

NAJ Graham · NK Dulvy · S Jennings · NVC Polunin

Size-spectra as indicators of the effects of fishing on coral reef fish assemblages

Received: 12 October 2003 / Accepted: 11 November 2004 / Published online: 25 January 2005
© Springer-Verlag 2005

Abstract The data requirements and resources needed to develop multispecies indicators of fishing impacts are often lacking and this is particularly true for coral reef fisheries. Size-spectra, relationships between abundance and body-size class, regardless of taxonomy, can be calculated from simple sizeabundance data. Both the slope and the mid-point height of the relationship can be compared at different fishing intensities. Here, we develop size-spectra for reef fish assemblages using body size-abundance data collected by underwater visual census in each of ten fishing grounds across a known gradient of fishing intensity in the Kadavu Island group, Fiji. Slopes of the size-spectra became steeper ($F_{9,69}=3.20$, $p<0.01$) and the height declined ($F_{9,69}=15.78$, $p<0.001$) with increasing fishing intensity. Regressions of numbers of individuals per size class across grounds were negative for all size classes, although the slope was almost zero for the smallest size class. Response to exploitation of each size class category was greatest for larger fish. Steepening of the slope with increasing fishing intensity largely resulted from reductions in the relative abundance of large fish and not from the ecological release of small fish following depletion of their predators. The slope and height of the size-spectrum appear to be good indicators of fishing effects on reef fish assemblages.

Keywords Ecosystem based fishery management · Size spectra · Coral reef fisheries · Community structure · Indirect effects · Fisheries management

Introduction

The world's fisheries provide important food sources for many countries (Watson and Pauly 2001) and coral reef associated fisheries are extremely important to many less industrialised nations (McManus et al. 2000; Russ 1991). Since the majority of the world's coral reefs are found in countries where human populations are likely to double within the next 30–50 years, pressure upon these ecosystems will inevitably increase (McManus 1997). Decline in the production of fisheries, the collapse of fisheries and the wider impacts of fishing on ecosystems have prompted calls for new approaches to assess the implications of fishing on the ecosystem (Gislason et al. 2000; Link 2002). Indicators of the status of marine ecosystems are required to underpin these objectives (Rice 2003). Although potential indicators have been identified, their data requirements often make application unfeasible, particularly in coral reef fisheries where the resources needed for assessment and management are usually very limited (Jennings et al. 1999; Johannes 1998; Reynolds et al. 2001).

Size-based analyses require fairly simple data collection techniques and may provide useful metrics of community responses to exploitation by fisheries (Rice 2000; Rochet and Trenkel 2003). The size composition of communities can usefully be described using size-spectra, relationships between abundance by body size class and body size of the aggregated assemblage regardless of taxonomy (Kerr and Dickie 2001). The resulting slopes and mid-point heights of the size-spectra respond to changes in mortality rates and the indirect effects of mortality. Steepening of the slope can be the result of a decrease in the number of large fish, an increase in the number of small fish, or both. The

Communicated by Biological Editor K.S. Sealey

NAJ Graham (✉) · NVC Polunin
School of Marine Science and Technology,
University of Newcastle, Newcastle-upon-Tyne,
NE1 7RU, UK
E-mail: n.a.j.graham@ncl.ac.uk
Tel.: +44-191-2225868
Fax: +44-191-2227891

NK Dulvy · S. Jennings
Lowestoft laboratory, Centre for Environment,
Fisheries and Aquaculture Science, Lowestoft,
NR33 0HT, UK

mid-point height value is an overall indication of the abundance of the community (Trenkel and Rochet 2003). Size-spectra have been applied to size composition data from demersal trawl surveys (Bianchi et al. 2000; Gislason and Rice 1998; Rice and Gislason 1996), but until recently (Dulvy et al. 2004) no attempt has been made to apply the technique to coral reef fishes.

In general terms larger bodied animals are exploited preferentially because they are more valuable and obvious to hunt (Purvis 2001). Fishing is no exception, but as the fishery develops and large fish are depleted, fishers target sequentially smaller individuals (Pauly et al. 1998). Since body size is broadly correlated with trophic level, these larger individuals are often top predators and a decline in their biomass is the most marked community response to exploitation by fisheries (Jennings and Polunin 1997; Russ and Alcala 1989). The indirect effects of the removal of large predators are not always easy to detect, since competition or predation effects are masked or mediated by environmental variation and recruitment variation (Jennings and Kaiser 1998). Indeed, the dynamics of individual predator and prey species or small groups of predator and prey species may or may not be linked (Graham et al. 2003; Holbrook and Schmitt 2002; Jennings and Polunin 1997; Jennings et al. 1995; Russ and Alcala 1989, 1998; Watson and Ormond 1994), while at the highest levels of aggregation (across all prey species and individuals in the food web) energetic considerations suggest that reduced predator abundance will result in prey release. The extent to which such prey release is observed in size-spectra is likely to depend upon the extent to which the sample reflects the total abundance of individuals in the foodweb.

Here, we examine the response of reef fish size-spectra to spatial variation in fishing effort and consider whether the slopes and mid-point heights of the spectra provide useful indicators of the effects of fishing on the community. Marine tenure systems in parts of the South Pacific lead to persistent spatial differences in fishing effort and provide an ideal opportunity to assess the responses of size-spectra to fishing at large spatial scales.

Methods

Study sites and data collection

The study was conducted within ten discrete fishing grounds (qoliqoli) on the northwestern coast of Kadavu Island, Fiji (Fig. 1). Inhabitants of specific villages have exclusive rights to fish the reefs enclosed in their qoliqoli and fisher exchange and poaching is negligible in this well-defended sea ownership system. Since the numbers of resident fishers vary among qoliqoli and since fish are caught almost exclusively for subsistence and provide the primary source of protein, an index of fishing intensity can be calculated by dividing the length of well-developed reef front by the number of people with

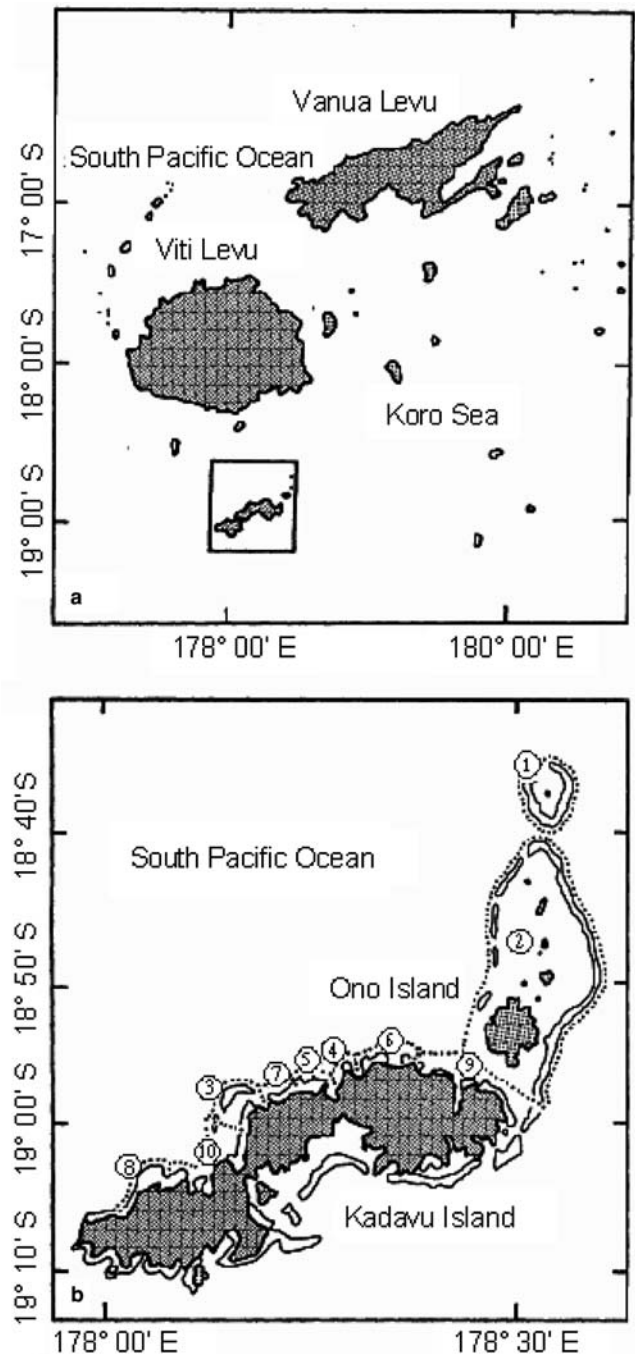


Fig. 1 a Location of Kadavu island group within Fiji, and b the ten qoliqoli surveyed in the study labelled in ascending order of fishing intensity. Land is shaded, unbroken lines indicate major reef areas, and broken lines indicate qoliqoli boundaries

fishing rights (Jennings and Polunin 1997). This fishing intensity index is robust and has been successfully related to fishing behaviour and activity and correlates well with catch rates and estimates of reef fish yields (Jennings and Polunin 1995, 1996). Furthermore, these fishing gradients have enabled large-scale assessments of both the direct and indirect effects of non-habitat destructive fishing on coral reefs (Dulvy et al. 2002, 2004; Jennings and Polunin 1997).

Fish were surveyed by underwater visual census at seven sites in each of the ten qoliqoli. Sites were randomly selected 100-m sections of well-developed reef on the outer slope. Within each of the seven sites, 12 point counts (Jennings and Polunin 1996; Samoils and Carlos 1992) were used to estimate the abundances and lengths of 144 species (non-cryptic diurnally active fishes > 8 cm fork length in families Epinephelinae, Lutjanidae, Scaridae, Labridae, Mullidae, and Chaetodontidae). The majority of the fish species surveyed were primary or secondary fishery targets (see Jennings and Polunin 1997 for full species list and details of the fishery). Fisheries-dependent surveys in the same area indicate that fish are targeted primarily on rocky and coralline areas and are targeted using non-destructive techniques, primarily hook and line and spear (Jennings and Polunin 1995). Point counts were centred on the 6-m depth contour to standardise counts and habitat type across sites and qoliqoli. The nested hierarchical sampling design enabled small-scale heterogeneity to be accounted for and summarised to the scale of the fishery. Fish length was estimated to the nearest 1 cm and accuracy of estimation was maintained by practising with objects of known length. Fish were surveyed sequentially with the most active, mobile species being counted first. Each point count took 6–13 min depending on the number and diversity of fish and complexity of habitat and all counts were made by S Jennings in 1995/1996 (see Jennings and Polunin 1997 for more detail). Percentage cover of different substrates (massive coral, branching coral, rock, rubble, and sand) and a six-point topographic complexity scale were used within the perimeter of each replicate count to assess habitat variables. These data were analysed in detail by Jennings and Polunin (1997) and indicated that there were no significant differences in habitat between the surveyed qoliqoli.

Data treatment and analysis

The individual fish censused in each qoliqoli were allocated to 11×5 cm body length classes from 11 to 65 cm, regardless of taxonomy, trophic, or other groupings. The slopes of the size-spectra were calculated from linear regressions of $\log_{10}(x + 1)$ numbers per size class on the rescaled \log_{10} mid-point of each length class. Centring of the independent variable gives a value for mid-point height as opposed to the intercept (Daan et al. 2003; Rochet and Trenkel 2003), which removes the correlation between slope and intercept. The mid-point height is effectively an index of community abundance-biomass (Trenkel and Rochet 2003). The significance of the relationship between slope or mid-point height and fishing intensity was tested using linear regression. Patterns of change in slope and height across the fishing intensity gradient were assessed using one-way ANOVAs (sites within qoliqoli as replicates). Tukey's test was used to identify significant differences in slope and mid-point height among qoliqoli. Normality of data was

examined with normplots and histograms, while Levene's test was applied to test for homogeneity of variances.

The significance of relationships between abundance and fishing intensity in each of the 11 size classes separately was also tested with linear regression. Changes in each length class category due to exploitation were calculated as the difference in predicted (from regression line) numbers between the lowest and highest fishing intensities.

Results

Slopes of the size-spectra were significantly steeper at high fishing intensity ($F_{9,69}=3.20$, $p < 0.01$) (Fig. 2). However, the data points were scattered and, in a comparison among qoliqoli, Tukey's test revealed that only qoliqoli 2 differed significantly from qoliqoli 5 (adjusted $p < 0.01$). Mean mid-point height of the size spectra declined significantly with fishing intensity ($F_{9,69}=15.78$, $p < 0.001$) (Fig. 3). Tukey's test indicated that mid-point height differed significantly between a number of the qoliqoli (Table 1).

Relationships between abundance and fishing intensity within size classes were all negative, although the decline in abundance with fishing was minimal for the

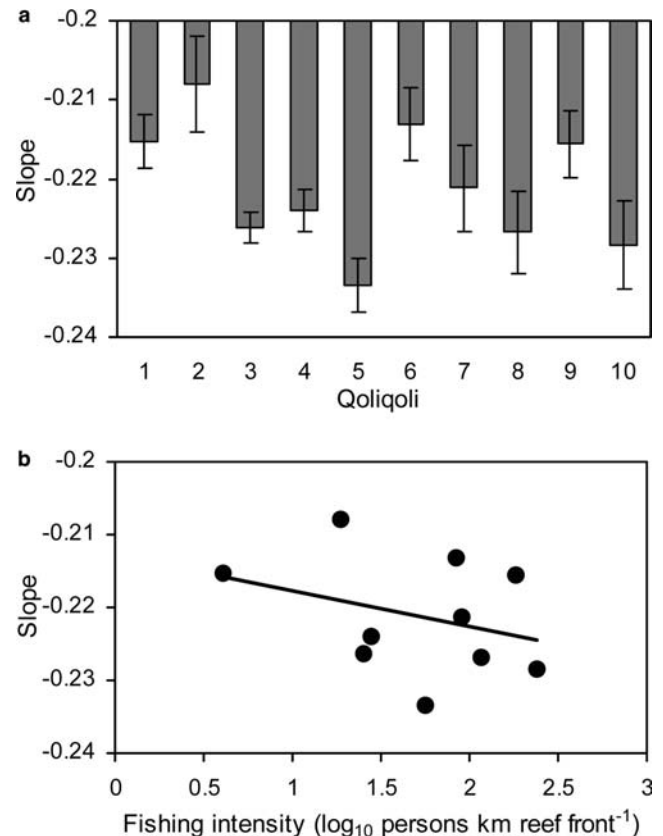
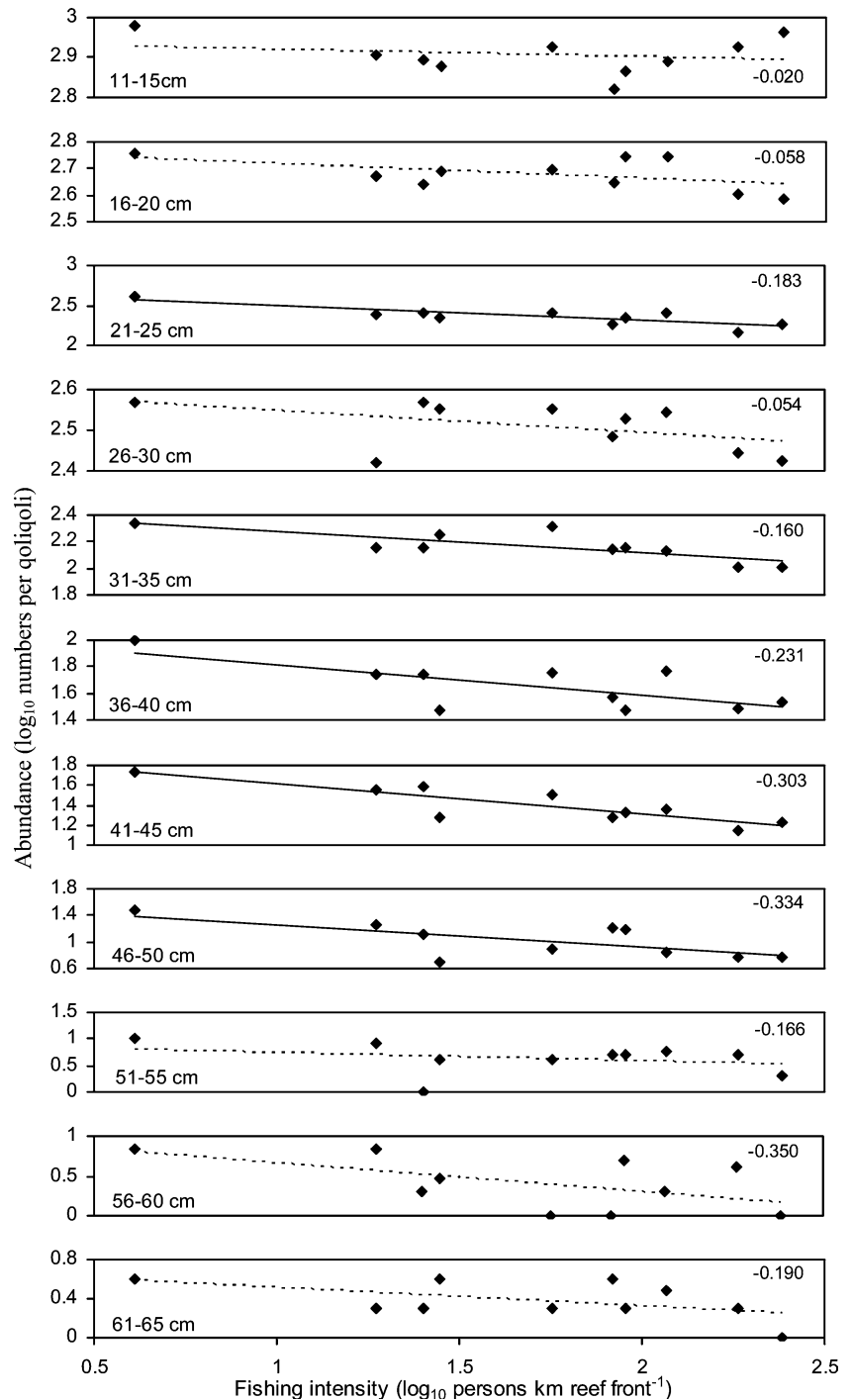


Fig. 2 Mean slopes of size-spectra for each qoliqoli \pm SE (a) and the relationship between slope and fishing intensity (b)

Fig. 4 Relationship between density and fishing intensity in 5 cm body size categories. *Dashed and solid lines* indicate non-significant and significant linear regressions, respectively. Slope of the regression line is given for each size class category. Note that the scale on the y -axis varies between size classes



This study provides good evidence of the size-spectra slope of coral reef fish assemblages steepening in response to exploitation. The greater reduction of larger size classes than smaller size classes may be explained by greater responses of larger fish to exploitation attributable to life history characteristics. Indeed, a previous study on the same data set demonstrated that larger species were more vulnerable to exploitation than their nearest relatives (Jennings et al. 1999). The extent to which the reduction in the mean size of fishes in the community corresponds to a

reduction in trophic level is not clear. This is because size and trophic responses to fishing can become decoupled when sampled communities do not reflect all the pathways of energy transfer in a marine ecosystem and when individual species show different relationships between body size and trophic level. In general, changes in size structure due to the differential effects of fishing on species and populations with different life histories will be a stronger and more universal indicator of fishing effects than changes in mean trophic level (Jennings et al. 2002).

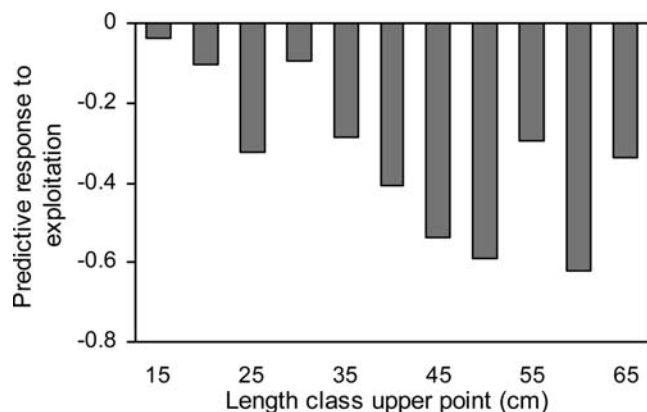


Fig. 5 Predicted responses to exploitation of 5 cm body size categories, calculated as the predicted difference in abundance (from regression line) between the lowest and highest fishing intensities

The relationships between fishing intensity and abundance by size class clearly demonstrate a decline in abundance of all size classes surveyed with increasing fishing pressure, and provide no evidence for the ecological release of smaller fish. Therefore, the steepening of the slope in the size-spectrum with increasing fishing intensity is principally a result of a greater reduction in the abundance of larger than smaller fish, and not ecological release of small fish from predation or competitive pressure.

Although no evidence of ecological release was apparent in this survey, it is important to highlight that (1) only a select number of species [144] and families [6] were included in the study, (2) many of the species surveyed are targeted by the fishery (see Jennings and Polunin 1997), and (3) no size classes < 11 cm were incorporated in the analysis. The minimal decline in abundance of fishes in the smallest size class suggests that they can withstand fishing impacts in the qoliqoli. This may be because these size classes are selected against or avoided by the fishers, or because many fish in these size classes have very high levels of productivity. However, much of the total biomass of animals in the food web in these size classes may be found in other fish and invertebrate species. Effects of predatory or competitive release might be detected if more of the individuals in these size classes were censused. Indeed, a similar study in the Lau Island group of Fiji incorporating 17 families of fish demonstrated weak ecological release of smaller size categories using size-spectra analysis (Dulvy et al. 2004). Further surveys of entire communities and smaller size classes may give a clearer picture of the extent of aggregated ecological release on coral reefs.

The majority of studies on coral reef fisheries conducted using underwater visual census methods, including this one, are limited to a certain depth range and standardised habitat type due to the constraints of SCUBA. However, as the depth and habitat are stan-

standardised among qoliqoli, and there is a high level of replication, the reef fish assemblage on the reef slope of these qoliqoli is well sampled, as reflected in the results. The fish assemblage is most homogeneous on these reef slope habitats, increasing the power to detect fishing effects. Furthermore, most of the fishing in these qoliqoli is on rocky and coralline reefs (Jennings and Polunin 1995). A further survey and analysis of lagoonal and deeper water fish assemblages would be needed to ascertain whether similar trends are apparent in other habitats.

In contrast to the many length-based methods used for single species stock assessments (see Pauly and Morgan 1987; Sparre et al. 1989), size-spectra analysis assesses the size structure of the whole sampled assemblage, regardless of taxonomy. Therefore, the technique may not be used to assess specific fishery target species, but is useful to assess the overall size structure of the assemblage. This is important as reef fisheries are multispecies and often opportunistic with an array of fishing methods targeting a wide size range. Size-spectra allow assessment at this multispecies level and can help elucidate both the primary and secondary impacts of fishing.

We conclude that size-spectra can be compiled for reef fish assemblages from easily collected size-abundance data and the slopes and mid-point heights of the size-spectra have the potential to be used as indicators of fishing effects. As size estimation is an easily trainable technique, the approach is likely to be very valuable in assessing the status of reef fish assemblages when the reliability of species identification is uncertain and/ or resources for conducting surveys are limited. However, a range of further work would be necessary to develop and test these indicators before they could be used to support any ecosystem approach to fishery management. Such work would need to include an assessment of the power of the indicators to detect fishing as opposed to environmental effects, development of methods for setting target and reference levels, and improved understanding of the relative effects of direct and indirect fishing effects on the slope of the size-spectrum.

Acknowledgements We thank Robin South and staff of the Marine Studies Programme at the University of the South Pacific, and the Fijian Government, Native Lands Trust Board, Fiji Fisheries Division, and Fijian Affairs for support. Much assistance came from the villagers of the ten qoliqoli surveyed. Original data collection was funded by the Natural Environment Research Council (UK).

References

- Beukers JS, Jones GP (1997) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114:50–59
- Bianchi G, Gislason H, Graham K, Hill L, Jin X, Koranteng K, Manickchand-Heileman S, Payá I, Sainsbury K, Sanchez F, Zwanenburg K (2000) Impact of fishing on size composition and diversity of demersal fish communities. *ICES J Mar Sci* 57:558–571

- Daan N, Gislason H, Pope JG, Rice J (2003) Changes in the North Sea fish community: evidence of indirect effects of fishing? *ICES CM N* 10:1–11
- Doherty PJ (1991) Spatial and temporal patterns in recruitment. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic, San Diego, pp 261–293
- Dulvy NK, Mitchell RE, Watson D, Sweeting C, Polunin NVC (2002) Scale-dependant control of motile epifaunal community structure along a coral reef fishing gradient. *J Exp Mar Biol Ecol* 278:1–29
- Dulvy NK, Polunin NVC, Mill AC, Graham NAJ (2004) Size structural change in lightly exploited coral reef fish communities: evidence for weak ecological release. *Can J Fisheries Aquat Sci* 61:466–475
- Gislason H, Rice J (1998) Modelling the response of size and diversity spectra of fish assemblages to changes in exploitation. *ICES J Mar Sci* 55:362–370
- Gislason H, Sinclair M, Sainsbury K, O'Boyle R (2000) Symposium overview: incorporating ecosystem objectives within fisheries management. *ICES J Mar Sci* 57:468–475
- Graham NAJ, Evans RD, Russ GR (2003) The effects of marine reserve protection on the trophic relationships of reef fishes on the Great Barrier Reef. *Environ Conservation* 30:200–208
- Holbrook SJ, Schmitt RJ (2002) Competition for shelter space causes density-dependent predation mortality in damselfishes. *Ecology* 83:2855–2868
- Jennings S, Kaiser MJ (1998) The effects of fishing on marine ecosystems. *Adv Mar Biol* 34:201–352
- Jennings S, Polunin NVC (1995) Comparative size and composition of yield from six Fijian reef fisheries. *J Fish Biol* 46:28–46
- Jennings S, Polunin NVC (1996) Effects of fishing effort and catch rate upon the structure and biomass of Fijian reef fish communities. *J Appl Ecol* 33:400–412
- Jennings S, Polunin NVC (1997) Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs* 16:71–82
- Jennings S, Grandcourt EM, Polunin NVC (1995) The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs* 14:225–235
- Jennings S, Reynolds JD, Polunin NVC (1999) Predicting the vulnerability of tropical reef fishes to exploitation with phylogenies and life histories. *Conservation Biol* 13:1466–1475
- Jennings S, Greenstreet SPR, Hill L, Piet GJ, Pinnegar JK, Warr KJ (2002) Long-term trends in the trophic structure of the North Sea fish community: evidence from stable isotope analysis, size-spectra and community metrics. *Mar Biol* 141:1085–1097
- Johannes RE (1998) The case for data-less marine resource management: examples from tropical nearshore finfisheries. *Trends Ecol Evol* 13:243–246
- Kerr SR, Dickie LM (2001) *The biomass spectrum: a predator-prey theory of aquatic production*. Columbia University Press, New York
- Link JS (2002) What does ecosystem-based fisheries management mean? *Fisheries* 27:18–21
- McClanahan TR, Arthur R (2001) The effect of marine reserves and habitat on populations of east African coral reef fishes. *Ecol Appl* 11:559–569
- McManus JW (1997) Tropical marine fisheries and the future of coral reefs: a brief review with emphasis on Southeast Asia. *Coral Reefs* 16:S121–S127
- McManus JW, Menez LAB, Kesner-Reyes KN, Vergara SG, Ablan MC (2000) Coral reef fishing and coral-algal phase shifts: implications for global reef status. *ICES J Mar Sci* 57:572–578
- Pauly D, Morgan GR (1987) Length-based methods in fisheries research. In: *ICLARM Conference Proceedings* 13, 468 p
- Pauly D, Christensen V, Dalsgaard J, Froese R, Torres Jr F (1998) Fishing down marine food webs. *Science* 279:860–863
- Purvis A (2001) Mammalian life histories and responses of populations to exploitation. In: Reynolds JD, Mace GM, Redford KH, Robinson JG (eds) *Conservation of exploited species, Conservation Biology* 6. Cambridge University Press, Cambridge, pp 169–181
- Reynolds JD, Jennings S, Dulvy NK (2001) Life histories of fishes and population responses to exploitation. In: Reynolds JD, Mace GM, Redford KH, Robinson JG (eds) *Conservation of exploited species, Conservation Biology* 6. Cambridge University Press, Cambridge, pp 147–168
- Rice JC (2000) Evaluating fishery impacts using metrics of community structure. *ICES J Mar Sci* 57:682–688
- Rice JC (2003) Environmental health indicators. *Ocean Coastal Management* 46:235–259
- Rice JC, Gislason H (1996) Patterns of change in the size spectra of numbers and diversity of the North Sea fish assemblage, as reflected in surveys and models. *ICES J Mar Sci* 53:1214–1225
- Rochet M-J, Trenkel VM (2003) Which community indicators can measure the impact of fishing? A review and proposals. *Can J Fisheries Aquat Sci* 60:86–99
- Russ GR (1991) Coral reef fisheries: effects and yields. In: Sale PF (ed) *The ecology of fishes on coral reefs*. Academic, San Diego, pp 601–635
- Russ GR, Alcala AC (1989) Effects of intense fishing pressure on an assemblage of coral reef fishes. *Mar Ecol Prog Ser* 56:13–27
- Russ GR, Alcala AC (1998) Natural fishing experiments in marine reserves 1983–1993: roles of life history and fishing intensity in family responses. *Coral Reefs* 17:399–416
- Samoilys M, Carlos GM (1992) Development of an underwater visual census method for assessing shallow water reef fish stocks in the south-west Pacific. Queensland Department of Primary Industries, Cairns
- Sparre P, Ursin E, Venema SC (1989) Introduction to tropical fish stock assessment. Part 1—Manual. *FAO Fisheries Technical Paper* 306/1. 375 p
- Steele MA (1999) Effects of shelter and predators on reef fishes. *J Exp Mar Biol Ecol* 233:65–79
- Trenkel VM, Rochet M-J (2003) Performance of indicators derived from abundance estimates for detecting the impact of fishing on a fish community. *Can J Fisheries Aquat Sci* 60:67–85
- Watson M, Ormond RFG (1994) Effect of an artisanal fishery on the fish and urchin populations of a Kenyan coral reef. *Mar Ecol Prog Ser* 109:115–129
- Watson R, Pauly D (2001) Systematic distortions in world fisheries catch trends. *Nature* 414:534–536