Habitat degradation and fishing effects on the size structure of coral reef fish communities

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Abstract

Overfishing and habitat degradation through climate change pose the greatest threats to sustainability of marine resources on coral reefs. We examined how changes in fishing pressure and benthic habitat composition influenced the size spectra of island-scale reef fish communities in Lau, Fiji. Between 2000 and 2006 fishing pressure declined in the Lau islands due to declining human populations and reduced demand for fresh fish. At the same time coral cover declined and fine-scale architectural complexity eroded due to coral bleaching and outbreaks of Crown-of-Thorns Starfish, *Acanthaster planci*. We examined the size distribution of reef fish communities using size spectra analysis- the linearised relationship between abundance and body-size class. Spatial variation in fishing pressure accounted for 31% of the variation in the slope of the size spectra in 2000, higher fishing pressure being associated with a steeper slope, which is indicative of fewer large-bodied fish and/or more small-bodied fish. Conversely, in 2006 spatial variation in habitat explained 53% of the variation in the size spectra slopes and the relationship with fishing pressure was much weaker (~12% of variation) than in 2000. Reduced cover of corals and lower structural complexity was associated with less steep size spectra slopes primarily due to reduced abundance of fish <20cm. Habitat degradation will compound effects of fishing on coral reefs as increased fishing reduces large-bodied target species, whilst habitat loss results in fewer small-bodied juveniles and prey that replenish stocks and provide dietary resources for predatory target species. Effective management of reef resources therefore depends on both reducing fishing pressure and maintaining processes that encourage rapid recovery of coral habitat.

Introduction

Unsustainable exploitation of fish has had a major impact on stocks globally, resulting in the collapse of fisheries and changes to the composition of fish communities (Jackson et al. 2001, Pauly et al. 2002). Fishing typically targets large-bodied individuals resulting in declines in target species size, density and biomass (Jennings and Kaiser 1998, Russ 2002). Targeting of predatory species (Pauly et al. 1998, Christensen et al. 2003, Myers and Worm 2003), may further result in trophic cascades, whereby abundance of prey species increase reducing the nature and quality of primary production (Pinnegar et al. 2000, Dulvy et al. 2004a, Mumby et al. 2006).

Environmental conditions underlie fisheries productivity (Finney et al. 2002, Rodwell et al. 2003, Wynne and Cote 2007); however, fishing can have a detrimental effect on the environment via the use of habitat moderating techniques (Dayton et al. 1995, Jennings and Polunin 1996a), or the removal of functionally important species (McClanahan and Shafir 1990, Hughes 1994; Dulvy et al. 2004a). Loss of habitat, directly and indirectly through fishing or other processes, poses a major threat to the continued existence of many marine species (Roberts and Hawkins 1999, Rodwell et al. 2003), particularly those that are already endangered (Wilcove et al. 1998). Indeed, exploitation is believed to have caused 55% of marine extinctions, while habitat degradation explains a further 37% (Dulvy et al. 2003), emphasising the importance of these two processes for both conservation and sustainability.

Coral reefs are a system of particular concern as millions of people on tropical coasts are dependant on the goods and services they provide (Moberg and Folke 1999). Human populations in tropical regions are increasing, adding to existing stressors (McManus 1997, Hughes et al. 2003, Bell et al. in press) and overexploiting of coral reef resources (Newton et al. 2007). Coral reefs are also highly susceptible to the effects of climate change, as the primary habitat builders, scleractinian corals, are living close to their thermal threshold (Hoegh-Guldberg 1999). Increased occurrence of thermal anomalies are expected to cause widespread coral mortality due to coral bleaching (Glynn 1993, Brown 1997, Hoegh-Guldberg 1999), disease (Harvell et al. 1999, 2002, Bruno et al. 2007) and severe storms (Emanual 2005, Webster et al. 2005), whilst beyond 2050 changes to water chemistry will inhibit growth of corals and reef accretion (Kleypas 1999, Hoegh-Guldberg et al. 2007). Most coral reef fish have a close association with the reef structure (Choat and Bellwood 1991), some species being highly dependent on particular biotic (e.g. Wilson et al. 2006, Cole et al. 2008, Munday et al. 2008) or physical (e.g. Risk 1972, Sano et al. 1987, Garpe et al. 2006, Graham et al. 2006) elements of the reef benthos. Loss of habitat, combined with overfishing, is therefore expected to have a severe impact on coral reef fish assemblages.

Previous studies have used spatial and temporal gradients in fishing intensity and habitat quality to demonstrate that both fishing and habitat are important determinants of fish abundance (e.g. McClanahan 1994, Jennings et al. 1996, Friedlander et al. 2003, McClanahan and Arthur 2001, Wilson et al 2008). Some studies have concluded that habitat is more important than fishing (e.g. Grigg 1994), whilst others have found that the effects of fishing are still prevalent when accounting for spatial variation in habitat (e.g. Chapman and Kramer 1999). The relative importance of these two processes is likely to depend on the extent of fishing pressure compared to changes in habitat (Russ et al. 2005) and will vary depending on species susceptibility to fishing versus habitat degradation (Wilson et al. 2008).

Sized-based indicators of fish communities have been recommended for monitoring fisheries and ecosystem based management because they represent the distribution of energy, and reveal energy flow through ecosystems (Jennings and Dulvy 2005, Shin et al. 2005). In particular, the use of size spectra descriptors have been correlated to fishing pressure in both temperate habitats (e.g. Rice and Gislason 1996, Zwanenburg 2000, Daan et al. 2005) and coral reefs (Dulvy et al. 2004b, Graham et al. 2005). These studies demonstrate that fishing can change the size distribution of fish communities directly, by decreasing abundance of large individuals, and indirectly, by increases in small individuals. Changes in habitat can also influence the size distribution of coral reef fish communities, resulting in a decline in abundance of small size classes, and some increases in larger sizes (Graham et al. 2007). Although the relative effect of fishing and environmental conditions on size spectra of temperate fish communities has been assessed (Blanchard et al. 2005), similar comparisons on coral reefs have not been made.

Here we examine how changes in both fishing pressure and habitat quality have affected the size distribution of fish communities on corals reefs surrounding the Fijian Lau islands. Fishing on these islands is restricted to subsistence fishing by local residents and a reduction in human populations and shift to alternate sources of income has resulted in a decline in fishing pressure over the past 10 years (Turner et al. 2007). Simultaneously, outbreaks of the crown-of-thorns starfish (COTS, *Acanthaster planci*) which may be linked to over-fishing (Dulvy et al. 2004a, Sweatman 2008) and coral bleaching have caused coral mortality in the region (Cummings et al. 2002, Dulvy et al. 2004a), changing the composition and structure of the benthic community. This is an unusual case study, as burgeoning populations on most tropical coasts increase the demands for marine resources and fishing intensity. However the current scenario in the Lau islands is analogous to management strategies which endeavour to reduce local fishing pressure by introducing marine protected areas. Moreover, changes in benthic composition on Lau reefs allow us to examine the interaction between the direct effects if fishing and habitat degradation on reef fish communities.

A previous study examined the influence of fishing and habitat degradation on trophic groups and species (Wilson et al. 2008), but here we assessed the influence of these two drivers on descriptors of size spectra. Size structure is a particularly useful indicator for fish assemblages as many life history characteristics, such as age at maturity, reproductive output and natural mortality, are positively related to size in marine fishes (Froese and Binohlan 2000, Jennings et al.1999, Denny et al. 2002) and it can be a useful proxy of overall productivity of fish assemblages (Kerr and Dickie 2001, Jennings et al. 2008). Size spectra are particularly suited to detecting change in communities dominated by species exhibiting indeterminate growth whose feeding ecology changes ontogenetically. Aggregation of data across species and individuals also affords greater statistical power to detect the direct and indirect effects of fishing (Jennings & Dulvy 2005, Dulvy et al. 2004b, Blanchard et al. 2009) and habitat degradation (Graham et al. 2007). Thus size spectra encompasses community characteristics not always captured using trophic or other groupings and can detect key changes passing through ecological communities, with the predictive ability to assess forthcoming change in ecosystem function and stability (Nyström et al. 2008). We predict that decreased fishing will increase the abundance of large-bodied fish, reducing the steepness of the size spectra slope. This may be exacerbated by a decline in small-bodied prey released from predation and competition pressures (Dulvy et al. 2004b). We also predict that reduced coral cover and structural complexity will have its greatest impact on small-bodied individuals and species, which will also cause a decrease in the size spectra slope.

Methods

The relationships between fishing, benthos and size distribution of fish communities were examined using data collected from five Lau islands: Kabara, Matuku, Totoya, Tavunasici and Vuaqava, located in the south-eastern Fiji division (see Turner et al. 2007 for map with island locations). Benthic and fish communities were assessed at three sites on the outer western reef slope of each island, at a depth of 7m. Benthic and fish counts were carried out at the same locations in 2000 and 2006, using GPS to relocate sites between years.

At each site, six point counts were used to assess size and abundance of 173 diurnal, non-cryptic fish species, from 17 families (see Wilson et al. 2008 for full species list). Point counts were carried out within a cylindrical area of 7m radius, encompassing a benthic area of approximately 154m^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 surveys were carried out by NKD in 2000 and SKW in 2006. Both divers are experienced in fish surveys and the influence of observer bias is therefore expected to be a small component of the variance in the underwater fish counts (Williams et al. 2006, McClanahan et al. 2007). Each diver also refined their ability to estimate fish lengths by estimating lengths of plastic pipe underwater and comparing estimates to actual values before surveys. To determine if there were any differences in the size estimates between the two observers we plotted size estimates of the plastic pipes against actual lengths for each observer and compared the slope and intercepts of the two relationships (Zar 1984).

No significant difference was detected in the slope (t_{64} = 0.24, P=0.813), or intercept (t_{65} = 1.25, P=0.218), suggesting size estimates of fish for the two divers were very similar.

The composition of the benthic community was assessed within the same circular survey area used for fish counts. In 2000, thirty digital images of the benthos, each covering an area of ~500cm^2, were collected from within survey areas and microhabitat was recorded from twenty random points on each image. In 2006, a 30m tape was unfurled within and around the survey area and microhabitat under 30 randomly marked points on the tape was recorded. Microhabitat categories used for both years were *Acropora*, *Pocillopora*, *Porites*, *Favites*, soft corals, sponges, coralline algae, turf algae and fleshy macroalgae (Wilson et al. 2008).

Structural complexity of the reef was measured at two spatial scales within each of the survey areas. At the seascape scale, topographic complexity was ranked on a scale of 0-5 where 0 represented reefs with no vertical relief, and extremely complex habitats, with numerous caves and overhangs, were given a value of 5 (Polunin and Roberts 1993). Rugosity was measured as the linear distance covered by a 3m chain draped over the reef surface (Risk 1972).

Fishing in the Lau islands is predominantly for subsistence purposes (Turner et al. 2007), each village having discrete fishing tenure areas known as *qoliqoli*. Fishing pressure may therefore be estimated as the human population per linear km of reef front, following Dulvy et al. (2002). This method correlates well with estimates of fishing pressure using log books (Jennings and Polunin 1995, 1996b) and community measures of the fish assemblage (Dulvy et al. 2004b). However, on some of the islands, there has been a decline in fresh fish consumption, as people have been engaged in more profitable occupations than fishing (Turner et al. 2007), suggestive of development driven impacts of humans on reef fish biomass (Cinner et al. 2009).

Hence, we calculated fishing pressure as human population divided by linear km of reef front, multiplied by proportional weekly consumption rate of fresh fish, estimated from household surveys of villages (Turner et al. 2007). This decline in fresh fish consumption represents a 40% reduction in fishing pressure across the five islands, although magnitude of decline varies among islands (Wilson et al. 2008). Population growth and decline is an exponential process henceforth estimates of fishing pressure were logged prior to analyses permitting linear comparisons with size spectra descriptors (Jennings and Polunin 1996a).

Data analyses

Spatial and temporal differences in habitat composition and the two measures of structural complexity were examined using principal components analysis (PCA). Variables were normalised prior to analysis, allowing them to be compared on a common scale. A biplot of the first two principal components and associated eigenvectors is presented in Wilson et al. (2008).

The size distribution of fish assemblages was assessed at each site using size spectra analysis. All fish were assigned to 5x10 cm size categories, covering the size range of 10-60 cm. Individuals <10cm were excluded from the analysis as their abundance is not adequately represented by underwater visual surveys (Ackerman and Bellwood 2000). The size distribution was measured as the slope and midpoint of a linear regression fitted to the size frequency distribution of the fish community. Frequency data was $\log_{10}(x + 1)$ transformed before analysis to ensure a linear relationship, and the midpoints of size classes were re-scaled to the size range and fixed at zero, removing the correlation between slope and midpoint (Daan et al. 2005, Rochet and

Trenkel 2003). When interpreting size spectra results, a steepening of the slope, whereby it becomes more negative, is indicative of an increase in small fish, a decrease in large fish or both. The mid-point height is an index of primary production and overall community biomass whereby greater values are indicative of greater community biomass (Dickie et al. 1987, Jennings 2005).

Spatial and temporal differences in the slope and midpoint attributable to fishing or habitat degradation were compared using ANOVA, where year and qoliqoli were entered as fixed factors. Multiple regression was used to assess the influence of fishing and habitat on size spectra descriptors. Fishing pressure and PC1, PC2 and PC3 scores from the habitat PCA were entered as independent variables and the slope and midpoint entered as dependant variables. Multiple regressions were carried out on 2000 and 2006 data to determine if the strength of trends changed between years.

Temporal changes in the size distribution were also examined by comparing total abundance of fish in 2000 and 2006, within each 10cm size class. To assess the influence of habitat change and fishing on the abundance of juvenile fish temporal comparisons of size distributions were carried out on all species and on species whose maximum total length was >20 cm. This removed the influence of small-bodied species whilst retaining information on juveniles and sub-adults of larger bodied conspecifics. Similar analyses were carried out on fish that feed with the epilithic algal matrix (EAM) and predatory species that feed predominantly on either fish or motile benthic invertebrates. Fish were placed into these feeding guilds based on information presented in Wilson et al. (2008)

Results

Benthic composition had changed significantly between 2000 and 2006, although the extent and type of change varied among islands. At three of the islands, namely Matuku, Totoya and Tavunasici, coral mortality of 50-70% had reduced coral cover to ~20%. In contrast, Kabara reefs had recovered from an outbreak of COTS in 2000 and coral cover had increased from <1 to 18%. At the island of Vuaqava coral cover had remained stable.

In 2000, coral communities were dominated by branching *Acropora* coral; however, in 2006, at sites where there had been some recovery or coral cover had remained high, *Pocillopora* and *Porites* were the prominent coral genera. At all sites, topography had not changed between 2000 and 2006, indicating reefs had retained structural complexity at this spatial scale. However, rugosity had declined at all sites, indicating structural complexity at the smaller spatial scale had been lost.

The first component of PCA used to describe spatio-temporal patterns in habitat explained 31% of the variation in habitat data and was positively correlated with *Acropora*, *Porites* and *Pocillopora* cover, as well as rugosity (Table 1). Topographic complexity was positively correlated with the second and third PCA components, which explained 18 and 15% of the variation in data respectively. Coralline algae and *Pocillopora* were also positively correlated with PC2, whilst rugosity was negatively correlated to this axis. Macroalgae and sponge cover were positively associated with PC3.

The structure of the fish communities, measured as the slope from size spectra analysis of size distribution, varied between islands (F_4=4.82, P=0.006), slopes being steeper at Matuku, than at either Tavunasici or Kabara (Figure 1a). There was also a tendency for size spectra slopes to be steeper in 2000 than 2006 (F_1=3.93, P=0.061). There was no significant interaction detected between year and islands. Midpoint of the size spectra analyses differed between years (F_1=40.37, P<0.001), higher values occurring in 2006 (Figure 1b).

Temporal variation in the size distribution of fish can be attributed to reduced abundance of small-bodied fish (<20cm TL) and an increase in medium sized fish (20-40 cm TL) in 2006 (Figure 2a). Abundance of small-bodied fish represented 76 ± 2 % (mean ± SE) of fish observed in 2000, but only 40 ± 3 % of the fish community in 2006. Small-bodied species (maximum total length < 20 cm) represent approximately 75% of the decline in small fish and these are predominantly small pomacentrids that feed on the EAM (Figure 2b), or invertebrate feeding labrids (Figure 2c). However, juveniles or sub adults of larger bodied conspecifics have also been affected, particularly among the roving EAM feeders. In 2000 the average number of small (TL< 20cm) scarids and acanthurids observed per island was 98 ± 39 and 87 ± 18 respectively. In 2006 the mean number of small scarids had fallen to 14 ± 4 and there were only 54 ±13 small acanthurids per island.

Spatial and temporal variation in the size structure of the fish community can be attributed to differences in both fishing intensity and habitat composition, although the relative importance of these predictors varies between years. In 2000 a negative relationship between fishing intensity index and size spectra slopes indicates sites with lower fishing pressure had more large fish and/or fewer small fish. This relationship accounts for 30% of the spatial variation in size spectra slopes in 2000, but by 2006 it had weakened ($F_{1,13}$=1.7, P= 0.210 R^2 = 0.118) and fishing is not included as a predictor variable in the multiple regression model (Table 2, Figure 3a). Instead the slope of the size spectra analysis in 2006 is best predicted by spatial heterogeneity in benthic habitat, scores from PC1 and PC3 accounting for 53% of the variation in data (Table 2). Fishing and PC3 are however correlated ($F_{1,28}$ =31.5, $P<0.001$, R^2=0.529) and fishing may contribute to spatial variation in slope data from 2006. A negative relationship between slope data and PC1 in 2006 suggests sites with higher coral cover and rugosity have a steeper or more negative slope. A positive relationship between the slope and PC3 in 2006 suggests sites with higher topographic complexity and macroalgae cover have a shallower or less negative slope (Figure 4).

The midpoint from size spectra analysis is also best predicted by a combination of fishing and habitat data when information from both years is pooled. Combined fishing and habitat account for 51% of the variation in midpoint data (Table 2). The midpoint tends to be greater when fishing pressure is lower (Figure 3), which suggests a reduction in fishing has increased overall fish biomass. The midpoint is also greater when cover by turf algae coralline algae and topographic complexity are high (Figure 4). The relationship between fishing pressure and size spectra midpoint is weaker when analysed by year, predictor variables accounting for < 30% of the variation in data.

The slope and midpoint of size spectra analysis were positively correlated ($F_{1,28}$=19.2, $P<0.001$, R^2= 0.406), despite rescaling of data prior to analysis. However, the best combinations of predictor variables differed between slope and midpoint, suggesting these two descriptors of size spectra still provide unique information.

Discussion

Fishing has a profound effect on the size distribution of fish on coral reefs as fishers typically target large-bodied individuals, which steepens fish community size spectra.

In addition, many fishers, including those in Fiji, target predatory species such as serranids and lutjanids (Jennings and Polunin 1995), which can result in release of prey and increased abundance of small-bodied fish (Graham et al. 2003, Dulvy et al. 2004b). These impacts of fishing were evident in the Lau islands of Fiji in 2000, but by 2006 the size structure of the fish assemblage was increasingly governed by and overwritten by habitat modification.

Coral bleaching and outbreaks of COTS (the latter of which may be driven by removal of starfish predators (Dulvy et al. 2004a; Sweatman 2008)) have brought about spatial variation in habitat composition and quality, which is having a greater impact on the size distribution of fish than the direct effects of fishing. The effects of coral habitat degradation are particularly severe on small individuals. Many of the fish that feed or shelter among the branches of live coral colonies are small-bodied and disturbances that reduce coral cover have a detrimental effect on their abundance (Wilson et al. 2006). In the Lau islands, loss of *Acropora* corals was identified as an important driver of change in the fish community which resulted in significant declines in coral feeding butterflyfish and small bodied damselfish that shelter amongst coral branches (Wilson et al. 2008). Maximum attainable size of these coral dependant species is < 20 cm (Randall 2005) and their loss has contributed to the decline of small-bodied fish in the Lau islands. However, coral-dependant fish represent only 5-10% of the species in reef fish communities (Jones et al. 2004; Pratchett et al. 2008), and the decline in small-bodied fish in the Lau Islands can be largely attributed to loss of small-bodied pomacentrids that feed on the EAM and invertebrate feeding labrids rather than coral dependant species. Thus decline of small fish species is most likely due to lost rugosity associated with corals, rather than the loss of live coral tissue (Sano et al. 1987, Garpe et al. 2006, Graham et al. 2006).

A decline in small-bodied fishes may also include reduced abundance of juvenile fish and have long term consequences for replenishment of adult fish stocks (Graham et al. 2007). Whilst small-bodied species account for 75% of the decline in fish <20 cm, juveniles of larger-bodied conspecifics are also likely to have been effected, particularly juveniles of roving EAM feeders. Abundance of adult roving EAM feeders was typically higher in 2006 than 2000 due to reduced fishing pressure and increased dietary resources (Wilson et al. 2008). But the size distribution of these fish in 2006 is skewed towards larger fish, with fewer juveniles. Importantly, a decline in these stocks due to poor recruitment could compromise reef resilience in the future, assuming a direct relationship between recruitment and stock size and the absence of compensatory density dependence (Hughes et al. 2007).

Reduced fishing pressure in the Lau islands, caused by emigrating human populations and reduced consumption of fresh fish (Turner et al. 2007), may also have contributed to temporal changes in size spectra slopes. Relaxed fishing pressure could have resulted in more large fish and increased predatory control on small-bodied fishes and invertebrates. This effect may have been facilitated by loss of refuge from predation and maintenance of topographic complexity, which measures structural complexity at a spatial scale relevant to medium sized predators (Wilson et al. 2007).

The observed temporal increase in size spectra mid-point height was a result of larger individuals (>20cm) in the assemblage and can also be partially attributed to reduced fishing pressure. This is consistent with increases in mid-point height and community biomass observed from fishery closures in Kenya (McClanahan and Graham 2005). The fish feeding groups responsible for the increase in Lau were roving EAM feeders, invertivores and piscivores (Wilson et al. 2008). These larger bodied species are major contributors to total biomass of reef fish communities (Ackerman and Bellwood

2000) and increased occurrence of these fish has more than compensated for lost biomass associated with small bodied fish. Higher midpoints in 2006 were also associated with greater coverage of turf and coralline algae, which may be indicative of high grazing pressure from roving fish (Scott and Russ 1987, McClanahan 1997, Hughes et al. 2007). Greater midpoints in 2006 also suggest that productivity of the system may have increased, although this increase may be temporary if juveniles of adult conspecifics are affected by reduced reef rugosity.

Whilst we can not definitively determine the primary driver of declines in small-bodied fish, the correlation between habitat quality and size spectra slope suggest loss of coral and associated rugosity will have a detrimental effect on small fish abundance. Consequently, habitat degradation, as observed following coral loss, exacerbates the effects of exploitation on fish stocks. Fishing will remove large-bodied individuals, whilst loss of coral and associated rugosity will reduce abundance of small-bodied fish and impair the replenishment of adult stocks. For this reason it is imperative that managers address both over-fishing and protect against habitat degradation, especially given the continuing impacts of climate change (Hughes et al. 2003).

Reducing fishing locally (e.g. implementing no-take areas) will protect exploited fish and may encourage reef recovery following some disturbances (Gell and Roberts 2003, Hughes et al. 2007), but will not necessarily protect corals against the large-scale effects of climate change (Rogers and Beets 1999, Graham et al. 2008). Consequently, effective conservation of reefs will require a combination of management policies that not only reduce fishing, but also protect functionally important structures (complexity) and processes (herbivory) (Rodwell et al. 2003, Mumby and Steneck 2008). This may involve protecting high quality, resilient habitats and prohibiting fishing practices that cause habitat destruction (McClanahan et al. 2008). Productivity of coral reefs is also tightly linked to coastal systems such as mangroves and seagrass meadows (Dorenbosch et al. 2005, Manson et al. 2005), which are essential juvenile habitats for many reef species and act as biological filters removing nutrients and sediments from the water column (Harborne et al. 2006). It is therefore imperative that these habitats are protected (Mumby and Steneck 2008). Finally, the underlying drivers of fisheries exploitation need to be addressed, which likely requires improving the economic development of coastal fishing communities to navigate socio-ecological traps (Cinner et al. 2009).

Our study demonstrates that a reduction in fishing pressure is positively correlated to a shallowing of the size spectra of coral reef fish communities and to an increase in the overall community biomass. However, we have also shown that coral degradation (through a combination of climate induced bleaching and the indirect effect of fishing-induced starfish outbreaks) and structural complexity loss can affect the size spectra of fish communities. Reduced habitat rugosity is associated with declines in small-bodied fishes, which lessens the steepness of the size spectra slope. Thus habitat degradation is likely to compound the direct effects that fishing has on the size distribution of fishes, as both small and large bodied fish will be negatively impacted when they occur concurrently. In a previous study (Wilson et al. 2008) we demonstrated that functional groups of fish do not accurately portray impacts of fishing and habitat loss because interspecific variation attenuates response within these groups. However, size spectra slope is a community measure that is sensitive to both fishing and habitat and therefore a valuable indicator of stress from both processes. As perturbation of reefs increases due to climate change, human population growth and expansion, the influence of habitat will have an increasingly important role in structuring reef fish communities, particularly in areas protected from fishing.

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Table 1. Co-efficients of habitat variables contributing to principle components 1,2 and 3 of habitat principle component analysis.

Habitat variable	PC1 (31%)	PC2 (18%)	PC3 (15%)
Topographic complexity	0.12	0.28	0.39
Rugosity	0.32	-0.45	0.07
Acropora	0.44	-.0.15	0.00
Coraline algae	-0.24	0.46	-0.15
Favites	0.44	0.09	0.23
Macroalgae	-0.18	0.15	0.46
Pocillipora	0.34	0.36	0.03
Porites	0.30	0.10	0.25
Soft coral	0.26	-0.05	-0.48
Sponges	-0.04	-0.35	0.42
Turf algae (EAM)	-0.29	-0.44	0.04

Table 2. Influence of fishing intensity and benthic composition on the size spectra of fish communities in the Lau islands, Fiji. Values are from forward stepwise multiple regression analyses. Partial correlation coefficients are in parentheses next to each of the variables included in the model.

year	df	F	P	R^2	Included variables
	Slope				
Both	3,26	5.1	0.007	0.371	Fishing (-0.2), PC1 (-0.3), PC3 (0.3)
2000	1,13	5.7	0.033	0.305	Fishing (-0.6)
2006	2,12	6.7	0.011	0.529	PC1 (-0.6), PC3 (0.7)
	Midpoint				
Both	4,25	6.5	0.001	0.511	Fishing (-0.5), PC1 (-0.5), PC2 (0.5), PC3 (-0.3)
2000	2,12	2.4	0.133	0.285	PC1 (0.5), PC2 (-0.4)
2006	2,12	2.3	0.141	0.276	PC2 (-0.4), PC3 (0.3)

Figure legends

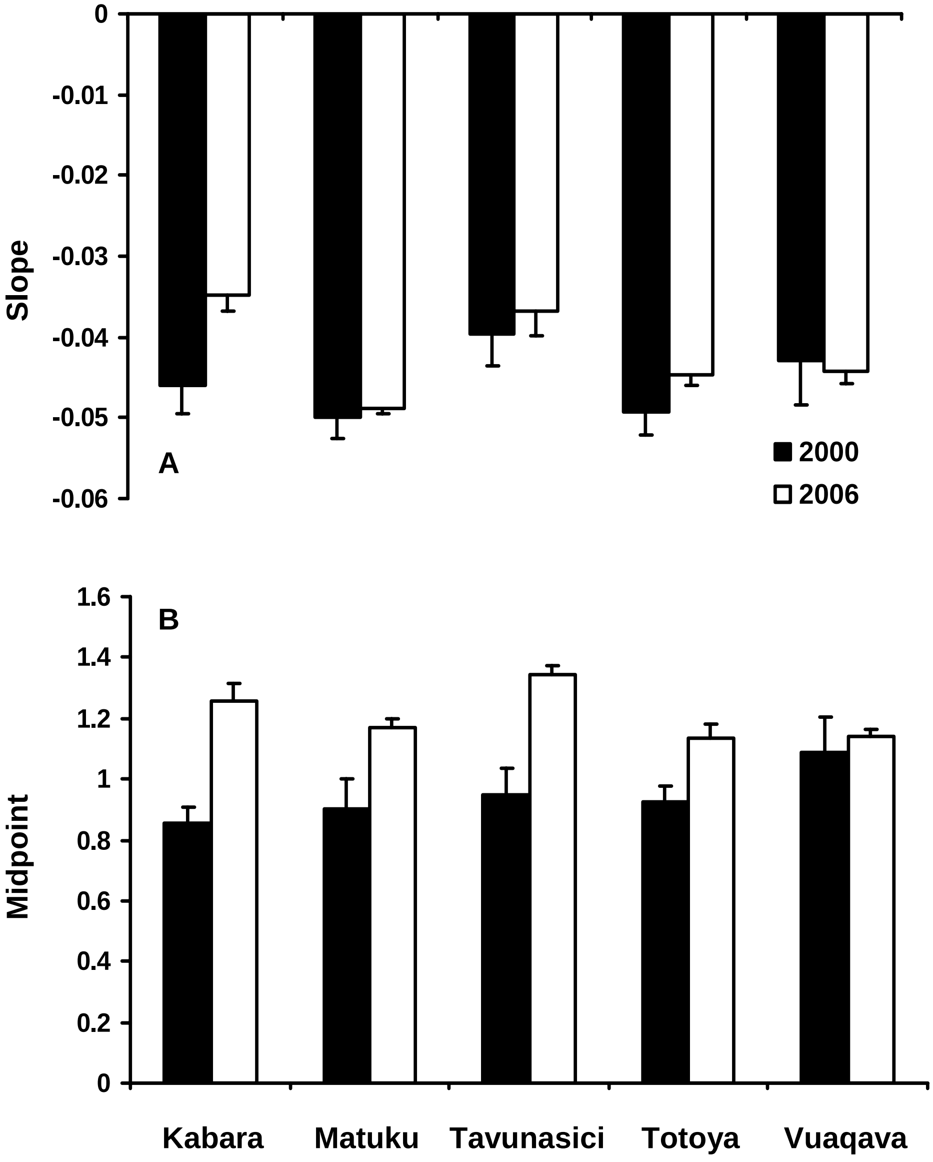
Figure 1. Spatial and temporal changes in size spectra descriptors of fish communities from five Lau islands. Means and standard errors calculated from three sites at each island.

Figure 2. Temporal shifts in the size distribution of coral reef fish at Lau Islands, Fiji. Bars represent the mean abundance difference of fish between 2000 and 2006. White bars are a subset of the data which only includes species that attain a maximum total length of 20 cm or less. Means and standard errors calculated from n = 5 islands

Figure 3. Influence of fishing on A. slope and B. midpoint from size spectra analyses of fish communities in the Lau Islands, Fiji.

Figure 4. Influence of habitat on the slope and midpoint of size spectra analyses of fish communities in the Lau Islands, Fiji. Habitat assessment based on scores from principle component analysis of 11 habitat variables. Percentages adjacent to PC1, 2 and 3 are the amount of variation in habitat data explained by that principal component. Habitat variables correlated with each component (correlation co-efficient > 0.3) are listed below each component. Trf *Turf algae*, Acr *Acropora*, Fav *Favites*, Poc *Pocillopora*, Por *Porites*, Rug *Rugosity*, Spo *Sponge*, CAlg *Coraline algae*, Top *Topographic complexity*, Sof *Soft coral*, Mac *Macroalgae*.

Figure 1.



0
-0.01
-0.02
-0.03
-0.04
-0.05
-0.06
Slope
A
■ 2000
□ 2006
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
Midpoint
B
Kabara
Matuku
Tavunasici
Totoya
Vuaqava

Figure 2.

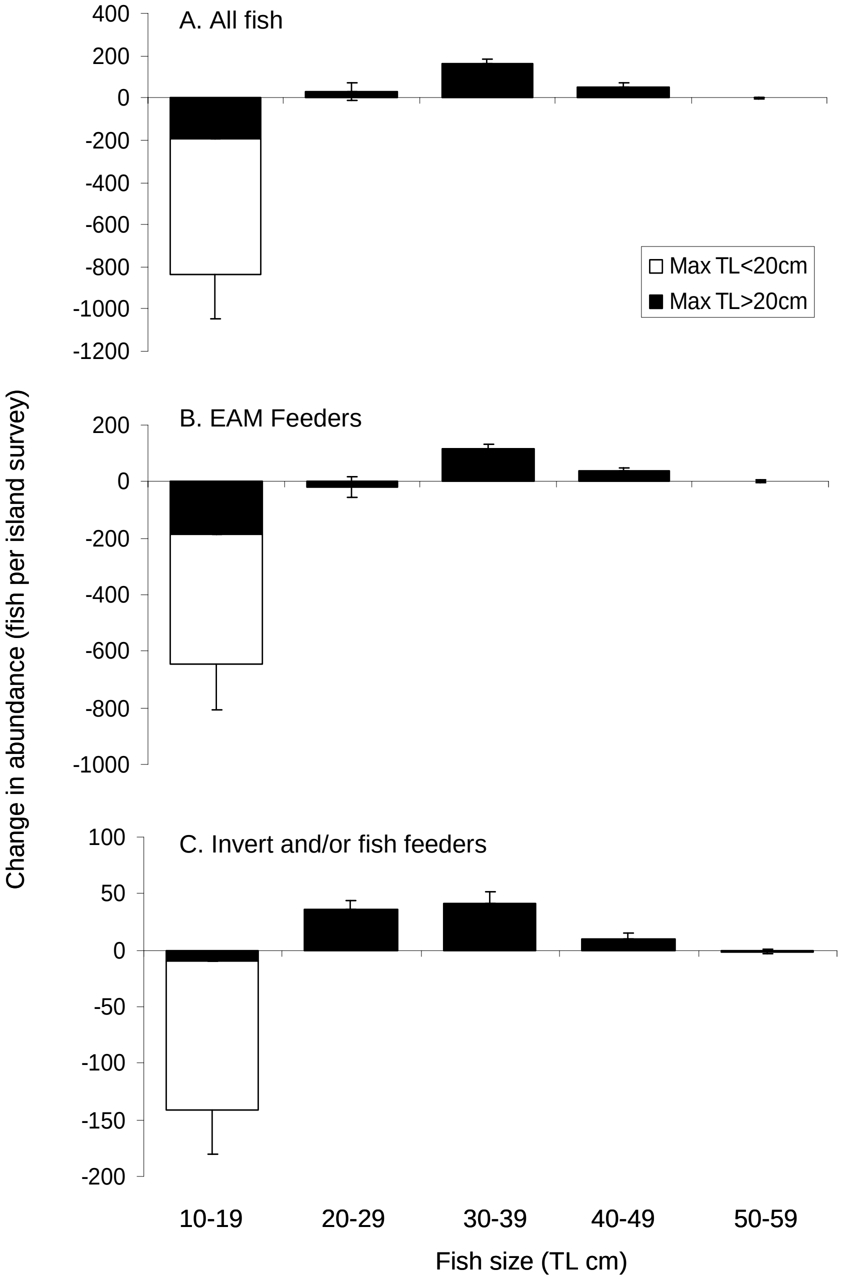

A. All fish
400
200
0
-200
-400
-600
-800
-1000
-1200
□ Max TL<20cm
■ Max TL>20cm
B. EAM Feeders
200
0
-200
-400
-600
-800
-1000
C. Invert and/or fish feeders
100
50
0
-50
-100
-150
-200
10-19
20-29
30-39
40-49
50-59
Fish size (TL cm)
Change in abundance (fish per island survey)

Figure 3.

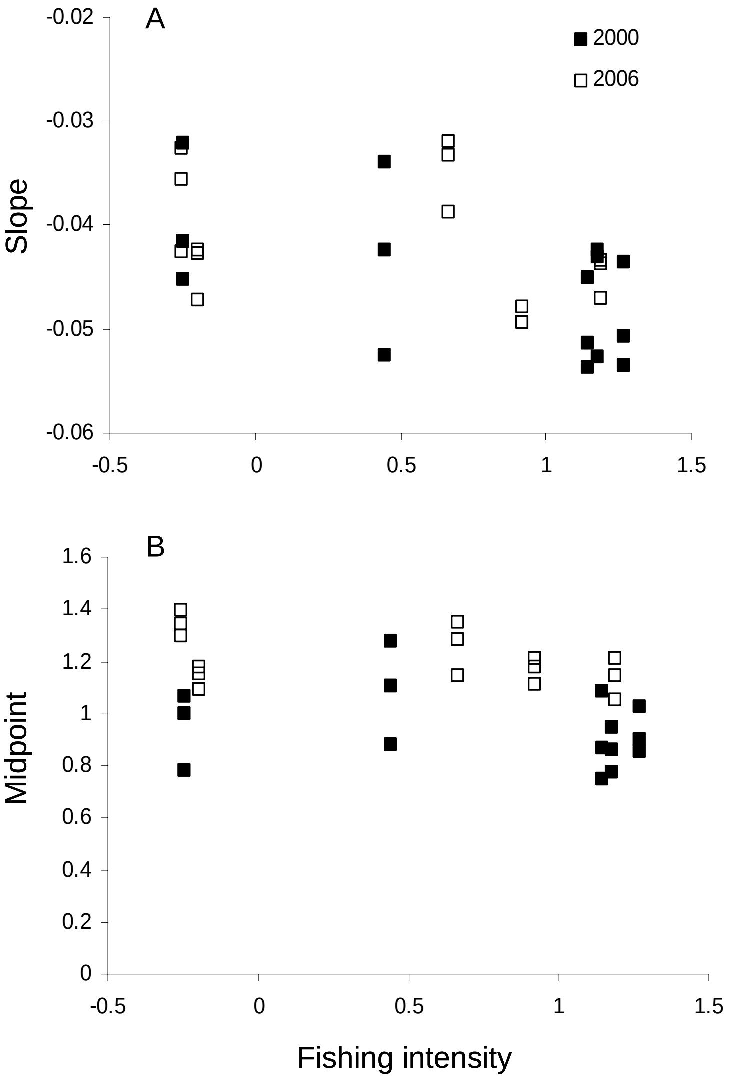
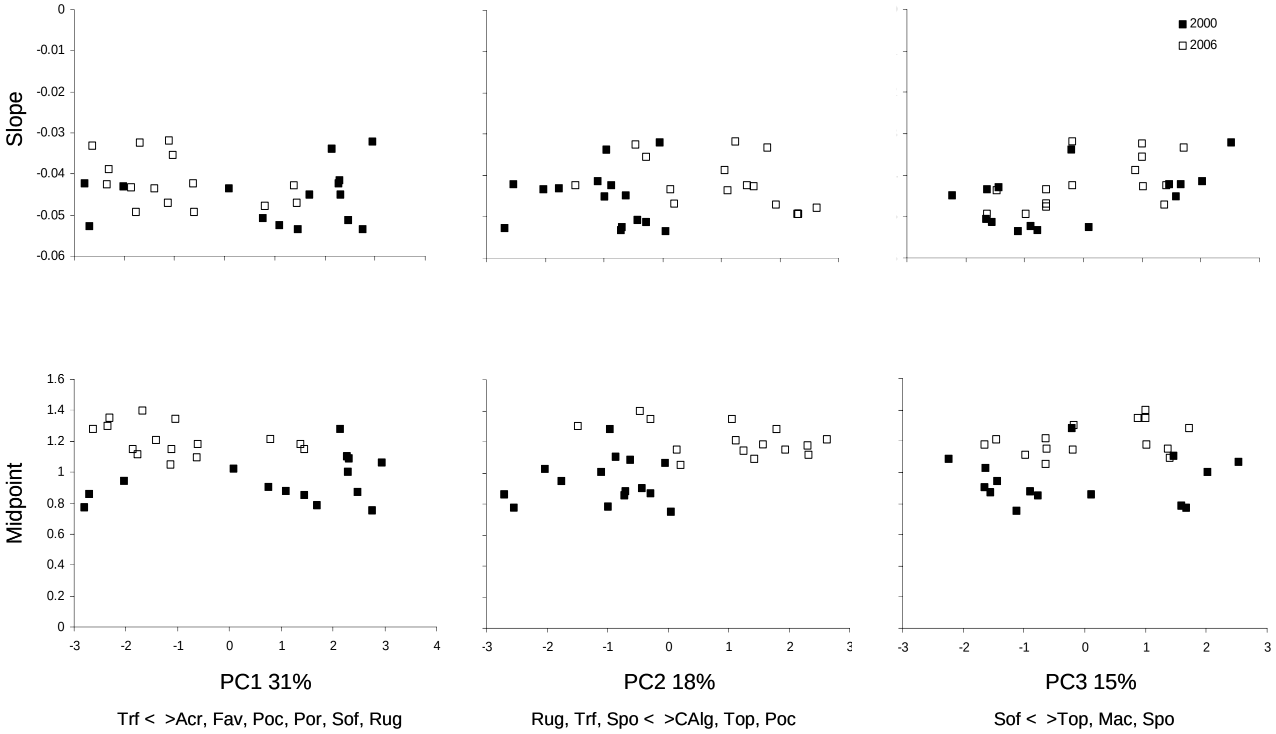

A
Slope
-0.02
-0.03
-0.04
-0.05
-0.06
■ 2000
□ 2006
-0.5
0
0.5
1
1.5
B
Midpoint
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-0.5
0
0.5
1
1.5
Fishing intensity

Figure 4.


Slope
0
-0.01
-0.02
-0.03
-0.04
-0.05
-0.06
■ 2000
□ 2006
Midpoint
1.6
1.4
1.2
1
0.8
0.6
0.4
0.2
0
-3
-2
-1
0
1
2
3
4
PC1 31%
Trf < >Acr, Fav, Poc, Por, Sof, Rug
PC2 18%
Rug, Trf, Spo < >CAlg, Top, Poc
PC3 15%
Sof < >Top, Mac, Spo