



## Relative importance of habitat and fishing in influencing reef fish communities across seventeen Pacific Island Countries and Territories

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### Abstract

Reef fish assessments were undertaken in 17 Pacific islands to describe the status of finfish resources in 63 villages where fishing is mainly artisanal. Surveys were performed by recording the number and size of edible fish species and benthic composition. Fishing impact was described through six proxies representing level of catch, alternative incomes, degree of commercial catch and country economic development derived from a simultaneous socioeconomic assessment. The relative importance of broadly defined habitat (geographical location, island and reef type, substrate composition) and fishing impact in controlling the distribution of fish trophic groups, families and species was measured through multivariate analysis. The extreme faunistic diversity was shown by the large variation in fish density (difference of up to an order of magnitude) and fish biomass (displaying a 20-fold difference across the region). Herbivores were dominant in the eastern part of the region, at what we classified as complex islands and at islands with small lagoon and at coastal reefs, while carnivores were dominant at oceanic islands and atolls and at outer reefs. Specific habitat associations were shown for Scaridae, Acanthuridae, Siganidae, Balistidae, Lethrinidae, Lutjanidae and Serranidae. Relative importance and size decrease of several fish families (Mullidae, Scaridae, Lutjanidae and Serranidae) were related to high fishing impact. Acanthuridae and Lethrinidae appeared to have a role as opportunistic groups in impacted sites. The relative impact from fishing and habitat on fishes accounted for, respectively, 20 and 30% of variance, demonstrating the effect of human impacts even at such large scale and taking into account only limited fishing impact variables.

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## Introduction

Coastal fisheries in Pacific Island countries and territories (PICTs) continue to support livelihoods and food security for millions of people. The average annual per capita consumption of fishes in PICTs ranges from 16 to 140 kg, covering 5–26% of total annual energy needs (M. Kronen *et al.* unpublished data). Reef fisheries are also important because of their social value to millions of people in terms of employment, traditions, community activity and more (Medley *et al.* 1993). However, information on the status of coastal resources and the sustainability of the present exploitation rates for the whole PICTs covering area is lacking. Managing coral reef fisheries in the Pacific Island region in the absence of such scientific information presents a major challenge. It is for this reason and because of the importance of sustainably managing their inshore fisheries that 17 PICT governments expressed an urgent need for information on the status of their coastal resources. Two parallel projects, the Pacific Regional Oceanic and Coastal Fisheries Development Programme (PROCFish) and the Pacific Regional Coastal Fisheries Development Programme (CoFish) funded by the European Union, were undertaken to address this need. The data acquired by these two projects represent the source for the first comprehensive multicountry baseline comparative assessment of reef fisheries (on both natural resources and human components) ever undertaken

in the Pacific Island region. The study used a standardized methodology in 63 sites (Fig. 1).

Owing to the lack of reference points for such a baseline study, defining fisheries resource conditions is a difficult task. This difficulty is amplified by the extremely wide geographical scale. The project sampling design comprises an area of  $9000 \times 4000$  km and habitat variables fluctuate considerably within such a large space; latitudinal and longitudinal gradients, as well as geomorphology and physical structure of islands and their coralline components at both large and intermediate scales, are primary causes of variability in coral reef fish communities (Mellin *et al.* 2009). Moreover, the potential impact from artisanal fishing on the composition and structure of fish communities may vary greatly because of the high diversity of social conditions throughout the region: distinct customs and social patterns in the different islands result in different fishing necessities, practices and preferential species targeted. Therefore, we envision that environmental variability, including geographical gradients, geomorphological type of island, reef and benthic composition, will act not only by directly influencing the fish communities but also by being one of the causes of variable levels of fishing impact imposed by different groups of people on the fish resources.

We studied the relative importance of natural and anthropogenic effects in influencing fish resources through a partition of variance in fish community structure. The major objectives of this study were to

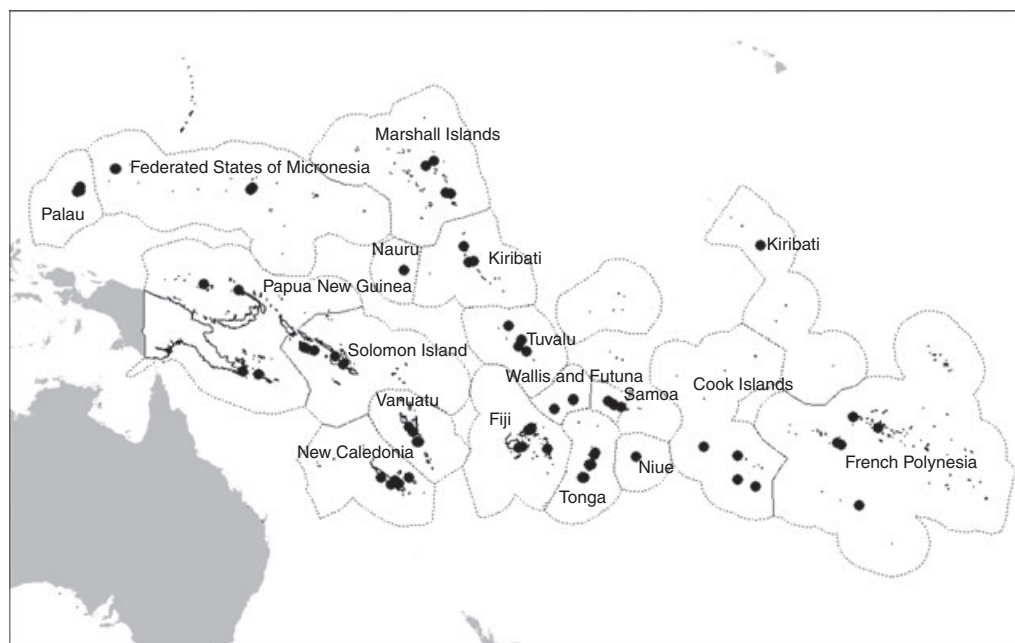


**Figure 1** Study region showing countries and sites (indicated by dots).

partition the role of habitat and people at different spatial scales and thus to provide useful information for fisheries managers. Data from anthropogenic impact were derived from the parallel study on socioeconomic conditions published by Kronen *et al.* (2010a,b) and recorded at the same 63 sites as part of the PROCfish and CoFish projects.

## Methods

### Site selection

A total of 63 sites in 17 PICTs were studied in the region, spreading from Palau in the west to French Polynesia in the east and from the Marshall Islands in the north to Tonga in the south (Fig. 1). In general, four sites or fishing villages were selected in each PICT, based on government recommendations and logistic constraints. However, five were chosen in the larger territories of New Caledonia and French Polynesia, while small PICTs (Niue, Nauru, Wallis and Futuna) were sampled in their entirety.

### Habitat definition

For the present work, habitat is defined as a combination of types of islands, types of reefs and substrate variables.

### Large-scale habitat – geography and Island type

Geography refers to the geographical location of sites indicated by their longitudinal and latitudinal positions. Islands were classified into four different schematic morphological types, based on their geological development and complexity of reefs (i.e. the extent and number of types of reefs and lagoon present) and following a description compiled by South *et al.* (2004): (i) islands with low reef complexity (here for simplicity indicated as ‘oceanic’), characterized by young fringing reefs that can be almost exposed at low tide and steep outer slopes; sometimes they might present shallow and small reef flat pools; this category includes systems with lagoon still forming; (ii) islands of medium reef complexity (here indicated as ‘islands with small lagoon’) with only small lagoons and a barrier reef further from shore; (iii) islands of higher complexity (here indicated as ‘complex islands’), including an extended barrier reef, a back reef, an intermediate reef and a deep and large lagoon; they might include sea grass beds and mangroves; (iv) atolls, generally the latest stage of a tropical island formation, characterized by a barrier reef at the perimeter and a well-developed central lagoon with some motus and submerged reefs; the land is made of old reef or beach rock and no native rocks are present.

*Medium-scale habitat – reef types*

Given the high diversity of reef types sampled, the different reefs were clustered into four broad categories: (I) coastal reefs (protected fringing reefs not far from land, along the coast), (II) intermediate lagoon reefs (patch reefs), (III) back reefs (on the inner lagoon side of barrier reef) and (IV) outer reefs (on the ocean side of fringing or barrier reefs). Sampling was stratified by these four simplified reef types with at least six transects per reef type at each site. Surface cover of each reef type within the fishing ground defined by the villagers of each site was calculated using (i) satellite images from Millennium Coral Reefs Landsat Archive, (ii) geomorphological Millennium Coral Reef Mapping products derived from Landsat imagery (Andréfouët *et al.* 2006) and (iii) *in situ* information from divers. The reef areas were then used as weight to calculate the values of weighted average fish density and biomass at site level.

*Small-scale habitat – substrate variables*

Substrate composition was assessed at each transect using the medium-scale approach described by Clua *et al.* (2006). The method consists of recording substrate parameters within twenty 5 m by 5 m quadrats located on both sides of the transect. Substrate information was then used at the scale of the site by calculating the weighted average of per cent cover of live coral, dead coral, rubble, sand, boulders, bedrock, soft algae and encrusting algae and of the ratio between hard and soft substrates, by using reef areas as averaging weights.

**Fish counts**

To assess edible finfish resources, distance sampling underwater visual census (Labrosse *et al.* 2002) was used, where species name, abundance, body length and distance of each fish or group of fishes from a 50-m transect are recorded up to the distance of maximum visibility. A total of twelve divers counted fishes at the 63 sites. Each diver underwent intense training prior to assessment consisting of *in situ* species identification and size and distance estimation at training sites throughout the region. Moreover, an estimation of visibility before each dive was performed by referring to the maximum distance at which the writing slate was visible along the tape. This analysis only included data on fishes within a distance of 5 m on each side of the transect. Only fishes of the most common edible species that can be

recorded underwater with good precision were counted. These belong to 11 major families: Acanthuridae, Balistidae, Holocentridae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Scaridae, Serranidae (Epinephelinae), Siganidae and Zaclidae. Fishes were assigned to four major trophic guilds – herbivores, invertebrate feeders, planktivores and piscivores – according to their most common diet, as recorded on FISHBASE (Froese and Pauly 2004) and from Kulbicki *et al.* (2005). The number of fishes counted was used to calculate density and biomass at each site. Weight of each individual was estimated using length–weight relationships (Kulbicki *et al.* 2005). Biomass ( $\text{g m}^{-2}$ ) was estimated using these weights.

**Fishing impact proxies**

The fishing impact matrix obtained from parameters gathered during the socioeconomic study included five variables at the community level: (I) total population and (II) total number of boats in each community as proxies for the level of finfish catch, (III) total yearly catches ( $\text{tonnes year}^{-1}$ ) as a direct measure of extraction, (IV) percentage of households with primary income from a salary to characterize the level of alternative and viable income sources, and (V) easiness of marketability as a proxy for the degree of commercial finfish catch (Kronen *et al.* 2010a,b); a further variable, the percentage of urbanized population at the national scale, was selected as a surrogate for overall economic development (Kronen *et al.* 2010a,b). These proxies were the most significant in explaining catch rates from a regionwide socio-economic analysis that included all 63 sites surveyed. It can therefore be concluded that they are of regional relevance and represent the best choice of proxies for this study.

**Data analysis**

One-way analyses of variance (ANOVAS) were calculated to test the differences in total reef surface areas, proportion of extension of reef types and cover areas of substrate descriptors among the fishing grounds of different island types and among reef types. Assumptions for ANOVA were met with variable transformation. A subset of the habitat descriptors at different scales were used as an explanatory matrix in the multivariate analysis. All possible subsets of the regression model selection

(Seber and Lee 2003) were applied to pick the subset of variables that best predict the logarithmic value of total fish biomass, using Akaike's Information Criterion to choose the optimal number of variables. A habitat matrix of 14 variables was thus obtained. All parameters (Table 1) were log-transformed or given extra quadratic terms (latitude and longitude) and then standardized to be used in ordinations to determine relationship between the faunistic assemblage and the habitat.

Relative fish density and biomass were calculated as density and biomass values of species, family and

trophic guild relative to the site average value of density and biomass of all fishes counted. Size was reported as the average value for each family.

Redundant analysis (RDA, terBraak and Smilauer 2002) on site density, size and biomass values of trophic groups, families and most abundant and frequent species (present in >80% of transects, Table 2) was computed to identify correlations of the faunal composition with the habitat.

Relative density and biomass of the 16 most important species were also analysed through linear multiple regressions on the standardized habitat

**Table 1** List of selected large-scale habitat variables used on the analysis, including transformed variables to linearize some of them.

| Definition and number of transformed parameters | Abbreviation                          | Unit of measure                                                                    |
|-------------------------------------------------|---------------------------------------|------------------------------------------------------------------------------------|
| Latitude                                        | lat1, lat2                            | Described by 2 values each for linearization of the variable                       |
| Longitude                                       | long1, long2                          | Described by 2 values each for linearization of the variable                       |
| Island types                                    | Atoll; Compl_isl;<br>Sml_lag; Oceanic | Described by binary values (presence/absence for each site)                        |
| Live coral cover                                | Live coral                            | Percentage cover of live coral as averaged among the four reef types for each site |
| Relative hard bottom cover                      | Hard bottom                           | Ratio percentage cover of hard bottom vs. soft bottom as average for each site     |
| Importance of coastal reef                      | Coastal                               | Percentage area covered by coastal reefs                                           |
| Importance of lagoon reef                       | Lagoon                                | Percentage area covered by lagoon reefs                                            |
| Importance of back reef                         | Back                                  | Percentage area covered by back reefs                                              |
| Importance of outer reef                        | Outer                                 | Percentage area covered by outer reefs                                             |

Compl\_isl, complex islands, i.e. islands of high reef complexity; Sml\_lag, islands with small lagoons, or islands of intermediate reef complexity; Oceanic, oceanic islands or islands of low reef complexity.

**Table 2** Species selected for the multivariate analysis owing to their frequency of presence (>80% of transects) and abundance.

| Family       | Species                          | Common name                  |
|--------------|----------------------------------|------------------------------|
| Acanthuridae | <i>Acanthurus lineatus</i>       | Striped surgeonfish          |
|              | <i>Acanthurus nigricauda</i>     |                              |
|              | <i>Acanthurus triostegus</i>     | Convict surgeonfish          |
|              | <i>Naso lituratus</i>            | Orangespine unicornfish      |
| Serranidae   | <i>Cephalopholis argus</i>       | Peacock grouper              |
| Labridae     | <i>Cheilinus chlorourus</i>      | Floral wrasse                |
| Lethrinidae  | <i>Monotaxis grandoculis</i>     | Bigeye emperor               |
| Mullidae     | <i>Parupeneus multifasciatus</i> | Multibanded goatfish         |
| Scaridae     | <i>Chlorurus microrhinos</i>     | Pacific steephead parrotfish |
|              | <i>Chlorurus sordidus</i>        | Bullethead parrotfish        |
|              | <i>Ctenochaetus striatus</i>     | Striped bristletooth         |
|              | <i>Scarus frenatus</i>           | Bridled parrotfish           |
|              | <i>Scarus ghobban</i>            | Bluebarred parrotfish        |
|              | <i>Scarus niger</i>              | Swarthy parrotfish           |
|              | <i>Scarus psittacus</i>          | Palenose parrotfish          |
|              | <i>Scarus schlegeli</i>          | Schlegel's parrotfish        |

matrix to measure the importance of habitat in controlling the community composition richness and the distribution and importance of such species.

To measure the relative importance of fishing activity and habitat on the structure of the fish community, partition of variance with partial principle component analysis, RDAs and partial RDAs (PRDAs) (Borcard *et al.* 1992) were calculated using CANOCO for Windows 4.5 (terBraak and Smilauer 2002) to extract the percentage of the variance in trophic, family and species composition that would be explained by the 14-variable habitat matrix and by the six-variable fishing impact matrix.

Although the fish density and biomass, and the substrate variables were measured at the transect level, the fishing, biogeographic and reef area variables were available at the village level. The relationships documented here between fishes and substrates are therefore at the latter higher spatial scale.

## Results

### Natural environmental conditions

The 63 sites illustrated a high geographical variation in island types (Table 1, Fig. 2). The highest vari-

ability in island types was found in the south; sampled complex islands were more concentrated in the west, while sampled atolls were more abundant in the north and east. Presence and composition of reefs varied considerably as well, showing a variation in available total reef area between 1 and 188 km<sup>2</sup> with a noticeably higher area towards the west and south-west. In this part of the region, there was also a higher presence of reef habitats. Sites at complex islands and atolls had higher cover of reefs available to fishing grounds compared with sites at islands with small lagoons and oceanic islands ( $P_{ANOVA} < 0.01$ , Fig. 3a). Sites located on complex islands and islands with small lagoons had higher percentage surface cover of coastal reefs compared with the other island types ( $P_{ANOVA} < 0.01$ ). Sites on complex islands also displayed larger percentage of lagoon reefs ( $P_{ANOVA} < 0.01$ ), while sites located on atolls had the largest percentage of back reefs ( $P_{ANOVA} < 0.01$ ) and sites on oceanic islands had the largest percentage of outer reefs ( $P_{ANOVA} < 0.01$ ). Back reef habitats displayed a larger proportion of area compared with coastal, lagoon and outer reef habitats available as fishing ground ( $P_{ANOVA} < 0.01$ , Fig. 3b).

Sites on atolls and complex islands had the highest percentage of live coral ( $P_{ANOVA} = 0.02$ ,

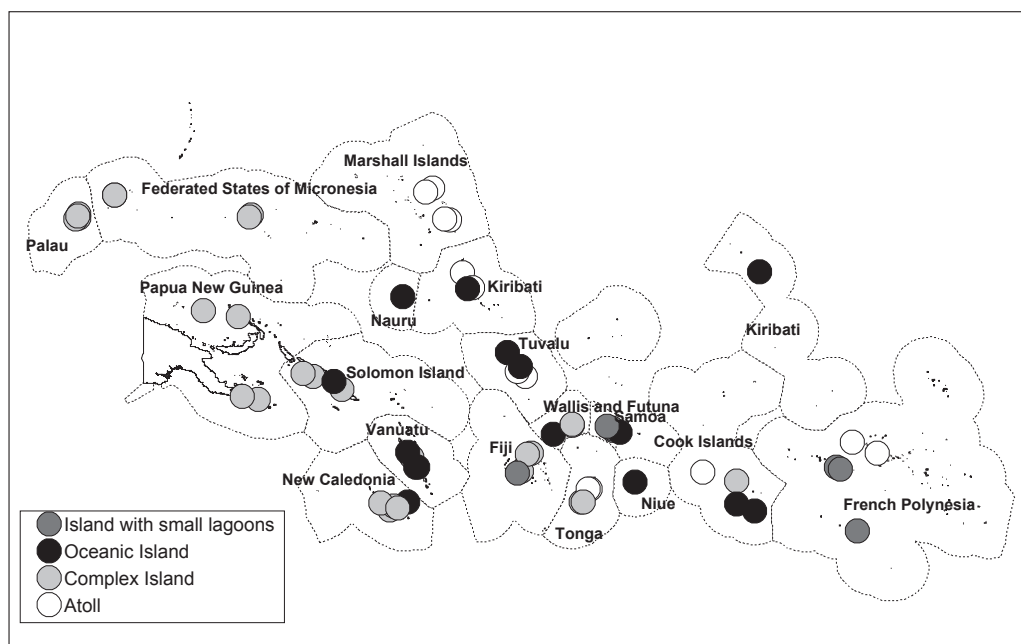


**Figure 2** Sites identified by island type, in order of decreasing age: atoll, complex island, island with small lagoon, oceanic island.

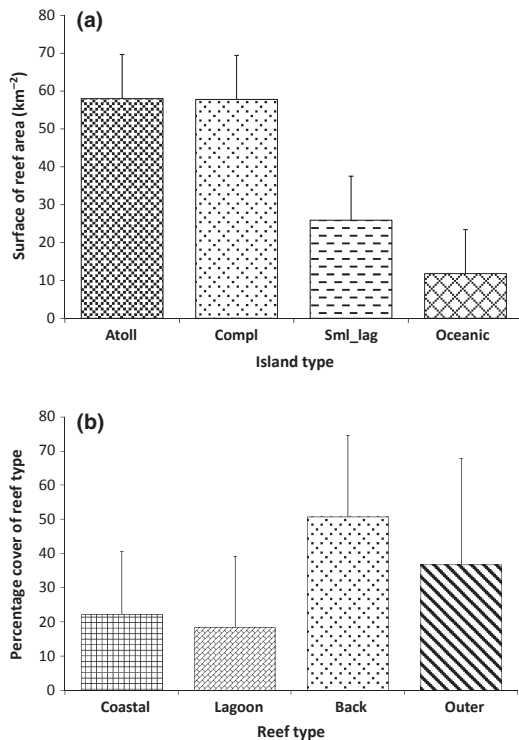


**Figure 3** Average and standard deviation of total reef areas in the four island types (a,  $P < 0.01$ ) and average and standard deviation of percentage cover of the four reef types throughout the region (b,  $P < 0.01$ ). Compl, complex islands; sml\_lag, islands with small lagoons.

Fig. 4), while sites on oceanic islands had the lowest percentage. Sites on complex islands also had the highest amount of rubble ( $P_{ANOVA} < 0.01$ ). Sites on

islands with small lagoons had the highest percentage cover of dead coral ( $P_{ANOVA} = 0.02$ ).

To summarize, at the large scale, it appears that sites located on oceanic islands and, to a lesser extent, islands with small lagoons are poorer compared with the sites on other island types in terms of presence and diversity of reefs, while sites located on complex islands and atolls have the richest reef environments, with a larger surface covered by reef, a larger variety of habitats and the largest cover of live coral (Table 3).

Cover of live coral and bedrock were significantly higher ( $P_{ANOVA} < 0.01$ ) and sand was significantly lower ( $P_{ANOVA} < 0.01$ ) at outer reefs. Soft algae did not show significant differences between the four reef habitats; however, encrusting algae had significantly ( $P_{ANOVA} < 0.01$ ) higher cover at outer reefs, but lower cover at back reefs, and the lowest cover at lagoon and coastal reefs.

#### Fish abundance and composition

The total sample size was 571 254 fishes recorded in 162 436 observations. A total of 91 commercial genera and 392 species were counted along a total of 1459 transects.

The mean number of surveyed fish species per transect was 37, with the range extending between 21 and 60. Average species density was 152 species per site, with values ranging between 93 and 239 species per site.

Four species were ubiquitous throughout the region, i.e. they were counted at all sites: Striped

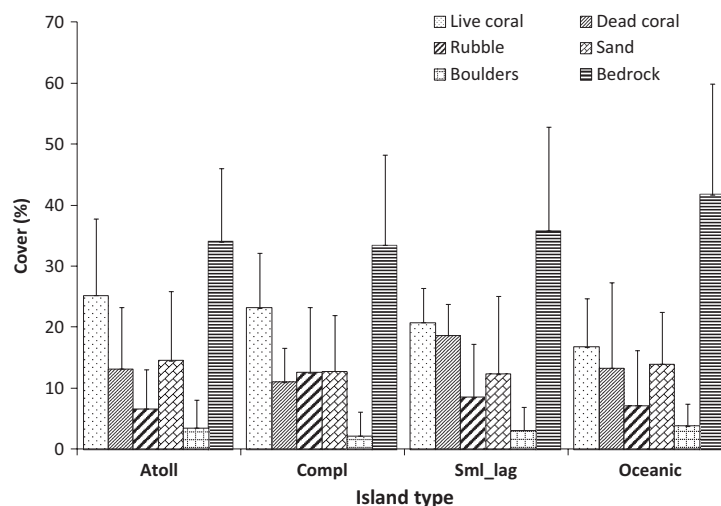


**Figure 4** Average and standard deviation of percentage cover of different substrate categories at the four island types.

bristletooth (*Ctenochaetus striatus*, Acanthuridae), Orangespine unicornfish (*Naso lituratus*, Acanthuridae), Multibarred goatfish (*Parupeneus multifasciatus*, Mullidae) and Moorish idol (*Zanclus cornutus*, Zanclidae). The most abundant species were Striped bristletooth, Bullethead parrotfish (*Chlorurus sordidus*, Scaridae), Striped surgeonfish (*Acanthurus lineatus*, Acanthuridae), Whitecheek surgeonfish (*Acanthurus nigricans*, Acanthuridae), Convict surgeonfish (*Acanthurus triostegus*, Acanthuridae), Palenose parrotfish (*Scarus psittacus*, Scaridae) and Humpback snapper (*Lutjanus gibbus*, Lutjanidae).

The mean regional value of weighted average density of edible finfish by site was 0.6 fish m<sup>-2</sup>, with minimum value of 0.2 fish m<sup>-2</sup>, a maximum value of 1.8 fish m<sup>-2</sup> and a standard deviation of 0.3 fish m<sup>-2</sup> (Fig. 5a). Mean weighted average biomass was 118 g m<sup>-2</sup>, with a minimum value of 17 g m<sup>-2</sup>, a maximum value of 363 g m<sup>-2</sup> and standard deviation of 78 g m<sup>-2</sup> (Fig. 5b). As many as 41 sites (65% of all sites) were below this average value.

Throughout the region, density and biomass were dominated by herbivores; they accounted for an average of 65% of total fishes counted (Fig. 6a). Second in importance were invertebrate feeders, then planktivores and piscivores. All carnivores together represented on average 35% of total density and biomass of all edible fishes; the figures varied between 8 and 82% of total density and between 11 and 81% of total biomass.

The 11 families had very different importance in composing the average regional and individual site density and biomass. The most relevant families when considering the regional average were Acanthuridae (39% of total biomass), Scaridae (25% of total biomass) and Lutjanidae (11% of total biomass, Fig. 6b).

#### Relative importance in structuring the fish community played by habitat and fishing as described by socioeconomic proxies

Through the combined use of RDAs and PRDAs, we obtained a partition of variance in trophic groups and families owing to habitat, fishing, fishing mediated by habitat and unexplained causes. The variability in the relative density of trophic groups caused by the combined effect of fishing and habitat (variance explained by both the direct effect of fishing and the combined effect of habitat and fishing on fish assemblages) was 15% of the total,

while 29% of total variance was attributable to the intrinsic effect of habitat (Fig. 7a). Comparatively, fish size appeared to be more influenced by fishing: 22% of total variance of average size of the four trophic groups was attributable to the combined influence of fishing and habitat and 38% was attributable to the direct influence of habitat. Variance in the relative biomass of trophic groups explained by the combined effect of fishing and habitat was 12%, while 39% was attributable to habitat alone acting directly on the fishing community.

The variance in the relative density and biomass of 11 selected fish families that was explained by the combined effects of habitat and fishing was 20 and 22%, respectively, while variance explained by habitat alone was 30% in both cases (Fig. 7b). Total variance in family size explained by habitat alone was 36%, while only 17% was related to the compounded effects of habitat and fishing impact.

The percentages of variance in the relative density and biomass of 16 selected fish species explained by habitat and fishing combined were 14 and 19%, respectively, while percentages of variance explained by habitat alone were 38 and 35%, respectively.

#### Interrelationship between habitat and the fish community

Analysis of direct relationship of density and biomass of trophic groups with habitat variables partialling out fishing impact showed that invertebrate feeders were more important than the other trophic groups at sites with large back and lagoon reefs but less important and smaller at sites located to the east and those with a high percentage of hard bottom. Piscivores and planktivores were more abundant than other groups at sites located on oceanic islands and atolls and at sites with large outer reefs and a high percentage of live coral, but less important at sites located on complex islands and sites with large coastal reefs. Herbivores were more abundant than other groups at sites located to the east and on islands with small lagoons and complex islands and sites with large coastal reefs, but they were less abundant than other groups at sites located on atolls and oceanic islands, sites with large back and outer reefs and those with a high percentage of live coral (Table 4).

The analysis of relationships of density, size and biomass of families with habitat when fishing effects

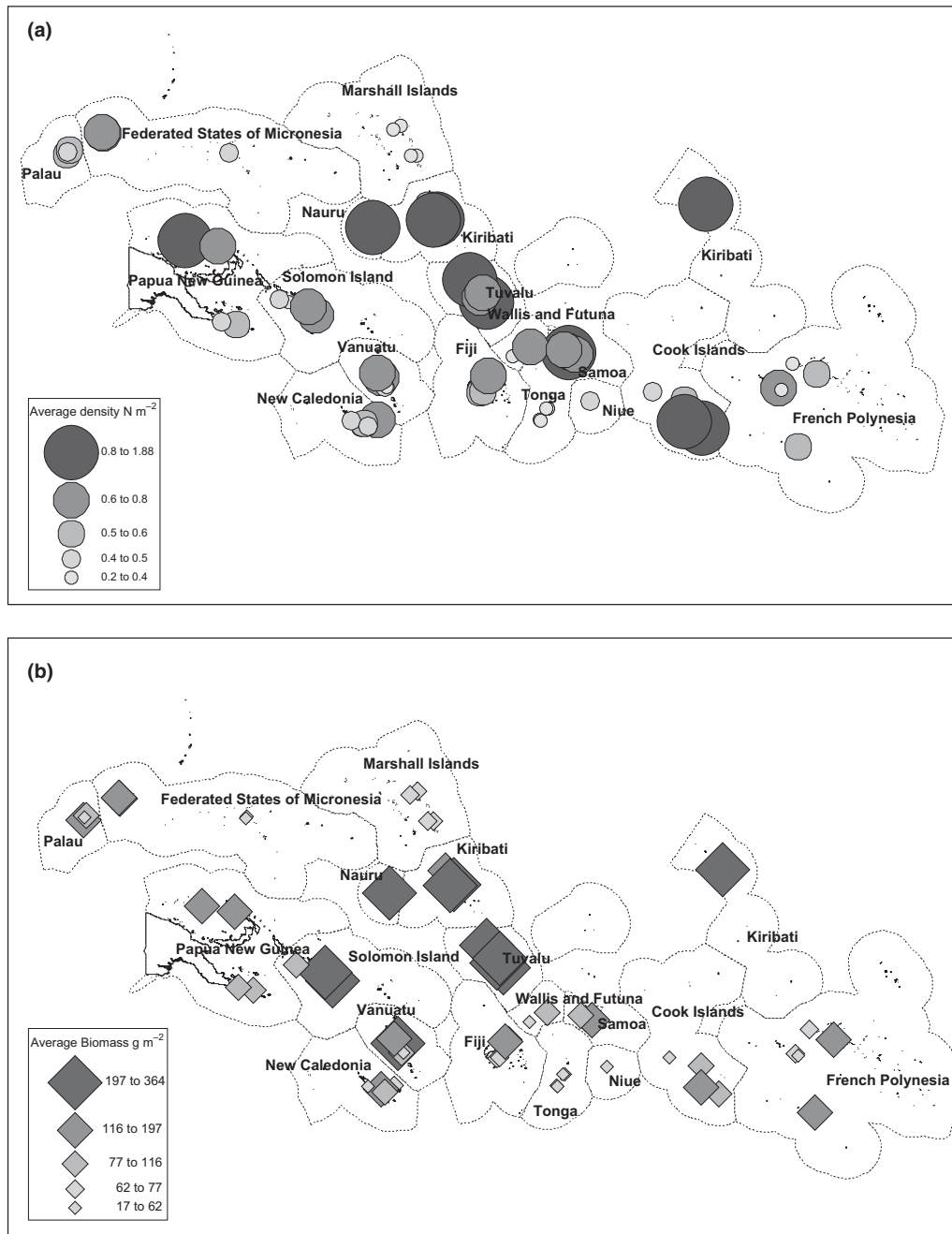


**Figure 5** (a) Values of weighted average density for all sites. (b) Values of weighted average biomass for all sites.

were partialled out showed that Acanthuridae were positively related to sites towards the east, to oceanic islands and to sites with large percentage area of hard bottom and were negatively related to complex islands and sites with large lagoons and back reefs and those with high percentage of live coral (Table 5). Scaridae were positively related to

islands with small lagoons and sites with large coastal reefs, but negatively related to atolls and oceanic islands and sites with large outer reefs and those with high percentage of hard bottom. Siganidae were positively related to oceanic, complex islands and islands with small lagoon and sites with large coastal and lagoon reefs, but negatively

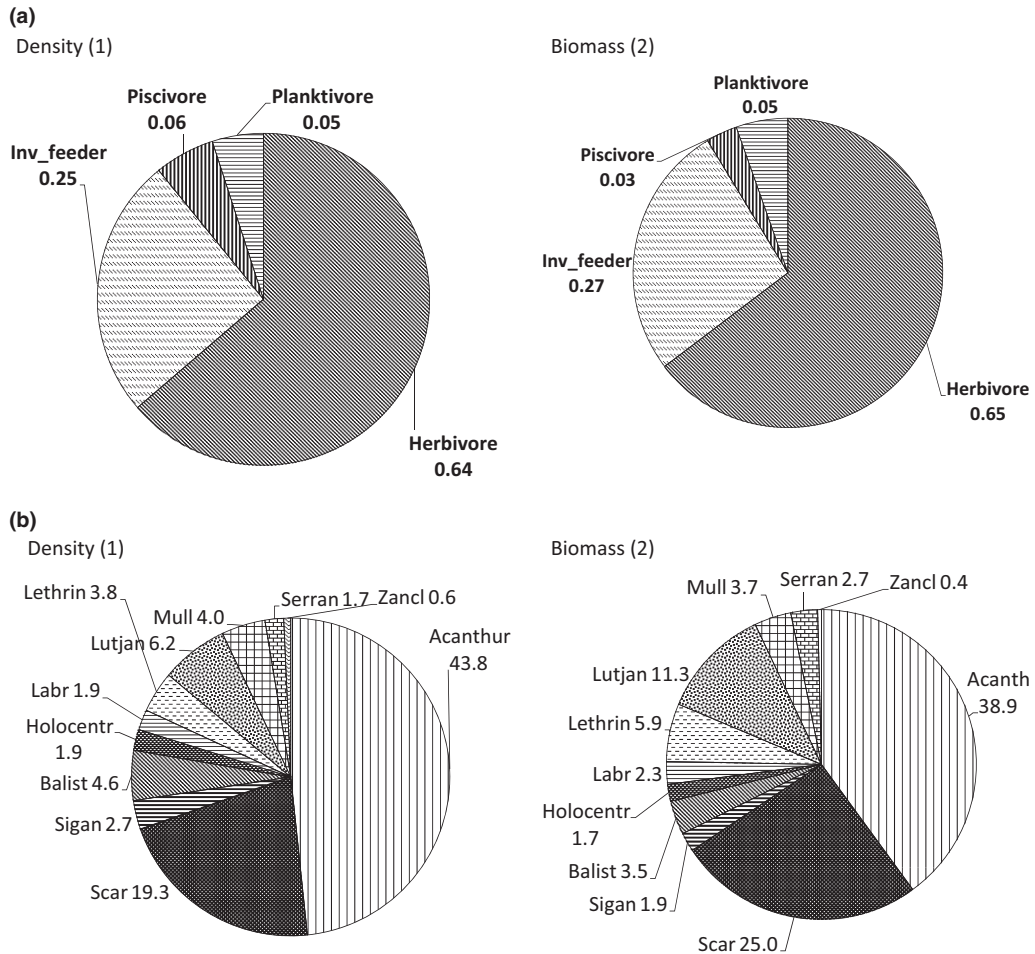


**Figure 6** (a) Relative density (1) and biomass (2) of the four trophic guilds. Values are calculated as regional mean of weighted average density and biomass by site. (b) Relative density (1) and biomass (2) for the 11 selected commercial families. Values are calculated as regional mean of weighted average density and biomass by site.

related to atolls and sites with large back and outer reefs and those with high percentage of hard bottom. Lutjanidae, Lethrinidae and Serranidae were positively related to atolls and sites with large outer reefs and high percentages of live coral, but negatively related to sites at the east, islands with small lagoons and sites with large coastal reef and high percentage of hard bottom. Balistidae were positively related to atolls and oceanic islands, but negatively related to islands with small lagoons and sites with large coastal reefs. Size of Acanthuridae, Scaridae and Lethrinidae was higher at oceanic islands, while size of Serranidae and Lutjanidae was larger at atolls.

Species richness and relative density and biomass of 4 of the 16 selected species showed a significant correlation with the habitat descriptors. Longitude

and latitude were significant explanatory variables for the number of species, as well as for the density of Convict surgeonfish. Specific island types characterized one species: both density and biomass of Bridled parrotfish (*Scarus frenatus*, Scaridae) were negatively related to atoll sites ( $P < 0.02$ ); particular reef types were preferred by three species: Ringtail surgeonfish (*Acanthurus blochii*, Acanthuridae; relative density was positively related to lagoon reefs and negatively related to back reefs,  $P < 0.01$ ), Bridled parrotfish (relative density and biomass were both positively related to back reefs,  $P < 0.01$ ) and Schlegel's parrotfish (*Scarus schlegeli*, Scaridae; biomass was positively related to coastal reefs,  $P < 0.01$ ). The density and biomass of Convict surgeonfish were negatively related to live coral cover ( $P < 0.01$ ).

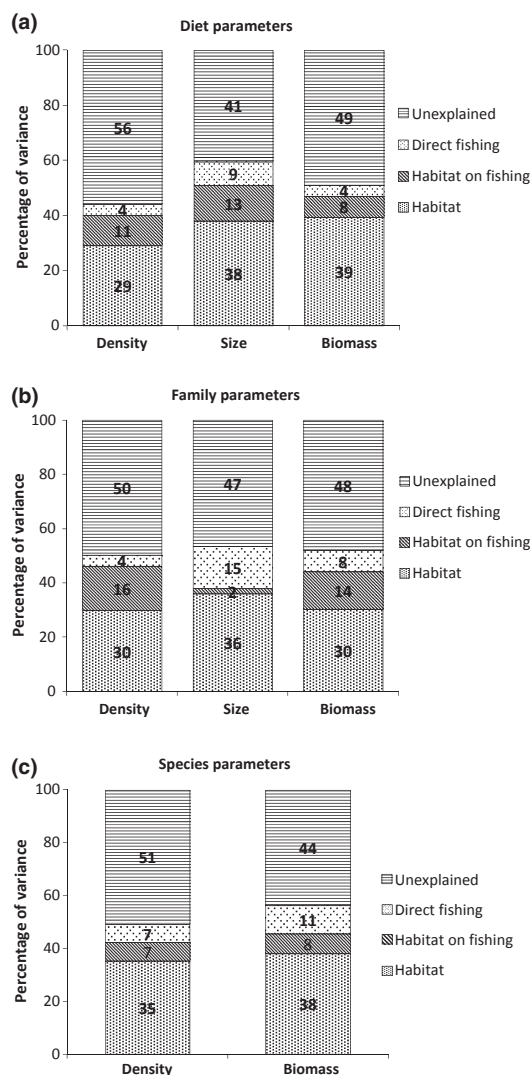


**Figure 7** Partition of percentage variance among the two main sets of explanatory variables, large-scale habitat and fishing pressure, of the relative biomass, density and average size of the four trophic guilds (a), 11 families (b) and 16 selected species (c). Total habitat effects, described by 14 parameters, are stronger than fishing pressure, described only by six major parameters, in explaining variability in density, biomass and size of the four trophic groups.

### Interrelationships between fishing and the fish community

The direct relationship of density and size of the four diet groups with fishing was obtained through RDAs and PRDAs where the influence of habitat was partialled out: less abundant planktivores and less abundant and smaller piscivores and invertebrate

**Table 3** Characteristics of the four island types – total surface area of fishing grounds, reef habitats and percentage cover of live coral, dead coral and rubble – that are higher in a particular island type compared with the others.

|                          | Total fishing ground | Reef habitats   | Live coral | Dead coral | Rubble |
|--------------------------|----------------------|-----------------|------------|------------|--------|
| Oceanic                  |                      |                 | –          |            |        |
| Island with small lagoon |                      | Coastal         |            | +          |        |
| Complex island           | +                    | Coastal, lagoon | +          |            | +      |
| Atoll                    | +                    | Outer, back     | +          |            |        |

Empty cells, non-significant.

feeders were associated with higher populations and numbers of boats. Smaller sizes of piscivores, invertebrate feeders and herbivores were associated with higher total annual catches. Larger piscivores were associated with higher percentages of urban population at a national scale. Less relatively abundant and smaller herbivores were associated with easier marketability and higher percentages of households with primary income from a salary.

When considering families, higher relative abundance of Acanthuridae and Lethrinidae and lower relative density of Scaridae and Siganidae (Fig. 8a, Table 6), as well as smaller sizes of Scaridae, Lutjanidae and Serranidae, were associated with higher percentages of urban population on a national level. Lower relative density and biomass of Siganidae and Scaridae, but higher relative density of Acanthuridae and Lethrinidae and higher relative biomass of Mullidae were associated with higher percentages of households earning primary income from a salary. Higher relative biomass of Acanthuridae, lower relative density of Mullidae and smaller sizes of Lutjanidae and Serranidae were associated with higher total annual catches (Fig. 8b). Lower relative density of Scaridae and Siganidae and lower biomass of Siganidae and lower sizes of Lutjanidae and Serranidae were associated with easier marketability (Fig. 8b).

**Table 4** Association of relative density, relative biomass and average size of diet groups with habitat variables (PRDA vs. habitat, influence of fishing partialled out).

|                | Herbivore |   |   | Invertebrate feeder |   |   | Planktivore |   |   | Piscivore |   |   |
|----------------|-----------|---|---|---------------------|---|---|-------------|---|---|-----------|---|---|
|                | D         | B | S | D                   | B | S | D           | B | S | D         | B | S |
| Geography      |           |   |   |                     |   |   |             |   |   |           |   |   |
| Latitude       |           |   |   |                     |   |   |             |   |   |           |   |   |
| Longitude      | +         |   |   |                     | - | - |             |   |   |           |   | - |
| Island type    |           |   |   |                     |   |   |             |   |   |           |   |   |
| Oceanic isl.   |           | - | + |                     |   |   | +           |   |   | +         |   |   |
| Isl. sml. lag. | +         | + |   |                     |   |   |             | - |   |           | - |   |
| Complex isl.   | +         | + |   |                     |   |   | -           | - |   | -         | - |   |
| Atolls         | -         | - | + |                     |   |   | +           | + |   | +         | + |   |
| Substrate      |           |   |   |                     |   |   |             |   |   |           |   |   |
| Live coral %   | -         | - |   |                     |   | - | +           | + |   | +         | + | - |
| Hard bott. %   |           |   | + |                     | - | - |             | + |   |           |   |   |
| Reef types     |           |   |   |                     |   |   |             |   |   |           |   |   |
| Coastal        | +         | + |   |                     |   |   | -           | - |   | -         | - |   |
| Lagoon         |           |   | - |                     | + | + |             |   | - |           |   |   |
| Back           |           | - |   |                     | + |   |             |   |   |           |   |   |
| Outer          | -         | - | + |                     |   |   | +           | + |   | +         | + |   |

D, relative density; B, relative biomass; S, average size by family; empty cells, no effect.

**Table 5** Associations of major families with large-scale habitat descriptors (results from PRDA on relative density, biomass and size of the 11 selected families where influence of fishing is partialled out).

|              | Scaridae |   |   | Acanthuridae |   |   | Siganidae |   | Balistidae |   | Lutjanidae |   |   | Lethrinidae |   |   | Serranidae |   |   |
|--------------|----------|---|---|--------------|---|---|-----------|---|------------|---|------------|---|---|-------------|---|---|------------|---|---|
|              | D        | B | S | D            | B | S | D         | B | D          | B | D          | B | S | D           | B | S | D          | B | S |
| Geography    |          |   |   |              |   |   |           |   |            |   |            |   |   |             |   |   |            |   |   |
| Latitude     |          |   | + |              |   |   |           |   |            |   |            |   |   |             |   |   |            |   |   |
| Longitude    |          |   |   | +            | + |   |           |   |            |   | -          | - |   | -           | - |   | -          | - |   |
| Island type  |          |   |   |              |   |   |           |   |            |   |            |   |   |             |   |   |            |   |   |
| Oceanic      |          | - | + |              | + | + |           | + | +          | + |            |   |   |             | + |   |            |   |   |
| Sml. lag.    | +        |   |   |              |   |   | +         |   | -          | - | -          |   |   | -           |   | - |            |   |   |
| Complex      |          |   |   | -            |   |   |           | + |            |   |            |   |   |             |   |   |            |   |   |
| Atolls       | -        |   |   |              |   |   | -         |   | +          |   | +          | + | + | +           | + |   | +          | + | + |
| Substrate    |          |   |   |              |   |   |           |   |            |   |            |   |   |             |   |   |            |   |   |
| Live coral % |          |   |   | -            | - |   |           |   |            |   | +          | + |   | +           | + |   | +          | + |   |
| Hard bott. % | -        |   | + | +            | + |   | -         |   |            |   |            | - |   |             | + |   |            | - |   |
| Reef types   |          |   |   |              |   |   |           |   |            |   |            |   |   |             |   |   |            |   |   |
| Coastal      | +        |   |   |              |   |   | +         |   | -          | - |            | - |   |             | - |   |            | - |   |
| Lagoon       |          |   |   | -            | - |   |           | + |            |   |            |   |   |             |   |   |            |   |   |
| Back         |          |   |   | -            | - |   |           | - |            |   |            |   |   |             |   |   |            |   |   |
| Outer        | -        |   | + |              |   |   | -         |   |            |   | +          | + |   | +           | + | + | +          | + | + |

D, relative density; B, relative biomass; S, average size by family; empty cells, no effect.

Higher relative biomass and density of Striped surgeonfish, Palenose parrotfish and Orangespine unicornfish and lower relative biomass and higher

relative density of Convict surgeonfish and Bigeye emperor (*Monotaxis grandoculis*, Lethrinidae) were associated with higher community populations.

**Table 6** Main associations of families with fishing impact descriptors (results from analysis on relative density, biomass and size of the 11 selected families).

|               | Scaridae |   |   | Acanth. |   | Sigan. |   | Mullidae |   |   | Lutjanidae |   |   | Lethr. |   | Serr. |   |
|---------------|----------|---|---|---------|---|--------|---|----------|---|---|------------|---|---|--------|---|-------|---|
|               | D        | B | S | D       | B | D      | B | D        | B | S | D          | B | S | D      | S | B     | S |
| Total pop.    | –        |   | – | +       |   | –      |   |          |   |   |            |   | – | +      |   |       | – |
| No. boats     | –        | – |   | +       |   | –      | – |          |   |   |            |   | – | +      |   |       | – |
| % Urban pop.  |          | + | + | –       |   |        | + |          |   | – |            |   |   | –      | + |       |   |
| % HH 1st inc. | –        | – |   | +       |   | –      | – |          | + |   |            |   |   | +      |   |       |   |
| Catch         |          |   |   |         | + |        |   | –        |   |   |            |   | – |        |   | –     | – |
| Market. easy  | –        |   |   |         |   | –      | – |          |   |   | +          |   | – |        |   |       | – |

D, relative density; B, relative biomass; S, average size by family; Acanth., Acanthuridae; Sigan., Siganidae; Lethr., Lethrinidae; Serr., Serranidae; Total pop., total population at the site; No. boat, total number of boats in each community; % urban pop., percentage of urbanized population at the national scale; % HH 1st inc., percentage of households with primary income from a salary; catch, total yearly catches (tonnes year<sup>-1</sup>); Market. easy, easiness of marketability; empty cells, no effect.

Higher relative density and biomass of Striped bristletooth were associated with lower percentages of urban population at national scale.

## Discussion

This study showed that fish resources in the PICTs vary widely and are majorly affected by the highly variable geographical and environmental conditions measured at different scales, throughout the region, among islands and reef types. Although this might appear as common sense, because there is little reason why an isolated atoll would have the same production level or have the same intrinsic fish trophic or size structure than a large continental island, our data start to fill a void of evidence of such differences on a large geographical scale.

Our results indicate wide fluctuations in fish density and biomass, essential indicator of production (e.g. Clarke and Johnston 1999, Fukami and Morin 2003), linked to large-scale gradients. Fish density varied by almost an order of magnitude between the lowest and the highest extremes, while biomass was 20 times higher at the richest sites compared with the poorest ones. These results therefore illustrate, with previously lacking regional data, the statement by Newton *et al.* (2007) that sustainable production level depends on large-scale factors.

Among the large-scale habitat variables, position along the longitude axis was the major factor in separating species and organizing communities: a decrease in the number of species from west to east was highly significant, as expected from the knowl-

edge of rarefaction of species with increasing distance from the centre of biodiversity (e.g. Stehli and Wells 1971; Bellwood and Hughes 2001). However, our results show, in addition, that only <1% of all species (i.e. four species: *C. striatus*, *N. lituratus*, *P. multifasciatus* and *Z. cornutus*) was shared by all sites. Such an observation should be seriously taken into account when making comparisons of faunal compositions and status on a regional approach.

In addition, interaction between species, families and trophic groups, which is of high relevance for determining the diversity and production of fish communities and for identifying a level of status or stocks (Medley *et al.* 1993), was also found to vary considerably. Although in several cases herbivores were the dominant trophic group, while, in a restricted number of dispersed and diverse sites characterized by very low fishing level, piscivores represented a larger proportion of the biomass, both suggesting the well-documented negative effect of fishing on trophic structure (Pauly *et al.* 1998; Pinnegar *et al.* 2000; Dulvy *et al.* 2004), a geographical variation in the proportion of herbivores and carnivores independent from fishing was also proven by the present study. A significant increase in herbivores to the east and correspondingly a significant increase in carnivores to the west suggest that the proportion of trophic groups is not entirely controlled by fishing and that biogeography (Floeter *et al.* 2004; MacNeil *et al.* 2009) or large-scale factors like island size (as in Kulbicki *et al.* 2004) and type play an important role.

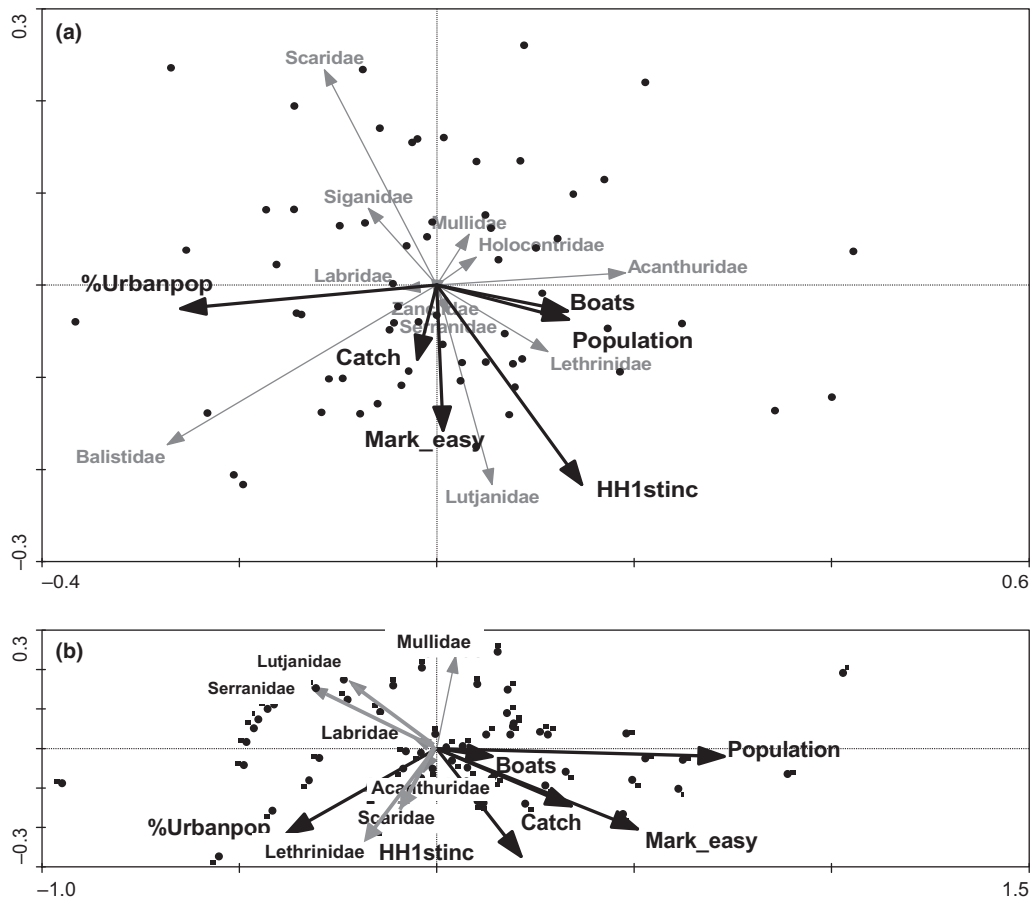


**Figure 8** PRDA on family density (a) and size (b) and fishing impact after excluding the influence of habitat. Relationships with the six fishing proxies are evident in the graphs. population, total population at the site; boats, total number of boats in each community; % urbanpop, percentage of urbanized population at the national scale; HH 1stinc., percentage of households with primary income from a salary; catch, total yearly catches (tonnes year<sup>-1</sup>); mark\_easy, easiness of marketability.

The spatial heterogeneity of habitat conditions in this study is remarkably significant, as can be expected considering the exceptional size of the area assessed. The 9000 × 4000 km area encompasses a high diversity of geomorphologic island types, which are under the effect of different climatic conditions as well as terrestrial and oceanographic inputs of nutrients. In turn, the typology of islands influences total reef area and the presence and composition of each reef type and their associated fauna. Total fishable reef area available to villages varies by two orders of magnitude and is higher at sites located in complex islands and atolls and in the west and south-west part of the region, where a higher presence of different reef types was also found. The sites located at oceanic islands, islands with small lagoons and complex islands present

large percentage surfaces of coastal reefs that are more directly under the terrigenous influence of both nutrients and pollutants. Their fish fauna was characterized by a high relative importance of Siganidae and Scaridae, compared with other fishes. On the other hand, atolls, with no inputs of nutrients from land, present large percentage surface of outer and back reefs but no coastal reefs. Atolls were characterized by the highest proportions of several carnivore families (Balistidae, Lutjanidae, Lethrinidae and Serranidae) as well as larger piscivores (Serranidae and Lutjanidae). In addition to geographical factors already mentioned, such proportions could be favoured by high coral cover and the autotrophy of oceanic reefs (e.g. Clavier and Garrigue 1999). Back reefs appeared to be the preferential habitat for invertebrate feeders, like

Lethrinidae and Balistidae, most probably because these reef habitats present more sand cover, a type of substrate where most of the species of this trophic group preferentially feed and hover.

However, association of specific fish families with different reef types should not be purely attributed to the preferential connection of some fish species to specific reef habitats; exposure should also be taken into account as a possible driving factor. In general, the four identified reef types show increasing exposure from coastal to intermediate to back and to outer reefs. The distribution of fishes in relation to exposure, as previously shown by Williams (1982, 1991), Williams and Hatcher (1983), Russ (1984), Ault and Johnson (1998), Friedlander and Parrish (1998), Syms and Jones (2000), Gust *et al.* (2001) and Gust (2002), is most probably due to the passive transportation of larvae unevenly carried by water movements in the differently exposed reefs and due to the specific choice of habitat for settlement as determined by wave action, illumination, depth, turbidity and presence of plankton (Williams and Hatcher 1983; Russ 1984; Williams *et al.* 1986; Hixon and Menge 1991; Hixon and Beets 1993).

Therefore, variation in island structure and reef types probably controls the level of production both directly, by limiting standing stocks via nutrient inputs, and indirectly, by affecting the number and quality of species that coexist, which in turn affects biomass production in itself (Williams 1983; Kulbicki *et al.* 2004; Cardinale *et al.* 2009).

The large variety of reefs (characterized by different surface area, exposure and composition) influences both the reef fish community structure and the fishing intensity, as differences in ease of access by fishers, depending also on the local availability of transportation, are one of the causes of different levels of subsistence fishing impact. As a consequence to such results, reef type and composition need to be taken into high account from both an ecological and a socioeconomical view point when comparing production of different locations in a fishing community.

The consideration of spatial heterogeneity at a smaller scale – at the station level – is especially relevant because of the characteristic high patchiness and discontinuity of coral reefs and associated fish abundance and community composition (Medley *et al.* 1993; Gust *et al.* 2001). The cover of live coral, often measured to assess the health of a reef community, was significantly higher, but also

most variable, at outer reefs. Live coral cover appeared to participate in controlling the distribution of some families, such as Lutjanidae, Lethrinidae and Serranidae, that depend on preys occurring more abundantly in association with live coral (Bell and Galzin 1984), as well as on the availability of shelter, which is often higher among healthy coral. Such findings should be carefully regarded in studies of the direct impact of climate change on live coral because of the possible negative effects it could have not only on coral-feeding fish but also on higher predators (Munday *et al.* 2008; Pratchett *et al.* 2008). Association of specific groups with live coral cover confirms what was shown at other locations, for example by Luckhurst and Luckhurst (1978), Carpenter *et al.* (1981), Bell and Galzin (1984), Bell *et al.* (1985), Findley and Findley (1985), Chabanet *et al.* (1997), Munday (2000), Gust (2002) and Wantiez and Chauvet (2003).

Herbivores (Scaridae and Acanthuridae), on the contrary, did not show a connection to live coral, in discordance with the usually positive correlation of live coral with abundance of fishes (Jones and Syms 1998). This could be probably explained by the fact that Scaridae do not display strict substrate requirements (Gust 2002) and comprise different species displaying stricter or looser coral associations (Gust *et al.* 2001) and because Acanthuridae preferentially browse on small turf growing on bedrock.

In addition to the profound causal relation to habitat, faunistic variability is also influenced by fishing and fishery-related human factors. Notwithstanding the large differences in habitat across the vast region, which controlled most of the variability (about 30%) in the fish community in terms of species richness and density, biomass and sizes at the level of species, family and trophic guild, a mere six indicators and proxies of fishing impact explained about 20% of the variability. Approximately half of this variation could be accounted for by the compounded effect of habitat and fishing, i.e. the differences in the nature of fishing activities (fishing techniques, culture, traditions etc.) related to location, island and reef type, while the other half was correlated with the direct effect of fishing impact on the fish community composition. More specifically, this means that global approaches such as offered by Newton *et al.* (2007) may give a false impression of a simple response of fish communities according to their production potential. Our results show clearly that we are confronted to a very complex situation with three levels of interaction between

resources, large- and local-scale habitat factors and fishing level. Therefore, adjusting this to a simple figure of production to separate sustainable from unsustainable production is very likely not correct.

The study also showed the well-known shift in species dominance with increase in fishing probably for the first time on such a wide geographical scale. Acanthuridae and some particular species such as Striped surgeonfish, Convict surgeonfish, Orange-spine unicornfish and Striped bristletooth appeared from the results to be opportunistic, increasing in relative abundance and biomass under higher fishing impact. Shifts in species dominance are a major concern in biodiversity loss; species may not easily disappear under the effect of fishing but may see their ecological impact drop drastically (Raffaelli 2006).

The results also showed that even some herbivorous species can be heavily impacted by fishing and that this factor acts in a complex way on the trophic structure of reef fish communities. Scaridae and Siganidae appeared to suffer the most from fishing impact, responding with lower relative density and biomass to more important fishing. Some carnivores displayed a more predictable negative response to fishing, as illustrated by the findings of lower density and smaller sizes among Mullidae and smaller sizes among Lutjanidae and Serranidae. The average sizes of these three major carnivore families could be used as easy-to-measure indicators to detect fishing impacts, as already suggested by Dulvy *et al.* (2004).

## Conclusion

Some of the previously missing information on the status of fish resources in Pacific Island countries and territories is filled by this first large-scale study. Although many studies have been carried out to determine the state of commercial fisheries resources and the level of the impact exerted by fishing (for example Pauly *et al.* 1998, 2003; Jackson *et al.* 2001; Hilborn 2002; Pauly 2002; Myers and Worm 2003; Rosenberg 2003; Daan *et al.* 2005; Mullan *et al.* 2005; Costello *et al.* 2008), very little attention has been given to the assessment of tropical coastal resources across the Pacific prior to the present research, except for the work by Dalzell *et al.* (1996). This study demonstrates how important it is to understand the natural variation in resources as related to environmental conditions at different spatial scales,

as recently shown by MacNeil *et al.* (2009), before analysing any possible effect from fishing. Environmental spatial variability produces fluctuations in fish species, populations and communities as well as their trophic relations and resulting fish stocks. Moreover, environmental variability is closely dependent on climate change, a matter of high urgency that must be now considered in any resource management decision (Friedmann and Wolff 2008; Munday *et al.* 2008).

Geographical variability is of fundamental importance when assessing the status of resources over large areas. In such an extensive area, the factor that showed the strongest influence on variability in the fish populations is location in terms of longitude and latitude. From the geographical patchiness of different types of islands in the Pacific area spring all differences in geomorphology, composition of coral-line structures and presence of different marine and terrestrial habitats affecting underwater production, described by fish abundance, biomass and community composition. Thus, if there is a need to manage resources at large spatial scales, for example in a regional or subregional coordinated recovery, conservation or development effort, it is necessary to consider the natural environmental conditions of each location to have the right measures of comparison and the right expectations. Similarly, local-scale management should take into account large-scale factors (like geomorphology and geographic location), which are still disregarded at the present time. Furthermore, in reef ecology studies at different spatial scales, for example examining relationships between reef fish structure (biodiversity, density, biomass and species associations) and habitat structure, strong consideration should be given to the variance driven by the impact of fishing practices (themselves related to diverse environmental situations) on fish populations, when not dealing with pristine systems.

In drawing conclusions about the level of fishing impacts and consequent conditions of the resources, one must keep in mind that the assessments were made as one-time visits. When the analysed parameters did not show clear trends associated with the fishing proxies used, this does not imply that fishing does not have strong direct impact on resources but only that the extent of the anthropogenic effects cannot be measured directly from such proxies, on such a large scale and without reference to previous or baseline conditions (Dalzell 1998; Pauly *et al.* 1998, 2003; Jackson *et al.* 2001; Hilborn 2002;

Pauly 2002; Rosenberg 2003). For instance, one site could already be under impact from fishing therefore at high risk of, or close to, collapse without showing signs of this in the parameters of fishing impact considered, as found, for example, by Labrosse *et al.* (2000) in New Caledonia. Alternatively, resources at a site under low fishing impact could be poor because of the site's naturally disadvantageous conditions, which might not be fully described by the parameters measured, as seen, for example, in French Polynesia by Mellin *et al.* (2006, 2008) and MacNeil *et al.* (2009).

The parameters used to define habitat at different spatial scales are only a very limited selection of the possible environmental factors affecting distribution and production of coral reef resources. Analysis of variables at similar spatial scales, such as currents and upwellings, temperature, nutrient inputs, primary productivity, sedimentation and bathymetry, would help improve the understanding of natural variability.

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