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# Exploitation and habitat degradation as agents of change within coral reef fish communities

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## Abstract

**Over-exploitation and habitat degradation are the two major drivers of global environmental change and are responsible for local extinctions and declining ecosystem services. Here we compare the top-down effect of exploitation by fishing with the bottom-up influence of habitat loss on fish communities in the most diverse of ecological systems, coral reefs. Using a combination of multivariate techniques and path analyses, we illustrate that the relative importance of coral cover and fishing in controlling fish abundance on remote Fijian reefs varies between species and functional groups. A decline in branching *Acropora* coral is strongly associated with a decline in abundance of coral-feeding species, and a decrease in coral-associated habitat complexity, which has indirectly contributed to reduced abundance of small-bodied damselfish. In contrast, reduced fishing pressure, brought about by declining human populations and a shift to alternate livelihoods, is associated with increased abundance of some piscivores and fisheries target species. However, availability of prey is controlled by coral-associated habitat complexity and appears to be a more important driver of total piscivore abundance compared with fishing pressure. Effects of both fishing and coral loss are stronger on individual species than functional groups, as variation in the relative importance of fishing or coral loss among species within the same functional group attenuated the impact of either of these potential drivers at the functional level. Overall, fishing continues to have an influence on Fijian fish communities; however, habitat loss is currently the overriding agent of change. The importance of coral loss mediated by climate change is expected to have an increasing contribution to fish community dynamics, particularly in remote locations or where the influence of fishing is waning.**

*Keywords:* climate change, density dependence, disturbance, food webs, trophic cascades

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## Introduction

Top-down and bottom-up control of populations is a central theme in ecology that is imperative to successful management of natural resources. The relative importance of these two processes is, however, spatially and temporally variable. For example, in temperate freshwater and hard substrate marine ecosystems, there is strong evidence for top-down control (Pinnegar *et al*., 2000); previous studies identifying keystone predators, which when removed, cause dramatic increases in prey and shifts in the ecosystem state (Estes *et al*., 1978) or diversity (Paine, 1966). Conversely, studies on the continental shelf and open ocean indicate that the influence of predators on prey abundance varies latitudinally, and systems at low latitudes, which are warmer and more diverse than those at higher latitudes, are more likely to be controlled by bottom-up processes (Worm & Myers, 2003; Frank *et al*., 2006). Even within the same system, the relative importance of top-down and bottom-up processes are temporally variable and liable to change

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with shifting regimes of exploitation and temperature (Wilmers *et al*., 2006; Frank *et al*., 2007).

In marine systems, fisheries exploitation typically targets larger individuals and species at higher trophic levels (Pauly *et al*., 1998) and is most likely to affect top-down processes, whilst disturbances that alter the availability of habitat resources will affect bottom-up processes. Over-exploitation and habitat loss account for >90% of all known marine population and species extinctions (Dulvy *et al*., 2003), emphasizing the importance of these disturbances within the marine environment. As human populations increase, the pressure on fish stocks from both fishing and habitat loss have increased, leading to increasing pressure on fishery resources (Newton *et al*., 2007). Moreover, loss of habitat induced by climate change may further exacerbate existing levels of stress on marine systems and fisheries (Hughes *et al*., 2003), and as the impacts of climate change are a relatively new phenomenon compared with over-exploitation, the full, long-term effects may be much greater than currently realized.

Coral reefs are particularly vulnerable to climate change, as the primary foundation species, scleractinian corals, are very susceptible to positive thermal anomalies (Hoegh-Guldberg, 1999). In 1998, high sea surface temperatures resulted in extensive coral mortality throughout the Indo-Pacific and the loss of 16% of the world's corals (Wilkinson, 2000). Over the past 30 years, coral bleaching, combined with other disturbances such as outbreaks of coral predators and disease, has led to regional declines of coral cover in the Caribbean (Gardner *et al*., 2003) and Indo-Pacific (Bruno & Selig, 2007). This loss of live coral represents a serious long-term threat to reef fish communities, as erosion of coral skeletons following coral mortality reduces the structural complexity of reefs, resulting in a decline in fish reliant on small refuges and overall diversity of fish communities (Garpe *et al*., 2006; Graham *et al*., 2006). Furthermore, many fish recruit directly to live coral, irrespective of adult habitat associations (Jones *et al*., 2004; Feary *et al*., 2007) and a loss of habitat, essential during early life history, may restrict the size of future adult stocks (Halpern *et al*., 2005; Graham *et al*., 2007).

Fishing is also prevalent on many of the world's coral reefs, with over-exploitation of fish stocks a common management dilemma. A recent analysis of coral reef fisheries on island countries found 55% are exploiting stocks in an unsustainable manner (Newton *et al*., 2007). The effects of fishing on fish communities and species may be direct and/or indirect. Direct effects at the species level include a decrease in abundance, biomass and size (Russ, 2002), whilst at a community level the size distribution of the assemblage may be altered (Dulvy *et al*., 2004a; Graham *et al*., 2005). Changes in size distribution of fish communities may also be attributed to indirect effects of fishing, as removal of predators can result in the release of small-bodied prey (Graham *et al*., 2003, 2005; Dulvy *et al*., 2004a). Some fishing techniques (e.g. blast and cyanide fishing) also cause severe habitat modification, often with detrimental consequences for fish diversity and abundance (Jennings & Polunin, 1996a).

Although fishing and habitat loss frequently occur concurrently on reefs, most studies examine the influence of these disturbances on fish communities in isolation. The few studies that have considered fishing and coral loss simultaneously have often failed to unequivocally identify the driver of changes in fish assemblages (e.g. McClanahan *et al*., 2002). Some studies identify changes predominantly due to fishing (McClanahan & Arthur, 2001; Grandcourt & Cesar, 2003), whilst others imply habitat (Grigg, 1994) and loss of coral are more important (Jones *et al*., 2004). Clearly, a key factor in determining the relative importance of fishing- vs. habitat-mediated disturbance is the extent of fishing pressure or habitat loss.

Here, we use a unique combination of multivariate techniques and path analyses to simultaneously assess the relative importance of fishing vs. coral loss to individual species, functional groups and the community structure of reef fish. The Lau Islands, Fiji, are an ideal location for this investigation. Reefs in this archipelago experienced severe bleaching in 2000 (Cumming *et al*., 2002) following outbreaks of the coral-feeding crown-of-thorns starfish (COTS), *Acanthaster planci*, in 2000 (Dulvy *et al*., 2004b). Variable levels of impact and recovery from these disturbances have resulted in a continuum of coral cover among islands. Furthermore, locally managed fishing grounds have measurably different levels of fishing pressure (Jennings & Polunin, 1995a, 1996b), which have been shown to influence the composition of local fish communities (Dulvy *et al*., 2004a), and destructive fishing techniques are not used by Lauan fishers (Dulvy *et al*., 2002), eliminating potentially confounding effects of fishing on habitat. Thus, the islands have a gradient of fishing pressure and coral cover, suitable for assessing the top-down impact of fishing, relative to the bottom-up effect of habitat changes on reef fish communities.

## Materials and methods

Extensive surveys of coral reef fishes and coral reef benthos were undertaken at five Lauan islands: Kabara, Matuku, Tavunasici, Totoya and Vuaqava, in the eastern division of Fiji, in 2000 and 2006. Each island represents a discrete fishing ground used for subsistence purposes by local villagers. At each island, fish and benthic surveys were carried out at three sites, in 2000, and again at the same geographical co-ordinates in 2006.

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Sites were located on the leeward (western) side of each island on the outer reef slope, at a depth of 7 m.

Abundance of 173 diurnal, noncryptic fish species, from 17 families, was estimated within six replicate point counts at each site. Surveyed fish included species from families targeted by Fijian fishers: lethrinids, lutjanids, serranids, acanthurids and scarids (Jennings & Polunin, 1995a, 1997), as well as species from families known to have strong habitat associations with coral: chaetodontids, pomacentrids, labrids and monocanthids (Wilson *et al*., 2006). Point counts of fish abundance were carried out within a cylindrical area of 7 m radius, encompassing a benthic area of approximately 154 $m^2$. Large mobile species were counted from outside the count area, before the area was thoroughly surveyed for other, more site attached, species. Any individuals entering the area once a count had started were excluded from abundance estimates.

Fish were placed into functional groups based on their diet and feeding behaviour (Froese & Pauly, 2007). Species known to have a strong association with live coral (Wilson *et al*., 2006) were categorized as coral dependant, which included obligate coral feeders (Pratchett, 2005), but excluded facultative coral feeders. Other functional groups were territorial and roving feeders of the epilithic algal matrix (EAM feeders), invertivores and piscivores (see Table S1 for full species list and functional group).

Benthic habitat was assessed within the same count areas used to assess fish communities. In 2000, 30 digital images were collected from each point count in a haphazard fashion. Each image covered approximately 500 $cm^2$ of benthos and microhabitat composition within each was later assessed from 20 random points. In 2006, benthos was assessed using point intercept transects. A 30 m tape was laid out in a haphazard fashion within and around each survey count area and microhabitat was recorded beneath 60 randomly marked points along each transect. Microhabitat categories used in both 2000 and 2006 were *Acropora*, *Pocillopora*, *Porites*, *Favids*, other living scleractinian corals, soft coral, *Millepora*, coralline algae, turf algae, macroalgae and sponges. Temporal comparisons were based on the proportional composition of the aforementioned taxa, which facilitated direct comparisons between surveys despite differences in sampling methodologies (Carleton & Done, 1995).

Topography and rugosity measures were used to assess the structural complexity of the benthos. Topographic measures provided an assessment of habitat complexity at the seascape level, whilst rugosity assessed complexity over a smaller spatial scale. Estimates of reef topography were made on a scale of 0–5, where reefs with no vertical relief were given a value of 0, and reefs with extremely complex habitats, with numerous caves and overhangs, were given a value of 5 (Polunin & Roberts, 1993). Rugosity was estimated by measuring the linear distance covered by a 3 m long chain fitted to the contours of the reef (Risk, 1972). Topographic and rugosity estimates were carried out within each count area, providing six estimates per site in both 2000 and 2006.

A fishing intensity index was calculated for each island, based on the number of people per linear km of reef front, following Dulvy *et al*. (2002). This index combines information on fishing behaviour and activity and correlates well with catch rates and estimates of reef fish yields (Jennings & Polunin, 1995a, 1996b). However, at some islands, there has been a shift to forms of subsistence other than fishing and an associated decline in fresh fish consumption (Turner *et al*., 2007). To account for differences in fish consumption, the fishing intensity index was modified to calculate the population size divided by the length of reef front, multiplied by the median weekly consumption rate of fresh fish per capita of local village households. Estimates of population size were obtained from the Lau provincial council, reef front was calculated from maps produced by Australian Aerial Mapping in 1994 and consumption rates were based on household surveys (Turner *et al*., 2007).

### *Statistical analyses*

Temporal and spatial variation in the abundance of fish within functional groups and total coral cover were analysed using repeated measures analysis of variance (ANOVA), with islands as a fixed factor. Abundance data were square-root transformed and percent coral cover arcsine transformed to meet the assumptions of homogeneity of variance and normality, which were assessed using Levene's test and residual plots. Any significant differences were investigated *post hoc* using Tukey's tests. Benthic composition of sites was further examined using principal components analysis (PCA), carried out on a correlation matrix of benthic and habitat complexity variables. Values for all environmental variables were normalized, allowing them to be compared on a common scale, and eigenvectors overlaid on a bi-plot of the first two components.

Fish assemblages at islands sites in 2000 and 2006 were compared using nonmetric multidimensional scaling (MDS) based on Bray–Curtis similarity measures. Data were fourth root transformed before analysis to reduce the influence of dominant species. Differences in fish assemblages between years were investigated using the nonparametric permutation procedure, ANOSIM. Significant differences were further

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assessed using SIMPER (Clarke & Warwick, 2001), which uses the average Bray–Curtis dissimilarity among samples to identify those species which contribute the most to differences between years. The percent contribution of species within functional groups was summed to indicate the relative importance of different functional groups in differentiating between fish communities in 2000 and 2006.

To assess which combination of environmental variables (benthic, habitat complexity and fishing intensity) best explained patterns in fish communities, Spearman's rank correlations between environmental and fish community matrices were calculated using BEST analysis with the BIOENV algorithm (Clarke & Warwick, 2001). Significance of correlations was tested with permutation tests.

The relative importance of coral cover and fishing intensity in driving the abundance of each of the functional groups and individual fish species were investigated using path analysis implemented in a structural equation modelling (SEM) framework. Path analysis is a method for partitioning relationships among variables on the basis of hypothetical pathways of interaction that are identified *a priori* (Elmhagen & Rushton, 2007). An *a priori* full model was developed for each functional group and fish species, with pathways and variables included depending on relevant ecological interactions. In all cases, the response variable was the average square-root abundance at each site for the group or species being examined. For path analyses we were explicitly interested in the relative importance of spatial differences in fishing and coral loss on fish abundance, rather than temporal changes in these potential drivers, hence time was not included as a model variable. However, for individual species, path analysis was only carried out on the five species within each functional group that contributed the most to temporal differences in MDS, as variation in abundance of these species was typically high.

All the potential paths used for the full models are shown in Fig. 1, but those actually included depended on the ecological characteristics of the species or functional group being examined. The full model was based on two alternative groups of pathways: (1) the bottom-up effects of habitat availability (coral cover; Fig. 1, paths c1–c4) and (2) the top-down effects of fishing (Fig. 1, paths f1–f2). For coral-related paths, it was assumed that coral cover would relate to both rugosity and topographic complexity. These measures of habitat complexity could then influence the response variables for specific fish functional groups and species. In addition, rugosity could affect abundance of small-bodied prey fish, and could, therefore, indirectly influence the abundance of piscivores. It was also

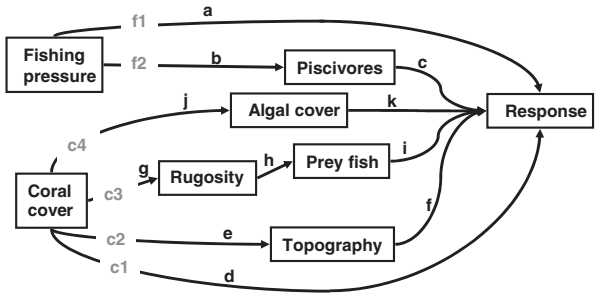


**Fig. 1** Paths used for the structural equation modelling (SEM) analysis. Fishing could influence the prey species via one of two alternate pathways (f1 and f2). A direct path between fishing and the response variable was only included for those species known to be targeted by Lau fishers (f1, path a). An indirect effect of fishing (f2) was included for all species that, based on body size, are potentially prey for fished species (paths b and c). Hard coral cover could influence the response variable via four potential pathways (c1–c4). A direct path between hard coral cover and the response variable (c1, path d) was only included for those species with a known dependence on live coral. For all models, an indirect pathway between coral cover and the response (c2) was formed via habitat topography or rugosity (paths e and f). For piscivorous species, there is an indirect pathway (paths g, h and i) between coral cover and the response, via rugosity and its potential effect on prey species (c3). For all EAM-feeding species, coral cover could indirectly influence the response variable via an effect on their food source, which is represented as algal cover (c4, paths j and k).

assumed that as benthic communities on reefs are space limited, coral cover would be inversely related to the cover of turf-forming algae, as turf rapidly colonizes space vacated by coral tissue following coral mortality (Diaz-Pulido & McCook, 2002). Turf-forming algae and associated detritus are also the primary food of EAM-feeding fishes (Choat, 1991; Wilson *et al.*, 2003) and changes in turf algae cover may influence abundance of these fish. Fishing effort is often determined by social factors and is not necessarily related to fish abundance or habitat, particularly in artisanal fisheries (Pet-Soede *et al.*, 2001; Abernethy *et al.*, 2007; Daw, 2008). Hence, fishing intensity was assumed to be independent of coral cover and was assumed to impact directly on all known fished species, as well as the abundance of piscivores, invertivores and roving EAM feeders. The total effect (TE) of top-down (fishing) and bottom-up (habitat) processes on the abundance of functional groups and species was calculated by multiplying the standardized coefficients within a pathway then summing these values for pathways associated with either fishing or habitat. All models were fitted in *R* using the SEM library (Fox, 2002). Goodness-of-fit and chi-squared values were used to assess the robustness of models.

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The type of habitat complexity measure used in models (topographic or rugosity) was determined based on the maximum observed body size of the functional group or species (calculated as an average across the sites). Topographic complexity was used for species with maximum sizes >20 cm, and rugosity for smaller species. For piscivorous fish, an indirect pathway between coral cover and the response, via rugosity and its potential effect on prey species was included (Fig. 1, c3). Rugosity was chosen here to represent habitat complexity for the prey species, because of their small size. Prey species abundance was the sum of all individuals counted that were below a critical 'prey' size, estimated to be 13 cm, which is 50% of the body length of the average-sized piscivore in counts. The relationship between predator/prey sizes was estimated by fitting a linear regression to the wide range of predator/prey size ratios presented in Scharf *et al.* (2000). Conversely, based on the same logic, piscivore abundance could influence abundance of species or functional groups considered potential prey.

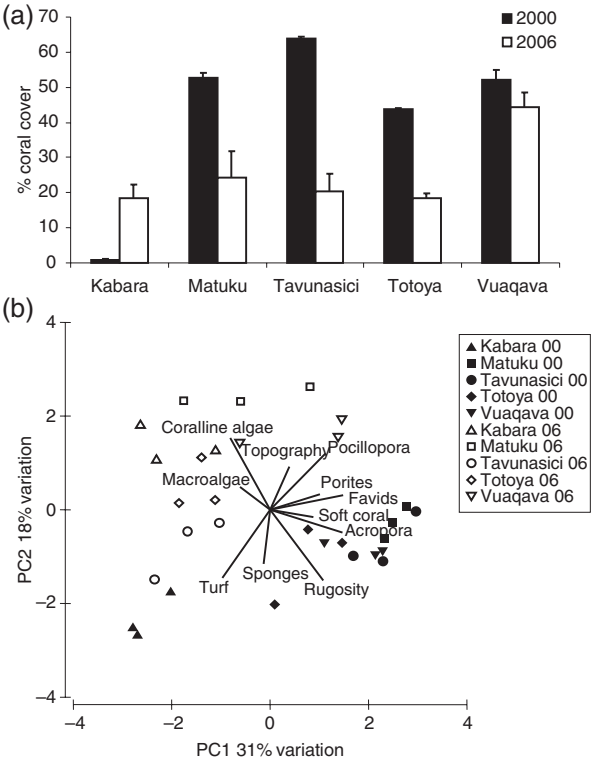


**Fig. 2** Spatial and temporal variation in (a) coral cover and (b) benthic composition on reefs within five Lau Islands. Average and standard error of coral cover calculated from three sites at each island. Benthic composition presented as bi-plot of first two components from principal component analysis, with normalized benthic and structural complexity variables presented as overlaid eigenvectors.

## Results

### *Spatial and temporal changes in benthos*

Total coral cover had changed markedly between 2000 and 2006, although the direction and extent of change varied among islands (islands × year interaction, $F_{4,10} = 26.2$, $P < 0.001$, Fig. 2a). At Matuku, Tavunasici and Totoya, coral had declined by 50–70%, and in 2006 was 18–24% at these islands. In contrast, coral cover at Kabara had increased from <1% to 18%, and was similar to 2006 coverage at the aforementioned islands. Coral cover at Vuaqava had remained relatively high (44%) compared with other islands and was similar to coral coverage in 2000.

Benthic communities in 2000 were mostly characterized by high cover of *Acropora*, *Faviidae*, *Porites* and *Pocillopora* corals and high levels of rugosity (Fig. 2b). At Kabara in 2000, live coral cover was <1% (attributed to local infestations of *A. planci*); however, mean rugosity at Kabara was 1.9, and similar to values recorded at other islands. In 2006, mean coral cover across all sites was 22% and reefs were dominated by macro and coralline algae. Moreover, all islands had lower rugosity than in 2000, although topography was similar to 2000 estimates. At Vuaqava, coral cover had remained high; however, the composition of the coral community had shifted and was characterized by *Pocillopora*, rather than *Acropora* corals, which were dominant in 2000.

### *Spatial and temporal changes in fishing pressure*

Fishing pressure at most islands declined between 2000 and 2006 (Table 1). The decline was greatest at Kabara and is attributable to a combination of reduced population size and a decrease in fish consumption (Turner *et al.*, 2007).

### *Spatial and temporal changes in fish communities*

Composition of fish communities in the five Lau Islands differed between the two sampling periods (ANOSIM, global $R = 0.859$, $P < 0.001$), an MDS plot revealing a distinct separation of sites surveyed in 2000 from those surveyed in 2006 (Fig. 3a). No single species contributed >3% to temporal differences in fish communities; however, when species contributions were summed as functional groups, the difference between years was driven by changes in the abundance of functional groups that are susceptible to coral loss or fishing (Fig. 3b).

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**Table 1** Spatio-temporal variation in fishing pressure

| | Fishing index | | | | |
|---|---|---|---|---|---|
| | Kabara | Matuku | Tavunasici | Totoya | Vuaqava |
| 2000 | 15.1 | 13.9 | 0.6 | 18.6 | 2.7 |
| 2006 | 4.6 | 8.3 | 0.6 | 15.4 | 0.7 |

Fishing index calculated as population per km of reef front multiplied by median weekly consumption rate of fresh fish per household.

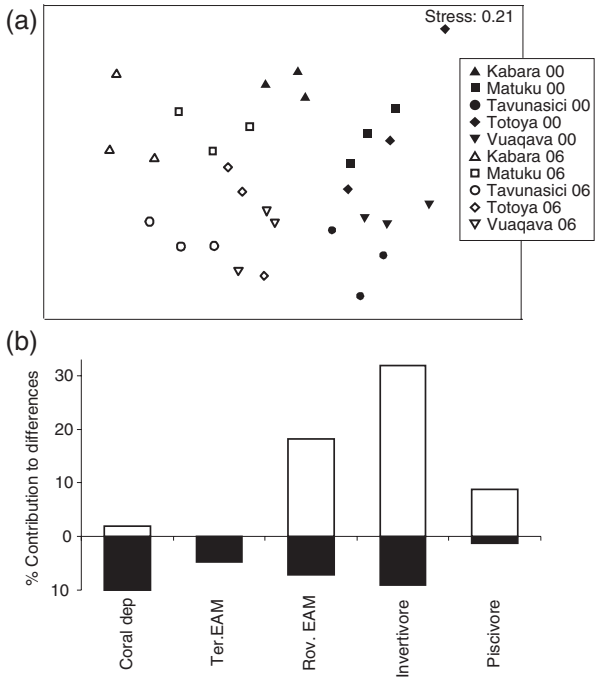


**Fig. 3** Spatial and temporal distribution of fish assemblages on reefs within five Lau Islands. (a) Nonmetric multidimensional (MDS) plot of fish assemblages at the five Lau Islands in 2000 and 2007. (b) Percent contribution by functional fish groups to temporal differences in Lau fish assemblages. Based on values from SIMPER analysis of species data used in MDS and calculated as the summed contribution of species within functional groups. Bars represent the summed contribution from species that were higher in abundance in 2000 (black) or 2006 (white).

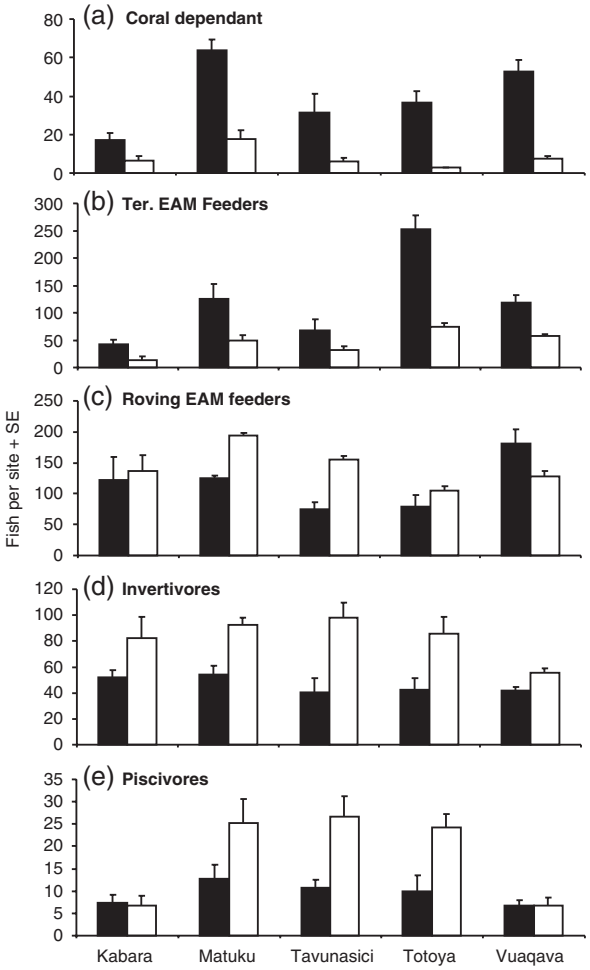


**Fig. 4** Spatial and temporal variation in abundance of functional fish groups on reefs within five Lau Islands. Average and standard error of abundance estimates calculated from three sites at each islands.

Abundance of coral-dependant species declined at all five islands (Fig. 4a, Table 2). Dramatic declines in this group can be attributed to reduced abundance of the coral-associated damselfish, *Plectroglyphidodon dickii* and *Plectroglyphidodon johnstonianus*, and obligate coral-feeding butterflyfish, such as *Chaetodon trifascialis*, although abundance of one coral-feeding species, *Chaetodon lunulatus*, increased following coral loss. Overall numbers of coral-dependant fish were lowest at Kabara, where coral cover was already negligible in 2000.

EAM-feeding fish represented a major proportion of the fish community, accounting for 45–70% of fish abundance estimates at the different islands; however, the relative contribution from territorial and roving species varied temporally. Abundance of territorial EAM feeders, which were all small-bodied pomacentrids, declined at all sites in 2006 (Fig. 4b, Table 2). In contrast, abundance of the larger bodied roving EAM feeders, which are primarily surgeon and parrotfish, had generally increased between 2000 and 2006 (Fig. 3c). Temporal changes in the abundance of roving EAM feeders were not consistent among islands and significant increases only occurred at Tavunasici and Matuku (Table 2).

The number of invertivore feeding and piscivorous fish also increased between 2000 and 2006 (Table 2, Fig. 4d and e). The invertivores were the most specious

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**Table 2** Statistical results from repeated measures analysis of variance (ANOVA) for each functional fish group

| | Islands | | Time | | Time × Islands | | |
|---|---|---|---|---|---|---|---|
| | $F_{4,10}$ | $P$ | $F_{1,10}$ | $P$ | $F_{4,10}$ | $P$ | Pairwise comparisons |
| Coral dependant | 4.3 | 0.007 | 59.1 | <0.001 | 1.7 | 0.231 | 2000 > 2006<br>Ma, Vu > Ka |
| Territorial EAM | 21.2 | <0.001 | 64.5 | <0.001 | 2.9 | 0.075 | 2000 > 2006<br>To > Vu, Ma, Ta, Ka; Vu, Ma > Ka |
| Roving EAM | 2.9 | 0.077 | 13.5 | 0.004 | 10.5 | 0.001 | Ma 2006 > Ma 2000<br>Ta 2006 > Ta 2000 |
| Invertivores | 2.5 | 0.110 | 33.2 | <0.001 | 1.2 | 0.358 | 2000 < 2006 |
| Piscivores | 12.8 | 0.001 | 11.8 | 0.006 | 2.4 | 0.120 | 2000 < 2006<br>Ma, Ta, To > Ka, Vu |

Pairwise comparisons from Tukey's test.
Ka, Kabara; Ma, Matuku; Ta, Tavunasici; To, Totoya; Vu, Vuaqava.

of all groups, accounting for 89/182 (49%) of species surveyed. Changes to the composition of this group accounted for 40% of the temporal variation in the fish community (Fig. 3b). Most invertivores (e.g. *Pseudocheilinus* species and *Parupeneus bifasciatus*) increased in abundance, although some (e.g. *Thalassoma hardwicke*) declined. Increases in piscivore abundance were most noticeable at Matuku, Tavunasici and Totoya, where the overall abundance of these fish was greater (Table 2, Fig. 4e).

A comparison of the fish community with environmental data found a combination of *Acropora* cover, fishing pressure and habitat rugosity were driving patterns in fish communities ($\rho = 0.511$, $P < 0.01$). However, when the analysis was restricted to single environmental variables, *Acropora* cover was the best predictor of change in fish communities, and explained a similar level of variation as the three-variable model ($\rho = 0.448$, $P < 0.01$).

### *Relative importance of fishing and coral loss to fish abundance*

In the path analyses, the relative influence of fishing pressure and coral cover as drivers for fish abundance varied between functional groups and among species within these groups (Table 3, Fig. 5). At a functional level, the TE of coral was clearly greater than fishing for coral-dependant and territorial EAM feeders, whilst the TE of fishing was greater for invertivores (Fig. 5). Among the 20 species analysed, coral had a strong TE (>0.3) on the abundance of eight, and fishing a strong effect on four fish species (Table 3). Coral or habitat complexity was identified as significant response paths for 12 fish species, whilst fishing or piscivore abundance was significant paths for four species.

The influence of coral and habitat on fish abundance was most evident among the coral-dependant fish (Table 3). A positive relationship was observed among coral cover and abundance of the coral-dependant group (Fig. 5a), as well as the obligate coral-feeding fish *C. trifascialis* (Table 3). However, the abundance of coral dwelling fish, *P. dickii* and *P. johnstonianus* and the corallivore *Chaetodon plebius*, was more strongly linked to habitat complexity (Table 3).

There was a strong negative relationship between coral and algal cover, the primary food source of many EAM-feeding fish (Table 3, Fig. 5). Abundance of territorial species was, however, inversely related to predator abundance and positively related to complexity, implying predation is a more important determinant of abundance than dietary resources (Fig. 5b). Indeed abundance of the territorial EAM feeders was negatively correlated to algae, although this relationship was primarily driven by *Plectroglyphidodon lacrymatus* (Table 3) and implies a positive relationship with coral and habitat rugosity. The trophic group, roving EAM feeders, were also more strongly affiliated with habitat topography than algae (Fig. 5c). Abundance of some species of roving EAM feeders such as *Naso literatus* and *Acanthurus lineatus* was positively linked to algal cover, although other species were more strongly linked with habitat topography and *Acanthurus nigricans* was negatively influenced by fishing pressure (Table 3). Models for all EAM feeders were, however, poorly fitted and response residuals indicate much of the variation in abundances had not been explained.

Fishing pressure was the main driver of invertivore abundance, although this was a positive relationship (Fig. 5d). Many of the invertivores surveyed were not directly targeted by fishers and a positive relationship implies increased fishing reduces competition and, or predation, resulting in an increase in abundance of

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**Table 3** Path analysis results for representative species from each functional group

| | | | | Total effect | | Response paths | | | | | | Associated paths | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Goodness-of-fit (SEM) | Chi-square | *P* | Coral | Fishing | Coral → response | Fishing → response | Algae → response | Complexity → response | Piscivores → response | Prey → response | Coral → algae | Coral → complexity | Fishing → piscivores | Complexity → prey | Response residual |
| Coral dependant | 1 | 0 | 1 | | | | | | | | | | | | | |
| *Plectroglyphidodon dickii* | 0.76 | 30.5 | <0.01 | 0.52 | 0.01 | 0.10 | | | **0.78** | −0.12 | | | **0.57** | −0.10 | | 0.24 |
| *Plectroglyphidodon johnstonianus* | 0.76 | 30.4 | <0.01 | 0.59 | 0.01 | 0.24 | | | **0.65** | −0.06 | | | **0.57** | −0.10 | | 0.31 |
| *Chaetodon trifascialis* | 1 | 0 | 1 | 0.68 | | **0.41** | | | **0.46** | | | | **0.57** | | | 0.40 |
| *Chaetodon lunulatus* | 1 | 0 | 1 | 0.13 | | **0.41** | | | **−0.50** | | | | **0.57** | | | 0.82 |
| *Chaetodon plebius* | 1 | 0 | 1 | 0.43 | | 0.23 | | | **0.36** | | | | **0.57** | | | 0.73 |
| Territorial EAM feeders | 0.76 | 39.0 | <0.01 | | | | | | | | | | | | | |
| *Plectroglyphidodon lacrymatus* | 0.77 | 38.9 | <0.01 | 0.46 | 0.02 | | | **−0.57** | −0.01 | −0.15 | | **−0.84** | **0.57** | −0.10 | | 0.63 |
| *Stegastes* spp. | 0.76 | 32.4 | <0.01 | 0.00 | 0.00 | | | 0.05 | 0.07 | 0.04 | | **−0.84** | **0.57** | −0.10 | | 0.86 |
| Roving EAM feeders | 0.82 | 22.7 | <0.01 | | | | | | | | | | | | | |
| *Naso lituratus* | 0.77 | 31.7 | <0.01 | −0.33 | −0.16 | | −0.16 | **0.45** | 0.29 | | | **−0.84** | 0.15 | | | 0.72 |
| *Acanthurus lineatus* | 0.80 | 26.2 | <0.01 | −0.34 | −0.09 | | −0.08 | **0.45** | 0.24 | | | **−0.84** | 0.15 | | | 0.76 |
| *Scarus schlegeli* | 0.78 | 29.5 | <0.01 | 0.13 | 0.21 | | 0.20 | −0.07 | **0.44** | | | **−0.84** | 0.15 | | | 0.83 |
| *Zebrasoma veliferum* | 0.82 | 21.7 | <0.01 | −0.08 | −0.12 | | −0.12 | 0.11 | 0.06 | | | **−0.84** | 0.15 | | | 0.97 |
| *Acanthurus nigricans* | 0.85 | 17.5 | <0.01 | −0.15 | −0.81 | | **−0.81** | 0.09 | **−0.50** | | | **−0.84** | 0.15 | | | 0.50 |
| Invertivores | 0.86 | 11.5 | <0.01 | | | | | | | | | | | | | |
| *Pseudocheilinus* | 0.77 | 26.3 | <0.01 | −0.49 | 0.01 | | | | **−0.81** | −0.09 | | | **0.57** | −0.10 | | 0.36 |
| *Parupeneus bifasciatus* | 0.81 | 16.6 | <0.01 | −0.02 | −0.46 | | **−0.45** | | −0.31 | | | | 0.15 | | | 0.83 |
| *Heniochus varius* | 0.96 | 1.7 | 0.19 | 0.05 | | | | | **0.30** | | | | **0.15** | | | 0.91 |
| *Bodianus loxozonus* | 0.98 | 0.7 | 0.41 | 0.01 | | | | | **0.06** | | | | **0.15** | | | 0.99 |
| *Thalassoma hardwicke* | 1 | 0 | 1 | 0.16 | | | | | **0.13** | | | | **0.57** | | | 0.96 |
| Piscivores | 0.65 | 60.7 | <0.01 | | | | | | | | | | | | | |
| *Cephalopholis urodeta* | 0.86 | 19.3 | <0.01 | −0.05 | 0.04 | | 0.04 | | **−0.40** | | **0.54** | | **0.57** | | **0.58** | 0.79 |
| *Parupeneus cyclostomus* | 0.67 | 62.4 | <0.01 | −0.04 | 0.15 | | 0.14 | | −0.27 | | **−0.39** | | 0.15 | | **0.58** | 0.85 |
| *Lutjanus bohar* | 0.67 | 55.5 | <0.01 | −0.03 | −0.20 | | −0.20 | | −0.20 | | −0.01 | | 0.15 | | **0.58** | 0.96 |
| *Cephalopholis argus* | 0.70 | 50.1 | <0.01 | −0.02 | −0.47 | | **−0.47** | | −0.15 | | 0.19 | | 0.15 | | **0.58** | 0.82 |
| *Lutjanus gibbus* | 0.71 | 47.8 | <0.01 | 0.00 | −0.46 | | **−0.46** | | −0.02 | | −0.18 | | 0.15 | | **0.58** | 0.71 |

Only the top five species that each contributed >1% to temporal differences in MDS are presented for each group. Values for response and associated paths are standardized coefficients for the full model (see Table S2 for unstandardized coefficients and statistical values), bold values indicate coefficients where significant relationships were detected. In all cases the response variable is the square-root abundance of the species. Total effects for fishing and coral have been calculated as the sum of the products of the standardized coefficients of the direct and indirect paths to the response. The response residual estimates how much variation is not explained by the model. High goodness-of-fit values and low chi-squared values are indicative of robust models.

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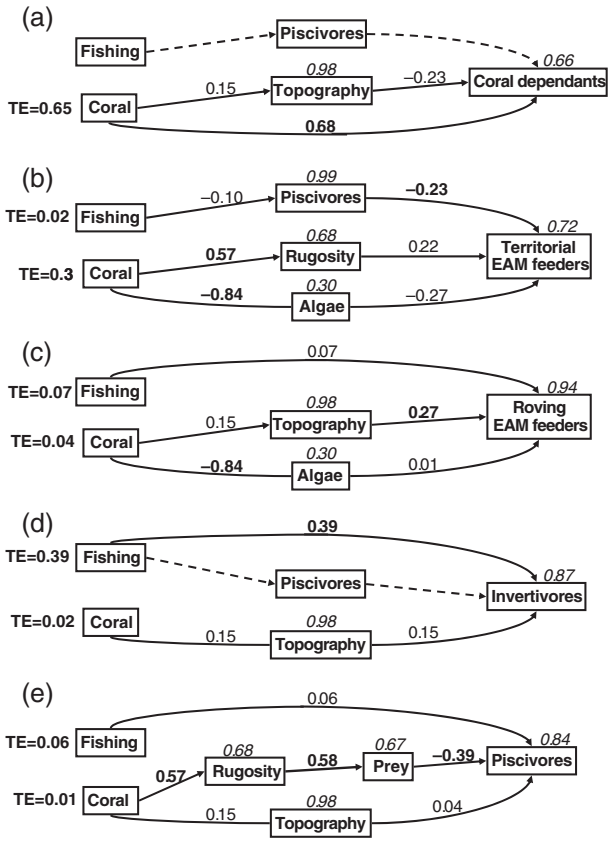


**Fig. 5** Path analyses models comparing the influence of fishing and coral on the abundance of (a) coral dependant, (b) territorial EAM feeders, (c) roving EAM feeders, (d) invertivores and (e) piscivores. Path arrows made with dashed lines were not included in the model for abundance of functional groups but were included for certain species within the group, when deemed appropriate. Values above arrows are path coefficients, which estimate the strength of the relationship among variables and if in bold are significant ($P<0.05$). Italicized values above boxes represent the amount of unexplained variation for that variable. The total effect (TE) gives an indication of the relative importance of fishing and coral on functional groups and was calculated by multiplying the standardized coefficients within a pathway then summing these values for pathways associated with either fishing or coral.

invertivores. Analysis at the species level revealed that whilst some invertivores are positively associated with habitat complexity, others were negatively associated with this variable, inferring a preference for low complexity or rubble type environments (Table 3). For species that are targeted by fishers, such as the goatfish, *P. bifasciatus*, there was a negative effect of fishing on abundance.

The overall abundance of piscivores was negatively linked to the abundance of prey, which was positively associated with rugosity (Fig. 5e). Models for piscivores and piscivorous species were, however, generally poor fits and path coefficients were not consistent among species (Table 3). Fishing had a direct effect on two of the piscivorous species, *Cephalopholis argus* and *Lutjanus gibbus*, both species declining in abundance with increasing fishing intensity (Table 3).

The most robust path analysis models in terms of goodness-of-fit and chi-squared values were those for coral-dependant fish (Table 3). For many of the other models, chi-squared analyses were significant and the goodness-of-fit indices were below 0.8, suggesting these postulated models miss some important predictors and associated descriptors of their interactions with responses in the reef fish communities. Although it appears that many of our models may miss substantial sources of variability in reef fish abundance, interpretation of the relative importance of coral and fishing in driving fish abundance are sound as we have considered all potential pathways for these variables to influence the response variables.

## Discussion

Over-exploitation and habitat degradation are the two primary drivers of population declines and species extinctions across a wide range of habitats (Ludwig *et al.*, 1993; Brooks *et al.*, 2002; Dulvy *et al.*, 2003). There are numerous examples where humans have hunted individual species to extinction (Flannery, 1994) and these events not only impact the target species but can also induce changes in community composition via the release of meso-predators (Crooks & Soule, 1999; Elmhagen & Rushton, 2007) and prey (Terborgh *et al.*, 2001; Gilg *et al.*, 2003; Frank *et al.*, 2005). This may have cascading effects on lower trophic levels, affecting diversity and primary productivity of the system (Crooks & Soule, 1999; Schmitz *et al.*, 2000). Alterations to habitat structure (e.g. through direct and indirect anthropogenic disturbances) also have obvious impacts on community structure and dynamics (Sousa, 1984; Walther *et al.*, 2002). For example, clearing of temperate woodlands for agricultural and mining purposes has reduced habitat heterogeneity and structural complexity resulting in a decline in reptile (Brown, 2001) and bird (Jansen & Robertson, 2001) diversity. Importantly, the combination of over-exploitation (top-down effects) and habitat degradation (bottom-up) can have potentially dire consequences for ecosystem function (Pace *et al.*, 1999; Travis, 2003).

Our study demonstrates that within an extremely diverse reef fish assemblage, both 'top-down' fishing and 'bottom-up' habitat disturbances play critical roles in determining abundance and community structure. However, the relative importance of fishing and habitat loss varies between functional groups and species of

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fish. Declines in fish that either feed or shelter within live coral can be directly attributed to coral loss, a result that has been widely reported in the literature (Wilson *et al*., 2006). Among these species, the impact of coral loss is greatest on specialists that feed or shelter within a narrow subset of species from the coral community (Munday, 2004; Pratchett *et al*., 2006; Wilson *et al*., 2008). Thus, as observed here, specialist corallivores such as *C. trifascialis* decline in abundance, whilst generalist feeders such as *Chaetodon lunula* may proliferate. Subtle shifts in a coral community can also favour some species over others, influencing the composition of coral-dependant fish communities (Berumen & Pratchett, 2006). For example, at Vuaqava, overall coral cover had not changed between 2000 and 2006, but a shift in coral composition resulted in dramatic declines in coral-dependant fish. This can be attributed to declines in *Acropora* feeding specialists and species that reside within branching corals.

Corals, particularly branching acroporids, also play a vital role in creating and maintaining habitat complexity, which is essential for the survival of many small-bodied reef fish (Graham *et al*., 2006). In the Lau Islands, topographic complexity, which is relevant to large- and medium-sized fish (Wilson *et al*., 2007), has been maintained; however, the loss of *Acropora* coral has reduced rugosity. This may explain why small, site attached fish such as the territorial EAM feeders have declined in abundance, whilst abundance of larger bodied roving EAM feeders has generally increased. In contrast, abundance of many small-bodied invertebrate-feeding fish, such as the Pseudochromids, was unaffected by changes in rugosity, a pattern also observed following widespread loss of coral and structural complexity throughout the Indian Ocean (Graham *et al*., 2008). The apparent stability of small-bodied invertivore abundance may partially relate to greater mobility of these fish compared with similar-sized species from other trophic groups. For example, EAM-feeding pomacentrids have territories that are often $<1\,m^2$ (Ceccarelli *et al*., 2005), whilst invertebrate-feeding wrasses of similar size forage over 30–150 $m^2$, including areas of low complexity, such as coral rubble (Jones, 2005). Some EAM-feeding pomacentrids (e.g. *P. lacrymatus*) also show a preference for habitats with skeletons of branching corals (Wilson *et al*., 2008), whilst invertivores tend to be habitat generalists (MacNeil *et al*., in press) and are therefore expected to be less susceptible to disturbance (Vasquez & Simberloff, 2002). Failure of coral recovery and protracted loss of fine scale complexity may, however, have serious long-term consequences, as most fishes probably depend on fine scale reef complexity to moderate predation and competition, particularly during vulnerable juvenile life stages (Almany, 2004; Graham *et al*., 2007).

Coral mortality instigated by bleaching or COTS is not always associated with an immediate decline in rugosity (Wilson *et al*., 2006). Coral skeletons may remain for several years after such disturbances, providing shelter for fish (Pratchett *et al*., 2008). For example, at Kabara, an outbreak of COTS caused coral cover to decline to $<1\%$ in 2000, but rugosity was similar to sites with 40–50% coral cover. High rugosity at Kabara probably allowed small fish, including some coral-associated species, to persist. However, by 2006, coral skeletons had eroded and although coral cover had increased, colonies were encrusting or small (S. K. Wilson, personal observations) and rugosity was lower than it was in 2000. Consequently, the relationship between structural complexity and coral cover may become decoupled when rugosity is retained immediately after disturbances or in the initial stages of recovery, when coral colonies are small.

Historic exploitation of marine resources has had an impact on the most remote of fish communities (Jackson *et al*., 2001). However, fishing is currently having a limited impact on Lauan fish communities. Path analysis detected direct effects on only a few species and patterns of piscivore abundance, which are targeted by many Fijian fishing communities (Jennings & Polunin, 1995a, 1997), are primarily linked to abundance of prey, which is closely associated with reef complexity. Furthermore, BEST analysis of fish community and environmental data matrices indicates that cover by *Acropora* corals alone explains almost the same level of variation in fish data as the combination of *Acropora*, fishing and rugosity. Similarly, results from the inner Seychelles found a loss of predominantly branching coral-reduced habitat complexity, resulting in a decline of small-bodied fish and their predators, even in areas where fishing is excluded (Graham *et al*., 2007).

Many invertebrate-feeding fish are also targeted by Lauan fishers, particularly those from the family Lethrinidae (Jennings & Polunin, 1995a). However, underwater visual surveys underestimate the abundance of lethrinids (Jennings & Polunin, 1995b), making it difficult to assess the direct impact of fishing on this family. This may explain why fishing has a positive impact on the abundance as invertebrate-feeding fish, as many of the smaller bodied invertivores are not targeted by fishers. Consequently, the removal of lethrinids could reduce competition for resources, encouraging an increase in the abundance of nonfished species. This implies a direct effect of fishing on lethrinids, but an indirect effect on invertivore competitors.

Indirect effects of fishing are also implied through the influence of predation on small-bodied EAM feeders.

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Fishing reduces the number of predators, which increases the number of prey; in this case pomacentrids. Such trophic cascades are not always observed at aggregated levels (e.g. Jennings & Polunin, 1997) and may relate to prey preferences of particular species (Graham *et al*., 2003). However, declines in fishing may result in changes to the size spectra of fish communities, whereby large fish become more abundant and, or, small fish less abundant (e.g. Dulvy *et al*., 2004a).

We have focused on two probable drivers of abundance in the path models: changes to habitat, brought about by disturbance mediated coral loss, and fishing. For some fish (e.g. coral dependants), coral variation and fishing are the basis of comparatively robust models; however, for more complex models there were poor fits. In these models, limited sample size may have contributed to poor model fits. However, high residual values on response variables for some fish imply factors other than coral cover and fishing pressure are important determinants of fish abundance. Our models do not consider supply rate of juvenile fish, which is spatially and temporally variable, and may substantially influence on the abundance of many fish species (Doherty, 1991). Furthermore, the high complexity inherent in diverse ecosystems such as coral reefs, mean a wide array of competitive and predatory interactions between fish and other co-habitants may occur. This means the number of potentially important driving pathways is vast, and may be highly variable on a species-specific basis. We found that path models were consistently stronger for species than for functional groups, supporting the notion that species level interactions are more common and detectable than those that occur at a community level (Polis *et al*., 2000). Indeed, abundance of species within the same functional group was often controlled by different drivers, effectively reducing the overall strength of the response at the functional level. Thus, community level responses to changes in exploitation or habitat are more likely to be attenuated when there is high diversity within a functional group (Schmitz *et al*., 2000).

## Conclusion

Fishing pressure has declined in the Lau Islands due to emigration of people and reduced reliance on live fish as a food source (Turner *et al*., 2007). This has reduced the direct impact of fishing on fish assemblages, though some effects of exploitation are still apparent. However, greater concern relates to coral bleaching and starfish outbreaks, which caused substantial declines in coral cover and small-scale complexity that are currently influencing coral-dependant fish and small-bodied species with potential long-term consequences for the assemblage. These results suggest that in sparsely populated remote locations, or where there is a decline in exploitation of marine resources, such as recently instigated reserves, loss of habitat is having an increasingly important influence on fish communities relative to fishing. Relative importance of top-down effects can however change (Frank *et al*., 2007), and increasing fishing pressure, which impacts different elements of the fish community, can put further pressure on a stressed system. The models presented here provide a basis for assessing the relative importance of fishing and habitat loss to other reef fish communities, providing spatial and temporal assessments of their relative impact. As fishing pressure increases and habitat disturbance becomes more severe, these models will provide a useful tool for identifying how complex top-down and bottom-up ecological processes interact with coral reef fish communities.

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## Supporting Information

The following Supporting Information for this article is available online:

**Table S1.** Functional group of surveyed fish species.

**Table S2.** Path analysis results for representative species from each functional group. Only the top 5 species that contributed >1% to temporal differences in MDS are presented. Values for Response Paths, Associated Paths and Residuals are un-standardised coefficients for the full model. In all cases the response variable is the square-root abundance of the species. Genus abbreviations; Pl, *Plectroglyphidodon*; Ch, *Chaetodon*; Na, *Naso*; Ac, *Acanthurus*; Sc, *Scarus*; Ze, *Zebrasoma*; Pa, *Parupeneus*; He, *Heniochus*; Bo, *Bodianus*; Th, *Thalassoma*; Ce, *Cephalopholis*; Lu, *Lutjanus*.

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Table S1. Functional group of surveyed fish species

| Species | Trophic group |
|---|---|
| *Acanthurus blochii* | EAM rover |
| *Acanthurus guttatus* | EAM rover |
| *Acanthurus lineatus* | EAM rover |
| *Acanthurus nigricans* | EAM rover |
| *Acanthurus nigricauda* | EAM rover |
| *Acanthurus olivaceus* | EAM rover |
| *Acanthurus pyroferus* | EAM rover |
| *Acanthurus triostegus* | EAM rover |
| *Acanthurus xanthopterus* | EAM rover |
| *Aluteres scriptus* | Invertivore |
| *Amanses scopas* | Invertivore |
| *Anampses caeruleopunctatus* | Invertivore |
| *Anampses neoguinaicus* | Invertivore |
| *Anampses twisti* | Invertivore |
| *Anyperodon leucogrammicus* | Piscivore |
| *Aphareus furca* | Piscivore |
| *Aprion virescens* | Piscivore |
| *Arothron mappa* | Invertivore |
| *Arothron nigropunctatus* | Invertivore |
| *Balistapus undulatus* | Invertivore |
| *Balistoides conspicillum* | Invertivore |
| *Balistoides viridescens* | Invertivore |
| *Bodianus anthioides* | Invertivore |
| *Bodianus axillaris* | Invertivore |
| *Bodianus diana* | Invertivore |
| *Bodianus loxozonus* | Invertivore |
| *Bodianus mesothorax* | Invertivore |
| *Cantherhines dumerilii* | Invertivore |
| *Cantherhines pardalis* | Invertivore |
| *Canthigaster valentini* | Invertivore |
| *Cephalopholis argus* | Piscivore |
| *Cephalopholis leopardus* | Piscivore |
| *Cephalopholis urodeta* | Piscivore |
| *Cetoscarus bicolor* | EAM rover |
| *Chaetodon auriga* | Coral dependant |
| *Chaetodon baronessa* | Coral dependant |
| *Chaetodon bennetti* | Invertivore |
| *Chaetodon citrinellus* | Invertivore |
| *Chaetodon ephippium* | Invertivore |
| *Chaetodon flavirostris* | Invertivore |
| *Chaetodon kleinii* | Invertivore |
| *Chaetodon lineolatus* | Invertivore |
| *Chaetodon lunula* | Invertivore |
| *Chaetodon lunulatus* | Coral dependant |
| *Chaetodon melannotus* | Invertivore |
| *Chaetodon mertensii* | Invertivore |
| *Chaetodon ornatissimus* | Coral dependant |

| | |
|---|---|
| *Chaetodon pelewensis* | Coral dependant |
| *Chaetodon plebeius* | Coral dependant |
| *Chaetodon quadrimaculatus* | Coral dependant |
| *Chaetodon rafflesi* | Invertivore |
| *Chaetodon reticulatus* | Invertivore |
| *Chaetodon trifascialis* | Coral dependant |
| *Chaetodon ulietensi* | Invertivore |
| *Chaetodon unimaculatus* | Invertivore |
| *Chaetodon vagabundus* | Invertivore |
| *Cheilinus chlorourus* | Invertivore |
| *Cheilinus fasciatus* | Invertivore |
| *Cheilinus oxycephalus* | Invertivore |
| *Cheilinus trilobatus* | Invertivore |
| *Cheilinus undulatus* | Invertivore |
| *Chlorurus frontalis* | EAM rover |
| *Chlorurus microrhinos* | EAM rover |
| *Chlorurus sordidus* | EAM rover |
| *Coris aygula* | Invertivore |
| *Coris gaimard* | Invertivore |
| *Ctenochaetus binotatus* | EAM rover |
| *Ctenochaetus striatus* | EAM rover |
| *Ctenochaetus strigosus* | EAM rover |
| *Diodon hystrix* | Piscivore |
| *Epibulus insidiator* | Piscivore |
| *Epinephelus fuscogutattus* | Piscivore |
| *Epinephelus hexagonatus* | Piscivore |
| *Epinephelus howlandi* | Piscivore |
| *Epinephelus maculates* | Piscivore |
| *Epinephelus polyphekadion* | Piscivore |
| *Forcipiger flavissimus* | Invertivore |
| *Forcipiger longisrostris* | Invertivore |
| *Gnathodentex aurolineatus* | Invertivore |
| *Gomphosus varius* | Invertivore |
| *Gracila albomarginata* | Piscivore |
| *Halichoeres hortulanus* | Invertivore |
| *Halichoeres margaritaceus* | Invertivore |
| *Halichoeres marginatus* | Invertivore |
| *Hemigymnus fasciatus* | Invertivore |
| *Hemigymnus melapterus* | Invertivore |
| *Heniochus chrysostomus* | Invertivore |
| *Heniochus monoceros* | Invertivore |
| *Heniochus singularis* | Invertivore |
| *Heniochus varius* | Invertivore |
| *Hipposcarus longiceps* | EAM rover |
| *Kyphosus cinerascens* | EAM rover |
| *Larbichthys unilineatus* | Coral dependant |
| *Lethrinus atkinsoni* | Piscivore |
| *Lethrinus erythracanthus* | Piscivore |
| *Lethrinus nebulosus* | Piscivore |
| *Lethrinus olivaceus* | Piscivore |

| | |
|---|---|
| *Lutjanus bohar* | Piscivore |
| *Lutjanus fulviflamma* | Piscivore |
| *Lutjanus fulvus* | Piscivore |
| *Lutjanus gibbus* | Piscivore |
| *Lutjanus kasmira* | Piscivore |
| *Lutjanus monostigma* | Piscivore |
| *Lutjanus russelli* | Piscivore |
| *Lutjanus semicinctus* | Piscivore |
| *Lutjanus vitta* | Piscivore |
| *Macolor niger* | Invertivore |
| *Macropharyngodon meleagris* | Invertivore |
| *Melichthys vidua* | Invertivore |
| *Monotaxis grandoculus* | Piscivore |
| *Mulloidichthys vanicolensis* | Piscivore |
| *Naso lituratus* | EAM rover |
| *Naso tuberosus* | EAM rover |
| *Naso unicornis* | EAM rover |
| *Ostracion meleagris* | Invertivore |
| *Oxycheilinus digramma* | Piscivore |
| *Oxycheilinus unifasciatus* | Piscivore |
| *Oxymonacanthus longirostris* | Coral dependant |
| *Parupeneus barbarinus* | Invertivore |
| *Parupeneus bifasciatus* | Piscivore |
| *Parupeneus ciliatus* | Invertivore |
| *Parupeneus cyclostomus* | Piscivore |
| *Parupeneus multifasciatus* | Invertivore |
| *Pervagor melanocephalus* | Invertivore |
| *Plectorhinchus chaetodontoides* | Invertivore |
| *Plectorhinchus obscurus* | Invertivore |
| *Plectorhinchus picus* | Invertivore |
| *Plectroglyphidodon dickii* | Coral dependant |
| *Plectroglyphidodon johnstonianus* | Coral dependant |
| *Plectroglyphidodon lacrymatus* | EAM territorial |
| *Plectropomus areolatus* | Piscivore |
| *Plectropomus laevis* | Piscivore |
| *Plectropomus leopardus* | Piscivore |
| *Plectropomus maculatus* | Piscivore |
| *Pomacentrus bankanensis* | EAM territorial |
| *Pomacentrus vaiuli* | EAM territorial |
| *Pseudocheilinus hexataenia* | Invertivore |
| *Pseudocheilinus octotaenia* | Invertivore |
| *Rhinecanthus lunula* | Invertivore |
| *Rhinecanthus rectangulus* | Invertivore |
| *Scarus altipinnis* | EAM rover |
| *Scarus chameleon* | EAM rover |
| *Scarus dimidiatus* | EAM rover |
| *Scarus forsteni* | EAM rover |
| *Scarus frenatus* | EAM rover |
| *Scarus ghobban* | EAM rover |
| *Scarus globiceps* | EAM rover |

| | |
|---|---|
| *Scarus longipinnis* | EAM rover |
| *Scarus niger* | EAM rover |
| *Scarus oviceps* | EAM rover |
| *Scarus psittacus* | EAM rover |
| *Scarus rubroviolaceus* | EAM rover |
| *Scarus schlegeli* | EAM rover |
| *Scarus spinus* | EAM rover |
| *Scolopsis bilineatus* | Invertivore |
| *Siganus doliatus* | EAM rover |
| *Siganus punctatus* | EAM rover |
| *Siganus stellatus* | EAM rover |
| *Siganus uspi* | EAM rover |
| *Stegastes fasciolatus* | EAM territorial |
| *Stegastes lividus* | EAM territorial |
| *Stegastes nigricans* | EAM territorial |
| *Stethojulis bandanensis* | Invertivore |
| *Sufflamen bursa* | Invertivore |
| *Sufflamen chrysopterum* | Invertivore |
| *Sufflamen fraenatus* | Invertivore |
| *Thalassoma harwicke* | Invertivore |
| *Thalassoma jansenii* | Invertivore |
| *Thalassoma lutescens* | Invertivore |
| *Thalassoma quinquevittatum* | Invertivore |
| *Variola louti* | Piscivore |
| *Zebrasoma scopas* | EAM rover |
| *Zebrasoma veliferum* | EAM rover |

Table S1. Path analysis results for representative species from each functional group. Only the top 5 species that contributed >1% to temporal differences in MDS are presented. Values for Response Paths, Associated Paths and Residuals are un-standardised coefficients for the full model. In all cases the response variable is the square-route abundance of the species. Genus abbreviations; *Pl, Plectroglyphidodon; Ch, Chaetodon; Na, Naso; Ac, Acanthurus; Sc Scarus; Ze, Zebrasoma; Pa, Parupeneus; He, Heniochus; Bo, Bodianus; Th, Thalassoma; Ce, Cephalopholis; Lu, Lutjanus.*

| | Response Paths | | | | | | Associated Paths | | | | Residuals | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Coral → Response | Fishing → Response | Algae → Response | Complexity → Response | Piscivores → Response | Prey → Response | Coral → algae | Fishing → piscivores | Complexity → prey | Coral → complexity | Algae | Complexity | Prey fish | Piscivores | Rugosity | Response |
| Coral dependant | 0.15 | | | -0.31 | | | | | | 0.09 | | 0.07 | | | | 0.12 |
| *Ch. plebius* | 0.06 | | | 0.59 | | | | | | 0.09 | | 0.07 | | | | 0.19 |
| *Ch. trifascialis* | 0.13 | | | 0.91 | | | | | | 0.09 | | 0.07 | | | | 0.15 |
| *Ch. lunulatus* | 0.13 | | | -1.02 | | | | | | 0.09 | | 0.07 | | | | 0.33 |
| *Pl. dickii* | 0.05 | | | 2.54 | -0.41 | | | -0.05 | | 0.09 | | 0.07 | | 0.09 | | 0.28 |
| *Pl. johnstonianus* | 0.09 | | | 1.61 | -0.16 | | | -0.05 | | 0.09 | | 0.07 | | 0.09 | | 0.20 |
| Ter. EAM feeders | | | -0.07 | 0.41 | -0.43 | | -0.90 | -0.05 | | 0.09 | 1.38 | 0.07 | | 0.09 | | 0.27 |
| *Pl. lacrymatus* | | | -0.26 | -0.05 | -0.49 | | -0.90 | -0.05 | | 0.09 | 1.38 | 0.07 | | 0.09 | | 0.62 |
| *Stegastes spp.* | | | 0.02 | 0.20 | 0.12 | | -0.90 | -0.05 | | 0.09 | 1.38 | 0.07 | | 0.09 | | 0.75 |
| Rov. EAM | | 0.04 | 0.00 | 0.20 | | | -0.90 | | | 0.03 | 1.38 | 0.19 | | | | 0.09 |

| | | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| feeders | | | | | | | | | | | | | | | |
| *Ac. lineatus* | | -0.10 | 0.15 | 0.41 | | | -0.90 | | | 0.03 | 1.38 | 0.19 | | | 0.40 |
| *Ac. nigricans* | | -0.95 | 0.03 | -0.81 | | | -0.90 | | | 0.03 | 1.38 | 0.19 | | | 0.26 |
| *Na. lituratus* | | -0.20 | 0.16 | 0.49 | | | -0.90 | | | 0.03 | 1.38 | 0.19 | | | 0.40 |
| *Sc. schlegeli* | | 0.21 | -0.02 | 0.66 | | | -0.90 | | | 0.03 | 1.38 | 0.19 | | | 0.32 |
| *Ze. veliferum* | | -0.12 | 0.03 | 0.08 | | | -0.90 | | | 0.03 | 1.38 | 0.19 | | | 0.39 |
| | | | | | | | | | | | | | | | |
| Invertivores | | 0.14 | | 0.07 | | | | | | 0.03 | | 0.19 | | | 0.04 |
| *Bo. loxozonus* | | | | 0.08 | | | | | | 0.03 | | 0.19 | | | 0.37 |
| *He. varius* | | | | 0.43 | | | | | | 0.03 | | 0.19 | | | 0.36 |
| *Pa. bifasciatus* | | -0.53 | | -0.21 | | | | | | 0.03 | | 0.19 | | | 0.41 |
| *Pseudocheilinus* | | | | -1.86 | -0.21 | | | -0.05 | | 0.09 | | 0.07 | 0.09 | | 0.17 |
| *Th. Hardwicke* | 0.03 | | | 0.28 | | | | | | 0.09 | | 0.07 | | | 0.45 |
| | | | | | | | | | | | | | | | |
| Piscivores | | 0.03 | | 0.03 | | -0.20 | | | 1.14 | 0.03 | | 0.19 | | 0.25 | 0.08 |
| *Ce. argus* | | -0.47 | | -0.22 | | 0.20 | | | 1.14 | 0.03 | | 0.19 | | 0.25 | 0.30 |
| *Ce. urodeta* | | 0.04 | | -0.87 | | 0.59 | | | 1.14 | 0.09 | | | | 0.25 | 0.36 |
| *Lu. bohar* | | -0.21 | | -0.30 | | -0.01 | | | 1.14 | 0.03 | | 0.19 | | 0.25 | 0.40 |
| *Lu. gibbus* | | -0.44 | | -0.02 | | -0.16 | | | 1.14 | 0.03 | | 0.19 | | 0.25 | 0.24 |
| *Pa. cyclostomus* | | 0.15 | | -0.41 | | -0.42 | | | 1.14 | 0.03 | | 0.19 | | 0.25 | 0.32 |