumpp et al., 1988; Klumpp and Polunin, 1990). The only study which examined the relative importance of these factors concluded that algal biomass was the major determinant of epifaunal density at small scales (<4 km) (Klumpp et al., 1988). Our data were consistent with this finding; at the smaller spatial scale algal biomass was the major determinant of motile epifaunal density. However, at the larger spatial scale rugosity was the most important determinant, and explained 99% of the variation in the density of small motile epifauna. Why should rugosity be an important determinant of epifaunal density? We

suggest that rugosity is a measure of epifaunal shelter availability or refugia from predation. Rugosity is strongly related to more direct measures of shelter availability such as the size of holes in the substrate (Friedlander and Parrish, 1998). Predation generally appears to have an important structuring role on coral reefs; shelter availability is a major determinant of coral reef fish community structure at large spatial scales (e.g. Caley and St. John, 1996; Friedlander and Parrish, 1998). Adult fish abundance is strongly determined by predator density and refuge availability, and the importance of shelter availability is underscored by the finding that juvenile survivorship of fishes is enhanced by providing more complex substrata (Beukers and Jones, 1998). Therefore, rugosity can be thought of as an indirect measure of predation risk or top-down control upon motile epifauna. If this assumption is valid, then top-down factors were a more important predictor of the density of small motile epifauna than bottom-up factors such as algal biomass at large spatial scales. To the best of our knowledge, scale dependence in the processes structuring the density of community components has not been described. However, it is becoming clear that diversity of communities is structured in a scale-dependent manner (Willis and Whittaker, 2002), so the finding of scale-dependent structuring of density is not unexpected.

If predation risk were a major structuring force of epifaunal communities, then one would predict that the reduction of fish biomass along the fishing gradient would lead to higher densities of motile epifauna via prey release. Predatory release of motile epifaunal prey is a prerequisite for the existence of a potential trophic cascade involving epifauna. There was no evidence for prey release and epifaunal densities did not vary with fishing intensity in this study (Fig. 10A); therefore, at these light fishing intensities, it is also unlikely that epifauna is involved in a trophic cascade. The absence of prey release suggests the reduction in predator biomass may be insufficient to invoke prey release or a consequence of the absence of any link between fishing intensity and rugosity at these light levels of fishing pressure. In more heavily exploited systems, fishing is known to reduce substrate complexity by facilitating the proliferation of bioeroding herbivorous urchins (McClanahan and Muthiga, 1988; McClanahan, 1992). The absence of a link between rugosity and fishing intensity is possibly due to the relatively low density of grazing urchins in this study, which is a tenth or less (< 1 urchins m^{-2}) than found in heavily fished coral reef systems, such as found in the Caribbean and also in East Africa (c. 10 urchins m^{-2}) (Carpenter, 1986; Lessios, 1988; McClanahan and Shafir, 1990; McClanahan and Kurtis, 1991; McClanahan, 1994; McClanahan and Mutere, 1994). The urchin densities in Fiji are possibly insufficient to measurably reduce substrate complexity at the comparatively low fishing intensities studied, but the potential for prey release of epifauna and a trophic cascade role should be borne in mind where fishing pressure is sufficiently high to influence substrate complexity.

4.2. Factors influencing motile epifaunal richness

Ultimately, understanding the forces structuring motile epifaunal diversity will be challenging because almost nothing is known of their life histories, dispersal strategies and niche ecology (Carpenter, 1986; Klumpp et al., 1988). The class richness and diversity of motile epifauna were independent of the structure of plate algal communities. This

evidence combined with the known rapid colonisation (<2 weeks) suggests the epifaunal communities on settlement plates reflected the larger benthic epifaunal pool (e.g. Caley and Schluter, 1997). Assuming this is true, then we can examine three possible explanations for monotonic decline in epifaunal class richness and diversity along the fishing intensity gradient, namely differential vulnerability, exploiter-mediated coexistence and decline in habitat quality. Larger-bodied animal species tend to have lower intrinsic population growth rates and lower resilience to mortality and would be expected to suffer most under a disturbance regime (Collie et al., 2000; Frisk et al., 2001; Reynolds et al., 2001). In these Fijian fishing grounds, increased fishing intensity should be associated with reduced predation pressure upon motile epifauna, unless there is an extra trophic group between target fishes and the motile epifauna. Therefore, large-bodied epifauna should exhibit elevated density at the most heavily fished grounds. However, there is no clear sign of increased densities of larger epifaunal classes (e.g. malacostracan crustaceans and gastropods) at the most heavily fished grounds (Table 5), which suggests the ‘differential vulnerability’ mechanism does not underlie the observed reduction in epifaunal richness and diversity. The second mechanism is exploiter-mediated coexistence, in which diversity is structured or maintained by frequency-dependent mortality; the most abundant taxa are preyed in proportion to their abundance, facilitating the coexistence of competitively inferior taxa (Lubchenco, 1978; Menge, 1995). At heavily fished grounds, the lower density of invertivorous fishes (and potentially lower predation) could have increased the dominance of competitively superior motile epifaunal taxa at the expense of less competitive taxa—resulting in a decline in motile epifaunal richness and diversity—which was consistent with the pattern described here. Another possible explanation for the change in epifaunal class richness and diversity is the change in the ‘habitat quality’ of the surrounding benthic community. Coral reef benthic communities are highly heterogeneous on a very small scale of <1 m (N.K. Dulvy, unpublished data) and a reduction in patch heterogeneity of surrounding habitat would be expected to result in lower diversity (Austen et al., 1998). Hard-coral cover declined and turf-algal cover increased along the fishing intensity gradient and the variation in benthic community structure was statistically correlated with the change in fish community structure. However, at present we cannot explain the causal mechanism(s) underlying this statistical link. The increase in motile epifaunal habitat (turf algae) on the coral reef and the possible homogenisation of benthos would be expected to result in a proliferation of primary colonising motile epifaunal taxa—which is also consistent with the pattern described here.

The spatial variance of abundance and diversity and the underlying structuring processes are not only of fundamental importance; spatial scaling is also a practical issue. If we are to understand and manage environmental impacts at large spatial scales, the analyses of underlying processes must be applied at the appropriate scale. Inferences drawn from small-scale studies may be erroneous because larger-scale structuring processes are not necessarily predictable from an understanding of small-scale processes (Willis and Whittaker, 2002). Finally, management must be feasible at the appropriate spatial scale. Fortunately, management can directly influence predator density at large scales through restricting fishing effort or the implementation of no-take zones, but not algal abundance, except by managing watersheds to reduce nutrient inputs.

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Appendix 1

Fish species in UVC, maximum lengths (cm) and tropic category (co—corallivore, he—herbivore, in—invertivore, om—omnivore, pi—piscivore, pl—planktivore, to—territorial omnivore, uf—urchin feeder).

Acanthuridae *Acanthurus albipectoralis* 33 pl, *A. blochii* 42, *A. guttatus* 26 he, *A. lineatus* 38 he, *A. nigricans* 21 he, *A. nigricauda* 40 he, *A. olivaceus* 35 he, *A. pyroferus* 25 he, *A. thompsoni* 27 pl, *A. triostegus* 26 he, *A. xanthopterus* 56 he, *Ctenochaetus binotatus* 22 he, *C. striatus* 26 he, *C. strigosus* 18 he, *Naso brevirostris* 60 pl, *N. caesius* 60 pl, *N. hexacanthus* 75 pl, *N. lituratus* 30 pl, *N. tuberosus* 60 pl, *N. unicornis* 70 pl, *N. vlamingii* 50 pl, *Zebrasomsa scopas* 20 om, *Z. veliferum* 40 om.

Balistidae *balistapus undulatus* 30 uf, *Balistoides conspicillum* 50 in, *B. viridescens* 75 uf, *Melichthys vidua* 35 om, *Rinecanthus rectangulus* 30 uf, *Sufflamen bursa* 24 uf, *S. chrysopterus* 30 uf, *S. fraenatus* 38 uf.

Chaetodontidae *Chaetodon auriga* 23 in, *C. baronessa* 15 co, *C. bennetti* 18 co, *C. citrinellus* 13 in, *C. ephippium* 23 in, *C. flavirostris* 20 C. *kleinii* 14 in, *C. ornatissimus* 20 co, *C. pelewensis* 12 in, *C. plebeius* 15 in, *C. quadrimaculatus* 16 co, *C. rafflesii* 15 in, *C. reticulatus* 16 co, *C. trifascialis* 18 co, *C. trifasciatus* 15 co, *C. ulietenis* 15 in, *C. unimaculatus* 20 in, *C. vagabundus* 23 in, *Forcipiger flavissimus* 22 in, *F. longirostris* 22 in, *Hemitaurichthys polylepis* 18 pl, *Heniochus acuminatus* 25 pl, *H. chrysostomus* 18 co, *H. monocerus* 23 in, *H. singularius* 25 in, *H. varius* 19 in.

Diodontidae *Diodon hystrix* 90 uf.

Haemulidae *Plectorhinchus chaetodonoides* 72 in, *P. obscurus* 100 uf, *P. picus* 84 uf.

Kyphoside *Kyphosus cinerascens* 45 he.

Labridae *Anampses caeruleopunctatus* 42 uf, *A. neoguinaicus* 15 in, *A. twistii* 18 in, *Bodianus anthiodes* 21 in, *B. axillaris* 20 in, *B. diana* 25 in, *B. loxozonus* 47 in, *B. mesothorax* 19 in, *Cheilinus chlorourus* 45 in, *C. fasciatus* 38 in, *C. oxycephalus* 17 in, *C. trilobatus* 45 uf, *C. undulatus* 229 in, *Coris aygula* 120 uf, *C. gaimard* 38 uf, *Epibulus insidiator* 35 pi, *Gomphosus varius* 28 in, *Halichoeres hortulanus* 27 in, *H. margaritaceus* 13 in, *H. marginatus* 17 in, *Hemigymnus fasciatus* 50 uf, *H. melapterus* 50 uf, *Labrichthys unileatus* 16 co, *Macrophargodon meleagris* 14 in, *Oxycheilinus diagrammus* 30 pi, *O. unifasciatus* 46 uf, *Pseudocheilinus hexataenia* 7 in, *P. octotaenia* 12 uf, *Stethojulius*

bandanensis 16 uf, *Thalassoma amblecephalum* 14 in, *T. hardwicke* 20 in, *T. janseni* 20 pi, *T. lutescens* 30 uf, *T. quinquevittatum* 16 uf.

Lenthrinidae *Gnathodentex aureolineatus* 24, *Lethrinus atkinsoni* 45 uf, *L. erythracanthus* 70 uf, *L. nebulosus* 86 uf, *L. olivaceus* 100 uf, *Montaxis grandoculis* 60 uf.

Lutjanidae *Aphareus furca* 40 pi, *Aprion virens* 100 in, *Lutjanus bohar* 90 pi, *L. fulviflamma* 35 pi, *L. fulvus* 40 pi, *L. kasmira* 35 pi, *L. monostigma* 53 pi, *L. russelli* 50 pi, *L. semicinctus* 35 pi, *L. vitta* 40 pi, *Macolor macularis* 55 in, *M. niger* 66 in.

Monacanthidae *Aluterus scriptus* 110 in, *Amanes scopas* 16 in, *Cantherhines dumerilii* 38 in, *C. pardalis* 25 in, *Oxmonacanthus longirostris* 12 co, *Pervagor melanocephalus* 10 in.

Mullidae, *Mulloidichthys vanicolensis* 38 uf, *P. bifasciatus* 35 in, *P. ciliatus* 38 in, *P. cyclostomus* 50 in, *P. miltifasciatus* 30 in.

Nemipteridae *Scolopsis bilineatus* 23 in.

Ostraciidea *Ostracion meleagris* 16 in.

Pomacentridae *Plectroglyphidodon dickii* 11 to, *P. johnstonianus* 9 to, *P. lacrymatus* 10 to, *Pomacentrus bankanensis* 9 to, *P. vaiuli* 9 to, *Stegastes fasciolatus* 15 to, *S. lividus* 13 to, *S. nigricans* 13 to.

Scanridea *Cetoscarus bicolor* 80 he, *Chlorurus frontalis* 50 he, *Hipposcarus longiceps* 60 he, *Scarus alptipinis* 60 he, *S. chameleon* 31 he, *S. dimidiatus* 30 he, *S. forsteni* 55 he, *S. frenatus* 47 he, *S. ghobban* 75 he, *S. globiceps* 27 he, *S. longipinnis* 40 he, *S. niger* 35 he, *S. oviceps* 30 he, *S. psittacus* 30 he, *S. rubroviolaceus* 70 he, *S. schlegeli* 38 he, *S. sordidus* 40 he, *S. spinus* 30 he.

Serranidae *Anyperodon leucogrammicus* 52 pi, *Cephalopholis argus* 40 pi, *C. leopardus* 24 pi, *C. urodeta* 27 pi, *Epinephelus fuscoguttatus* 90 pi, *E. hexagonatus* 26 pi, *E. howlandi* 44 pi, *E. maculatus* 50 pi, *E. polyphekaion* 75 pi, *Gracila albomarginata* 40 pi, *Plectropomus areolatus* 73 pi, *P. laevis* 110 pi, *P. leopardus* 70 pi, *P. maculatus* 70 pi, *Variola louti* 80 pi.

Siganidae *Siganus doliatus* 24 he, *S. punctatus* 40 he, *S. stellatus* 35 he, *S. uspi* 24 he.

Tetraodontidae *Aronthron mappa* 65 in, *A. nigropunctatus* 33 uf, *Canthigaster valentini* 10 he.

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