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REPORT

Coral reef cascades and the indirect effects of predator removal by exploitation

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Abstract

Fisheries exploitation provides the opportunity to examine the ecosystem-scale biodiversity consequences of predator removal. We document predatory reef fish densities, coral-eating starfish densities and coral reef structure along a 13-island gradient of subsistence exploitation in Fiji. Along the fishing intensity gradient, predator densities declined by 61% and starfish densities increased by three orders of magnitude. Reef-building corals and coralline algae declined by 35% and were replaced by non-reef building taxa (mainly filamentous algae), as a result of starfish predation. Starfish populations exhibited thresholds and Allee-type dynamics: population growth was negative under light fishing intensities and high predator densities, and positive on islands with higher fishing intensities and low predator densities. These results suggest the depletion of functionally important consumer species by exploitation can indirectly influence coral reef ecosystem structure and function at the scale of islands.

Keywords

Allee effect, biodiversity, ecosystem function, outbreaks, resilience, stability, sustainability.

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INTRODUCTION

Human exploitation of the seas has resulted in a greater than 90% decline in predator abundance worldwide (Jackson *et al.* 2001; Myers & Worm 2003). The collapse in predatory fishes is reflected by the local and regional extinction of more than 50 fish populations in the last century (Bellwood *et al.* 2003; Dulvy *et al.* 2003; Baum & Myers 2004). This rapid loss of a large functional component of shallow water marine biodiversity would be expected to have wider ecosystem consequences. The removal of consumers may have diverse and surprising outcomes (Menge 1997; Webster & Almany 2002) and the effects may be sufficient to influence aspects of marine ecosystem structure and function (Paine 1966; Dayton 1985; Estes & Duggins 1995; Shears & Babcock 2002; Duffy 2003; Steneck *et al.* 2003). Consequently, there is concern that the depletion of consumer fishes by exploitation may indirectly modify the structure and function of marine ecosystems, particularly of diverse systems such as coral reefs (Roberts 1995; Hughes *et al.* 2002; McClanahan *et al.* 2002).

The consequences of removing herbivores from ecosystems are relatively well understood compared with our understanding of the effects of removing predators (Hughes *et al.* 2003; Hawkins & Roberts 2004). Exploitation is thought to influence ecosystems via trophic cascades where predator removal results in elevated prey abundance, which in turn influences the base of the food web (Kitchell & Carpenter 1993; Pace *et al.* 1999; Pinnegar *et al.* 2000; Shurin *et al.* 2002). Cascades are more prevalent in less diverse systems such as rocky reefs and lakes, but there is some evidence for urchin and starfish-mediated cascades on coral reefs (Pace *et al.* 1999; McClanahan *et al.* 2002). In addition to cascading effects there is concern that anthropogenic impacts, such as exploitation or eutrophication, have the potential to cause unexpected shifts among multiple stable ecosystem states (May 1977; Scheffer *et al.* 2001; McClanahan *et al.* 2002).

Here, we examine a putative trophic cascade involving predatory fishes, the coral-eating crown-of-thorns starfish (*Acanthaster planci*) and reef-building corals (Ormond *et al.* 1990). The crown-of-thorns starfish feeds upon live corals causing the largest known pest-related disturbances on Indo-Pacific coral reefs and it is regarded as a major management problem (Birkeland & Lucas 1990; McClanahan *et al.* 2002). A number of mechanisms, including hydrography, hurricane disturbance, nutrient inputs and predator removal, have been suggested as potential causes or modulators of starfish outbreaks (Birkeland & Lucas 1990; Bradbury & Antonelli 1990; Ormond *et al.* 1990). Furthermore, predators can maintain prey in a state of negative population growth at small prey population sizes – an Allee effect (May 1977; Knowlton 1992). A search for dome-shaped patterns of prey population growth with negative growth at small population sizes would provide a test for an Allee effect.

Understanding the ecosystem effects of exploitation may be hindered by time lags (decades to centuries) between the onset of overfishing and the consequent changes in ecological communities, the confounding effects of destructive fishing techniques and other anthropogenic influences (Hughes 1994; Jackson *et al.* 2001). We study a series of 13 relatively pristine Fijian islands to construct a spatial gradient of fishing intensity over which we explore the structure of predatory fish and coral reef communities and starfish dynamics. Here, we show how exploitation-mediated predator removal is linked to starfish outbreaks via an Allee effect, which in turn modulates coral reef ecosystem structure and function.

METHODS

The Fijian study system consists of a series of 13 oceanic islands varying in area of coral reef and human population size (Table 1). An index of fishing intensity was calculated for each island by dividing the human population (1996 census) by the length of reef front (Jennings & Polunin 1997; Dulvy *et al.* 2002). This fishing intensity index has been found to be related to fishing behaviour and activity and correlates well with catch rates and estimates of reef fish yields (Jennings & Polunin 1995, 1996). Fijian fishing gradients have provided considerable insight into the direct and indirect ecological effects of non-habitat destructive fishing practices on coral reef systems (Jennings & Polunin 1996; Dulvy *et al.* 2002, 2004). The underlying assumption of spatial fishing gradients is that processes structuring the ecological communities of individual islands, e.g. large-scale hydrography or recruitment, are approximately equal across the archipelago and the only differences among islands are variations in human densities and the extent of coral reef (Jennings & Polunin 1997). The validity of this approach depends upon the integrity of replicates, i.e. no movement or interchange of fishers among islands and no poaching by external fishers. Fisher interchange and poaching were negligible owing to the well-defended sea ownership system, the large inter-island distances and paucity of ocean-going craft in the island group. Subsistence fishing for food only was practised using non-destructive fishing gears, mainly spears and hook and line (Dulvy *et al.* 2004). Agriculture is non-intensive, minimizing the degree of terrestrial sediment and nutrient inputs and there is no industrial development or other sources of pollution within 150 km radius of the Lau islands, Fiji.

Predatory fishes, starfish and barrier reef communities were surveyed at 13 islands each varying in fishing intensity (Fig. 1). Ecological censusing was conducted on shallow (7 m chart datum) leeward (western) outer reefs at a total of 13 islands, six of which were surveyed three times over a year (Table 1). Fish and starfish densities were estimated using SCUBA underwater visual census (UVC) in replicate 7 m radius point counts (Jennings & Polunin 1997; Samoilys & Carlos 2000). Six replicate point counts were haphazardly distributed within each area. For the purposes of this study we restricted the definition of predators to include all non-

Table 1 Survey locations and dates, number of areas surveyed, human population size, length of reef front, reef area and fishing intensity index (data sources in Appendix S1)

Island code	Fishing ground (Island)	Cruise 1, April 1999	Cruise 2, November 1999	Cruise 3, February 2000	Number of areas surveyed	Human population	Reef front length (km)	Reef area (km^2)	Fishing intensity (human population km^{-1} reef front)
A	Marabo		✔		3	10	7.6	3.5	1.3
B	Tavunasici	✔	✔	✔	3	20	7.6	4.0	2.6
C	Oneata			✔	3	156	48.6	95.0	3.2
D	Namuka-i-lau		✔		3	134	23.5	50.0	5.7
E	Vanuavatu			✔	5	89	14.8	12.5	6.0
F	Vuaqava	✔	✔	✔	3	100	15.1	17.0	6.6
G	Komo		✔		3	150	21.4	34.0	7.0
H	Tuvuca			✔	5	181	17.0	21.0	10.7
I	Totoya	✔	✔	✔	5	806	44.7	19.3	18.0
J	Matuku	✔	✔	✔	6	854	35.0	20.1	24.4
K	Moala	✔	✔	✔	8	1596	60.9	n/a	26.2
L	Kabara	✔	✔	✔	5	1012	23.4	44.5	43.3
M	Lakeba			✔	6	1982	39.8	155.0	49.8

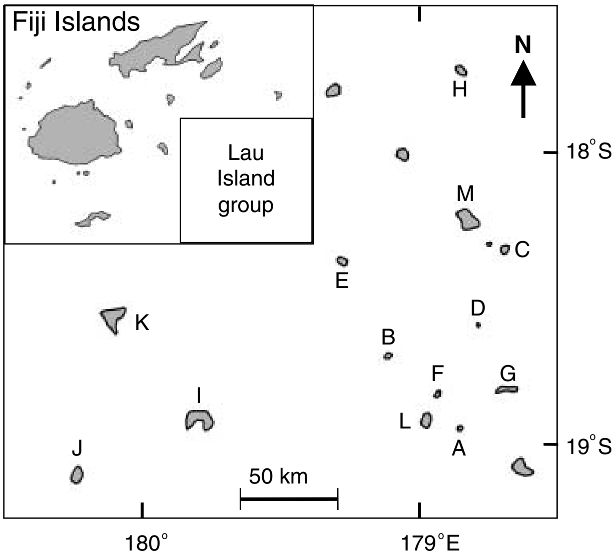

Figure 1 Map of the fishing grounds (islands) studied. Fishing grounds are labelled in ascending alphabetical order of fishing intensity (see Table 1). Inset shows the location of the Lau islands within Fiji.

pelagic reef-associated piscivorous and invertivorous fishes, which totalled 111 species (Table S1). Individuals >8 cm fork length were censused, length was estimated visually and converted to biomass estimates using published length : weight relationships (Dulvy *et al.* 2002, 2004). The surveyor (NKD) was trained in fish size estimation using objects of fixed sizes presented at 3 and 7 m distance underwater and fish size estimation was accurate to within 1 cm (Dulvy *et al.* 2004). Mobile species were censused first followed by sedentary and cryptic species. Individual fish entering the point count during the survey were not recorded (Samoilys & Carlos 2000). Following the fish count, starfish numbers were visually estimated within the area of the point count. The boundary of each point count was first visually estimated, and the radius was confirmed using a tape measure on completion of each count. Underwater visual radius estimates were accurate to within 5 cm. Underwater visibility was >20 m throughout the study and all surveys were conducted in daylight at least 1 h after sunrise and 1 h before sunset. Count time was not standardized because this was dependent on fish abundance, diversity and habitat complexity (Jennings & Polunin 1997). Fish density may be influenced by reef architectural complexity. Rugosity was measured by fitting a 3 m length of small-link chain to the reef surface perpendicular to the reef crest at the centre of each replicate point count. The corresponding horizontal distance was measured by tape and the ratio of chain length : horizontal length calculated. There was no significant variation in chain measures of reef rugosity along the fishing intensity gradient (Dulvy *et al.* 2002).

Percentage cover of each benthic category was calculated by overlaying transparent acetate sheets containing 20 randomly located 1 cm diameter circles over 30×500 cm^2 digital photographs recorded randomly in each of the UVC point counts (Dulvy *et al.* 2002). Reef building benthos included hard corals and coralline algae and non-reef building benthos included ascidians, blue–green algae, filamentous turf algae, fleshy macroalgae, *Palythoa* spp. soft corals and sponges. A stratified sampling design was used to appropriately summarize the small-scale heterogeneity into a large scale perspective, and three to eight areas were surveyed at each island and data were aggregated across survey periods then hierarchically, across replicates, areas and islands (Dulvy *et al.* 2002).

We used a general linear modelling framework to test for the existence of an Allee effect in starfish dynamics. Rates of starfish population change dn/dt could be calculated using two points in time for each of three islands, i.e. $n = 3$, and at three points in time for each of two other islands, i.e. $n = 4$, resulting in a total of $n = 7$. Rates were scaled to per capita rates $(1/n)$. A general linear model was then constructed using per capita rate of starfish population change, i.e. $n(t)^{-1}\,[n(t+1) - n(t)]$ as the response variable, and both $n(t)$ and $n(t)^2$ as predictors. The null expectation is of a negative linear relationship with a positive intercept, consistent with classical Lotka–Voltera dynamics where per capita population growth rate declines as intraspecific competition increases with density, whereas a statistically significant positive quadratic term indicates the dome-shaped relationship of an Allee effect.

RESULTS

The densities of predatory fishes were 61% lower at the most heavily fished islands compared with the most lightly fished islands ($r^2 = 0.59$, $F_{1,11} = 16.3$, $P < 0.001$; Fig. 2a). Starfish were absent at seven islands and present in six islands. At the islands where starfish were present their densities were positively related to fishing intensity ($r^2 = 0.71$, $F_{1,4} = 13.1$, $P < 0.05$; Fig. 2b). The consumption of coral by starfish resulted in mass coral mortality at the island scale. We observed an almost complete evolution of a starfish outbreak over the course of a year at only one of the islands. Starfish densities increased from 8000 to 113 000 individuals km^{-2} and declined to 50 000 individuals km^{-2} over the course of a year at Kabara Island (Fig. 3a). At this island hard coral cover declined from 44 to 8% and the cover of microfilamentous turf algae increased from 22 to 60% (Fig. 3b). The structure of the coral reef communities varied with predator density, the cover of carbonate-accreting reef building benthos was positively correlated with predator density (Fig. 4, $\rho = 0.56$, $t_{11} = 2.314$, $P < 0.05$). Overall, the reefs of lightly fished islands with high predator densities

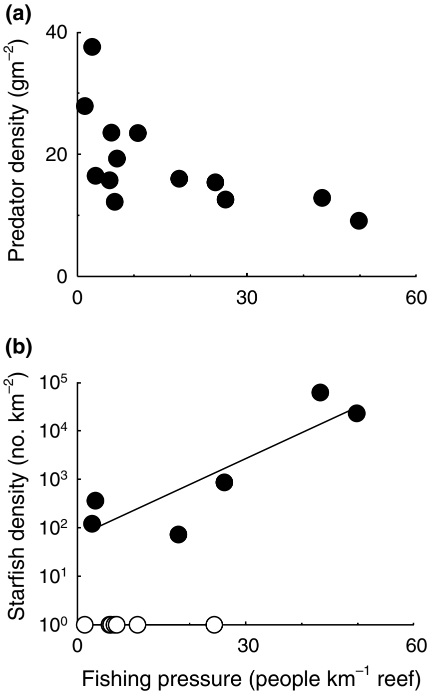

Figure 2 The relationship between fishing intensity and (a) average density of predatory fishes. (b) The relationship between fishing intensity and average density of crown-of-thorns starfish islands where starfish were present (●). Islands without starfish are denoted as (○).

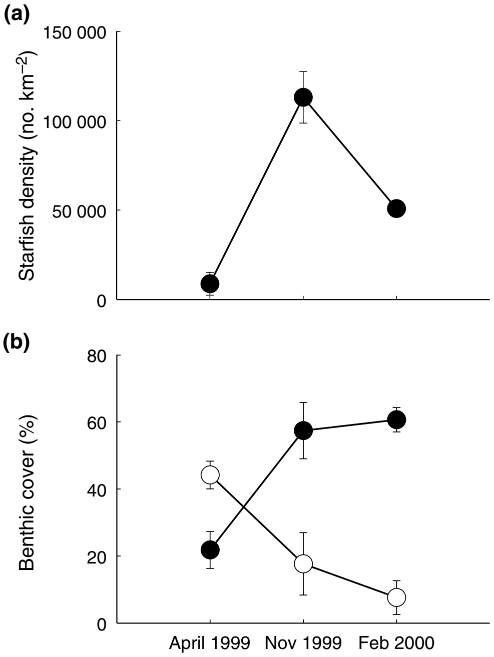

Figure 3 The change in (a) starfish density and (b) percentage cover of hard coral (○) and microfilamentous algae (●) at three time intervals at Kabara Island, which has the second highest fishing intensity, 43.3 people km^{-1} reef front (mean values ± 95% confidence intervals).

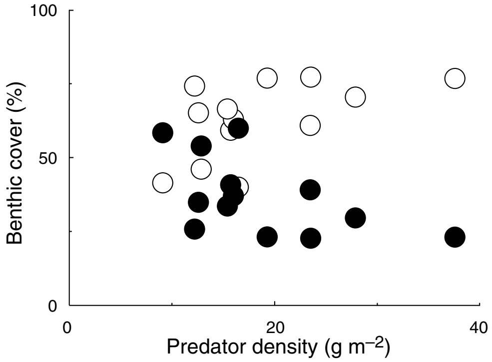

Figure 4 The relationship between predatory fish biomass and per cent cover of reef building (○) and non-reef building (●) benthos. Note the 95% confidence intervals averaged 5% and were less than the point diameter.

were dominated by carbonate-accreting reef building organisms – scleractinian hard corals and coralline algae (60–75% cover, Fig. 4). In contrast the reefs of the starfish-infested, heavily fished islands with low predator densities were dominated by rapid-colonizing fast-growing non-reef-building species, mainly turf algae (41–60% cover, Fig. 4).

Although the number of observations is small, there is a statistically significant domed relationship between starfish density and per capita population growth rate (significant quadratic term: $F_{1,4} = 8.22$, $P < 0.025$). The outbreak threshold was *c.* 250 (±235 estimated 95% confidence interval) starfish km^{-2} barrier reef (Appendix S1 in Supplementary Material). Starfish populations below this density exhibited declining population growth and above the threshold starfish populations exhibited positive population growth (Fig. 5a). Small declining starfish populations occurred at islands with lightest fishing intensities (Fig. 5b) and highest densities of predatory fishes (Fig. 5c). Large increasing starfish populations occurred at islands with higher fishing intensities (Fig. 5b) and lowest predator densities (Fig. 5c).

DISCUSSION

Changes in ecosystem state and Allee effects have been suspected in the sea but they have proven exceedingly difficult to detect at large spatial scales in marine systems (Hughes 1994; Estes & Duggins 1995; McClanahan 1995; Liermann & Hilborn 2001; Scheffer & Carpenter 2003; Steneck *et al.* 2003). Our data suggest that predator removal by subsistence exploitation may be sufficient to allow outbreaks of the crown-of-thorns starfish indirectly resulting in cascading changes in ecosystem structure and

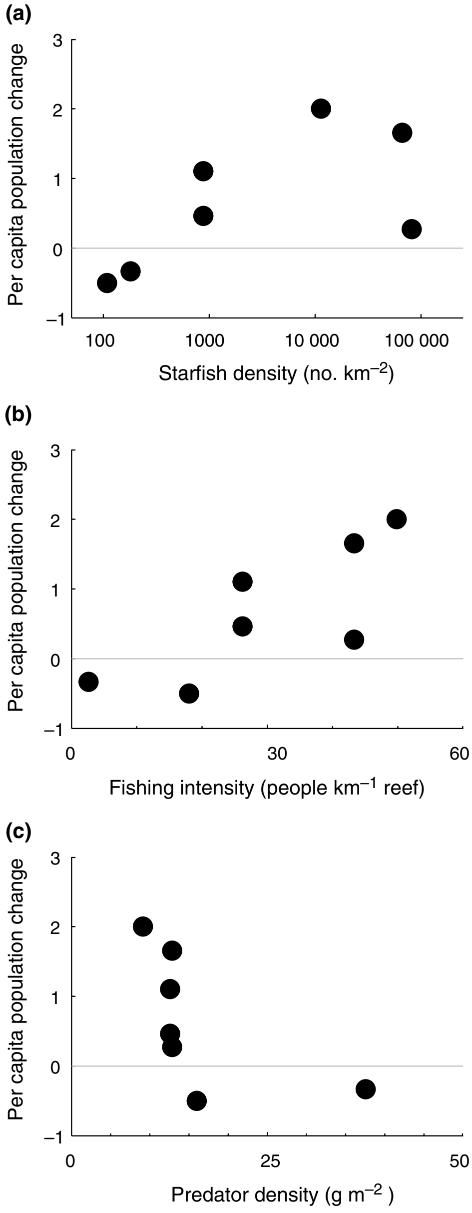

Figure 5 The relationship between per capita population growth of starfish and (a) average starfish density, (b) fishing intensity and (c) average density of predatory fishes. See methods for details of calculation of per capita population growth rate.

function. The higher densities of the coral-feeding starfish associated with subsistence fisheries exploitation have resulted in repeated shifts in benthic community structure from that dominated by carbonate accreting reef building organisms to domination by non-reef building organisms. This mechanism is consistent with other experimental and smaller-scale studies of terrestrial and aquatic systems which suggest consumer removal can have cascading effects upon ecosystem structure, function and diversity (Duffy 2003).

We have used a correlational approach to infer mechanistic links across trophic levels and in particular to infer that fishing intensity is the underlying causal factor. It should be borne in mind that causality can only be determined through experimental manipulation, thus we cannot exclude the possibility that the correlational link might be due to some other unknown factor associated with human population density and extent of coral reef. The relatively small spatial (1–100 km) and temporal (1 year) scale of our study limits the degree to which these findings can be extrapolated to other geographical areas and outbreak events. We attempted to include all possible starfish predators, but this broad-brush correlative approach using an aggregated carnivore guild runs the risk of attenuating or obscuring any single species predator-prey signal. This means our approach is conservative with respect to the hypotheses tested, at the expense of providing species-specific details of predator-prey interactions.

Our study focuses on the potential role of predators in controlling starfish dynamics and the evidence is elaborated upon in Appendix S2 (see Supplementary Material). However, this role must only be part of the explanation of starfish dynamics. Starfish were not observed at seven islands in this study, yet some islands overlapped in fishing intensity and predator density with islands where outbreaks occurred. We have only considered the link between starfish density and dynamics and an aggregated index of predator abundance, it is possible that a detailed examination of changes in species composition and functional attributes of the predator communities may help further explain variation in starfish density and dynamics. However previous work also suggests starfish outbreaks result from an interaction between predation and the variation in starfish recruitment – the recruitment-initiated predation hypothesis (Bradbury & Antonelli 1990; Ormond *et al.* 1990). Recruitment events of greater magnitude are required to swamp predators and outbreak in systems with higher predatory capacity. While bottom-up input of starfish recruitment is required to initiate events, the top-down predatory control modulates starfish recruitment into outbreaking or non-outbreaking populations. Both regional and local factors are thought to influence starfish recruit production and it may be worth quantifying recruitment and predation rates and processes to understand starfish dynamics and outbreak thresholds in Fiji and elsewhere in the Indo-Pacific region where outbreaks are known to occur.

The detection of phase shifts is fraught with difficulty, because of the nonlinear and dynamic nature of systems, and the problem of discerning causality at large spatial scales (Scheffer & Carpenter 2003). There are three features of these data which are consistent with thresholds and phase shifts (May 1977; Scheffer *et al.* 2001; Scheffer & Carpenter 2003). These features include the bimodal distribution of starfish among islands, i.e. outbreaking vs. non-outbreaking populations (Fig. 2b), the observation that slightly differing initial states (predator densities/fishing intensities, Fig. 2a) lead to substantially differing final states (reef building vs. non-reef building taxa, Fig. 4) and the existence of thresholds and Allee-type dynamics (Fig. 5a–c). These results are entirely consistent with the existence of strong nonlinearity and threshold dynamics as a consequence of subsistence exploitation in one of the most pristine reef systems remaining today. While these islands may not be pristine in a historical context (*sensu* Jackson *et al.* 2001), they exhibit among the lowest known contemporary human population densities relative to coral reef area, on average Fiji has 83 people km^{-2} reef area and these Lau Island study sites have human population densities ranging between two and 42 people km^{-2} reef area (Table 1). By comparison, other major coral reef study sites are based in countries with comparatively high population densities, e.g. Australia, 391; St Lucia, 975; Hawaii, 1711; Jamaica, 2140; Philippines, 32 380; Kenya, 48 158 people km^{-2} reef area (Appendix S1).

The rate of coral reef loss, at least in some parts of the world, is proceeding at a rate similar to or in excess of the rates of rainforest clear-felling (Gardner *et al.* 2003; Pandolfi *et al.* 2003). There is a good understanding of the mechanisms and importance of impacts such as hurricane disturbance, disease, coral bleaching and the effects of herbivore removal upon coral cover and reef health (Hughes *et al.* 2003; Hawkins & Roberts 2004). By comparison the impacts of predator removal on coral reefs have been relatively unstudied; this is not surprising given the large spatial scale of study required, the paucity of suitable study systems, the nonlinear dynamics and cross trophic level effects outlined above. These findings provide an additional challenge for biodiversity protection and coral reef management strategies. Starfish outbreaks have occurred on some Australian reefs nearly every decade in recent history despite the protection of the Great Barrier Reef Marine Park. These data suggest the maintenance of a minimum level of predators across reefs may be a useful management approach (Fig. 5c). Marine protected areas provide patches of elevated fish abundance in the face of exploitation (Roberts *et al.* 2001; Halpern & Warner 2002) and their utility in protecting reefs from pest outbreaks is worth exploring further.

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SUPPLEMENTARY MATERIAL

The following material is available from http://www.blackwellpublishing.com/products/journals/suppmat/ELE/ELE593/ELE593sm.htm

Appendix S1 Additional study details
Appendix S2 Can predators control starfish dynamics?

REFERENCES

Baum, J.K. & Myers, R.A. (2004). Shifting baselines and the decline of pelagic sharks in the Gulf of Mexico. *Ecol. Lett.*, 7, 135–145.

Bellwood, D.R., Hoey, A.S. & Choat, J.H. (2003). Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecol. Lett.*, 6, 281–285.

Birkeland, C. & Lucas, J.S. (1990). *Acanthaster planci: Major Management Problem of Coral Reefs*. CRC Press, West Palm Beach, FL.

Bradbury, R.H. & Antonelli, P.L. (1990). What controls outbreaks? In: *Acanthaster and the Coral Reef: A Theoretical Perspective* (ed. Bradbury, R.H.). Springer-Verlag, Berlin, pp. 278–290.

Dayton, P.K. (1985). Ecology of kelp communities. *Annu. Rev. Ecol. Syst.*, 16, 215–245.

Duffy, J.E. (2003). Biodiversity loss, trophic skew and ecosystem functioning. *Ecol. Lett.*, 6, 680–687.

Dulvy, N.K., Mitchell, R.E., Watson, D., Sweeting, C. & Polunin, N.V.C. (2002). Scale-dependant control of motile epifaunal community structure along a coral reef fishing gradient. *J. Exp. Mar. Biol. Ecol.*, 278, 1–29.

Dulvy, N.K., Sadovy, Y. & Reynolds, J.D. (2003). Extinction vulnerability in marine populations. *Fish Fisher.*, 4, 25–64.

Dulvy, N.K., Polunin, N.V.C., Mill, A.C. & Graham, N.A.J. (2004). Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. *Can. J. Fish. Aquat. Sci.* (in press).

Estes, J.E. & Duggins, O.D. (1995). Sea otters and kelp forests in Alaska: generality and variation in a community ecological paradigm. *Ecol. Monogr.*, 65, 75–100.

Gardner, T.A., Cote, I.M., Gill, J.A., Grant, A. & Watkinson, A.R. (2003). Long-term region-wide declines in Caribbean corals. *Science*, 301, 958–960.

Halpern, B.S. & Warner, R.R. (2002). Marine reserves have rapid and lasting effects. *Ecol. Lett.*, 5, 361–366.

Hawkins, J.P. & Roberts, C.M. (2004). Effects of artisanal fishing on Caribbean coral reefs. *Conserv. Biol.*, 18, 215–226.

Hughes, T.P. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*, 265, 1547–1551.

Hughes, T.P., Bellwood, D.R. & Connolly, S.R. (2002). Biodiversity hotspots, centres of endemicity, and the conservation of coral reefs. *Ecol. Lett.*, 5, 775–784.

Hughes, T.P., Baird, A.H., Bellwood, D.R., Card, M., Connolly, S.R., Folke, C. *et al.* (2003). Climate change, human impacts, and the resilience of coral reefs. *Science*, 301, 929–933.

Jackson, J.B.C., Kirby, M.X., Bergoer, W.H., A., B.K., Botsford, L.W., Bourque, B.J. *et al.* (2001). Historical overfishing and the recent collapse of coastal ecosystems. *Science*, 293, 629–637.

Jennings, S. & Polunin, N.V.C. (1995). Comparative size and composition of yield from six Fijian reef fisheries. *J. Fish Biol.*, 46, 28–46.

Jennings, S. & Polunin, N.V.C. (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, N.V.C. (1997). Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs*, 16, 71–82.

Kitchell, J.F. & Carpenter, S.R. (1993). Cascading trophic interactions. In: *The Trophic Cascade in Lakes* (eds Carpenter, S.R. & Kitchell, J.F.). Cambridge University Press, Cambridge, pp. 1–14.

Knowlton, N. (1992). Thresholds and multiple stable states in coral reef dynamics. *Amer. Zool.*, 32, 674–682.

Liermann, M. & Hilborn, R. (2001). Depensation: evidence, models and implications. *Fish Fisher.*, 2, 33–58.

McClanahan, T.R. (1995). A coral reef ecosystem-fisheries model: impacts of fishing intensity and catch selection on reef structure and processes. *Ecol. Model.*, 80, 1–19.

McClanahan, T.R., Polunin, N.V.C. & Done, T.J. (2002). Ecological states and the resilience of coral reefs. *Conserv. Ecol.*, 6, 18.

May, R.M. (1977). Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature*, 269, 471–477.

Menge, B.A. (1997). Detection of direct vs. indirect effects: were experiments long enough? *Am. Nat.*, 149, 801–823.

Myers, R.A. & Worm, B. (2003). Rapid worldwide depletion of predatory fish communities. *Nature*, 423, 280–283.

Ormond, R., Bradbury, R., Bainbridge, S., Fabricius, K., Keesing, J., De Vantier, L. *et al.* (1990). Test of a model of regulation of crown-of-thorns starfish by fish predators. In: *Acanthaster and the Coral Reef: A Theoretical Perspective* (ed. Bradbury, R.H.). Springer-Verlag, Berlin, pp. 189–207.

Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999). Trophic cascades revealed in diverse ecosystems. *Trends Ecol. Evol.*, 14, 483–488.

Paine, R.T. (1966). Food web compexity and species diversity. *Am. Nat.*, 100, 65–75.

Pandolfi, J.M., Bradbury, R.H., Sala, E., Hughes, T.P., Bjorndal, K.A., Cooke, R.G. *et al.* (2003). Global trajectories of the long-term decline of coral reef ecosystems. *Science*, 301, 955–958.

Pinnegar, J.K., Polunin, N.V.C., Francour, P., Badalamenti, F., Chemello, R., Harmelin-Vivien, M.-L. *et al.* (2000). Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environ. Conserv.*, 27, 179–200.

Roberts, C.M. (1995). Effects of fishing on the ecosystem structure of coral reefs. *Conserv. Biol.*, 9, 988–995.

Roberts, C.M., Bohnsack, J.A., Gell, F., Hawkins, J.P. & Goodridge, R. (2001). Effects of marine reserves on adjacent fisheries. *Science*, 294, 1920–1923.

Samoilys, M.A. & Carlos, G. (2000). Determining methods of underwater visual census for estimating the abundance of coral reef fishes. *Environ. Biol. Fish.*, 57, 289–304.

Scheffer, M. & Carpenter, S.R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.*, 18, 648–656.

Scheffer, M., Carpenter, S., Foley, J.A., Folke, C. & Walker, B. (2001). Catastrophic shifts in ecosystems. *Nature*, 413, 591–596.

Shears, N.T. & Babcock, R.C. (2002). Marine reserves demonstrate top-down control of community structure on temperate reefs. *Oecologia*, 132, 131–142.

Shurin, J.B., Borer, E.T., Seabloom, E.W., Anderson, K., Blanchette, C.A., Broitman, B. *et al.* (2002). A cross-ecosystem comparison of the strength of trophic cascades. *Ecol. Lett.*, 5, 785–791.

Steneck, R.S., Graham, M.H., Bourque, B.J., Corbett, D., Erlandson, J.M., Estes, J.A. *et al.* (2003). Kelp forest ecosystems: biodiversity, stability resilience and future. *Environ. Conserv.*, 29, 436–459.

Webster, M.S. & Almany, G.R. (2002). Positive indirect effects in a coral reef fish community. *Ecol. Lett.*, 5, 549–557.

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Appendix S1 Additional study details

Data sources

Human population data came from the 1996 Fiji population census (Anonymous 1998), the length of reef front was measured from measured from aerial photographs (scale = 1:50,000, Australian aerial mapping, available from the Department of Lands and Surveys, Suva, Fiji) and Lau Island reef areas were derived from geological surveys and maps (Woodhall 1984). Note that in these oceanic islands that the length of reef front is proportional to area. Total population by country came from 2000 United Nations Population Division (http://www.un.org/esa/population/unpop.htm) and national reef areas were extracted from the World Atlas of Coral Reefs (Spalding *et al.* 2001).

Choice of study species

We included carnivorous fishes of all dietary habits, including species that are largely piscivorous as they are known to opportunistically consume invertebrates (Jennings & Polunin 1997), species with crushing teeth and powerful jaw morphology which suggests they are capable of consuming spiny, well-defended invertebrates, e.g. triggerfishes (Balistidae) and wrasses (Labridae) (Table S1). In addition we included relatively specialised small-mouthed invertivores such as the butterflyfishes (Chaetodontidae) and goatfishes (Mullidae). Little is known of the species thought to feed on the crown-of-thorns starfish and little is known about the points of the starfish life cycle at which it is vulnerable to predation (Birkeland & Lucas 1990;

Sweatman 1995). We included these small-mouthed groups of invertivores, as it is possible that the predatory control of starfish occurs at the early settlement stage, where the starfish are relatively undefended (Sweatman 1995). It is also possible that predation events are extremely transient, e.g. occurring soon after a wave of larval settlement, under such conditions many species could opportunistically switch diet to focus on starfish. If this were the case then restricting the predator species list solely to documented predator may be unconservative. We regard this study as a relatively coarse and conservative approach to understanding fish-starfish predator-prey dynamics and recommend that further work, such as focal observation and prey tethering (McClanahan 1995; 2000) be undertaken to add detail to our findings.

Fish species and starfish correlations

Starfish density is negatively correlated to the density of 15 of our study species and all apart from three were also negatively correlated with fishing intensity (Table S1). Species with the strongest correlations fall into two groups. Those species with crushing teeth and powerful jaw morphology which could plausibly tackle this well-defended starfish, such as the blackedge thicklip and band cheek wrasses (*Hemigymnus melapterus*, *Oxycheilinus diagrammus*), the clown triggerfish (*Balistoides conspicillium*) and the emperor (*Monotaxis grandoculis*) and also large-bodied piscivores which are also known to eat small size classes of defended invertebrates, such as gastropods and lobsters, these include the black saddled grouper (*Plectropomus laevis*), camouflage grouper (*Epinephelus polyphekiodon*), two-spot red snapper (*Lutjanus bohar*), one-spot snapper (*Lutjanus monostigma*) (Allen 1985). However, these correlations should be interpreted cautiously because of because of the low statistical power of single-species density estimates, the problem of determining statistical and biological significance when multiple tests are conducted and the potential non-linearity of predator-prey relationships (May 1977, Fig 5c.).

Starfish census power

The variance in starfish densities increased with density, and our census method had good power even at lowest starfish densities. The confidence intervals for the observed outbreak threshold were calculated based on linear model fits between the mean density and 95th percentile of density estimates. It could be argued that there is considerable observer error associated with the census method, which involved a rapid search (1-2 minutes) of a relative large area (154 m^2) of topographically complex reef. However this larger scale method had lower coefficient of variation (1.2) and outperformed a concurrent quadrat survey using 70 * 1 m^2 quadrats per area (CoV = 3.2) at the area within island scale (R. E. Mitchell, unpublished data).

Table S1 Details of fish species including family, trophic category, trophic level and whether fishers targeted species. Pearson correlations between individual species density (g m^{-2}) versus fishing intensity (people km^{-1} reef) and individual species density (g m^{-2}) versus starfish density (individuals m^{-2}) with associated *n* values for each test. Trophic category was based on (Lieske & Myers 1994; Jennings & Polunin 1996; 1997; Myers 1999) and trophic level was derived from FishBase (www.fishbase.org). Species were categorised as targeted based on informal interviews of fisher preferences and fishing practices and fish catch observations (e. g. Jennings & Polunin 1995; 1997; Dulvy & Polunin 2004). Species negatively correlated both with fishing intensity and starfish density are indicated with and asterisk (a cut-off was arbitrarily set to > 0.25 level).

Species	Family	Trophic category	Trophic level	Targeted	Fishing pressure vs. species biomass	n	Starfish density vs. fish biomass	n
Balistapus undulatus	Balistidae	iv	3.3	yes	-0.19	13	0.30	6
Balistoides conspicillum *	Balistidae	iv	3.3	yes	-0.37	9	-0.59	5
Balistoides viridescens	Balistidae	iv	3.3	no	n/a	1	n/a	1
Rhinecanthus rectangulus	Balistidae	iv	2.9	yes	n/a	1	n/a	0

Sufflamen bursa	Balistidae	iv	3	yes	0.16	11	0.56	4
Sufflamen chrysopterus	Balistidae	iv	3.5	yes	-0.58	3	n/a	2
Sufflamen fraenatus	Balistidae	iv	3.4	yes	n/a	1	n/a	0
Chaetodon auriga	Chaetodontidae	iv	3.2	no	0.14	11	-0.10	4
Chaetodon citrinellus	Chaetodontidae	iv	3.1	no	0.02	10	0.29	5
Chaetodon ephippium	Chaetodontidae	iv	3.1	no	-0.17	12	0.16	5
Chaetodon flavirostris	Chaetodontidae	iv	3.3	no	-0.52	8	0.49	4
Chaetodon kleinii	Chaetodontidae	iv	2.7	no	-0.26	3	n/a	1
Chaetodon lineolatus	Chaetodontidae	iv	3.3	no	-0.77	5	n/a	0
Chaetodon lunula	Chaetodontidae	iv	3.3	no	-0.38	8	n/a	2
Chaetodon mertensii	Chaetodontidae	iv	2.9	no	0.05	7	n/a	2
Chaetodon pelewensis	Chaetodontidae	iv	3.3	no	-0.07	13	0.18	6
Chaetodon plebeius	Chaetodontidae	iv	3.3	no	0.20	12	-0.24	5
Chaetodon rafflesi	Chaetodontidae	iv	3.3	no	0.22	13	0.84	6
Chaetodon ulietensis	Chaetodontidae	iv	3.3	no	0.56	10	0.33	4
Chaetodon unimaculatus	Chaetodontidae	iv	3.1	no	0.14	11	0.97	5
Chaetodon vagabundus	Chaetodontidae	iv	3.2	no	0.28	12	0.88	5
Forcipiger flavissimus	Chaetodontidae	iv	3.1	no	n/a	1	n/a	1

Forcipiger longirostris	Chaetodontidae	iv	3.5	no	-0.21	12	-0.01	5
Heniochus monoceros	Chaetodontidae	iv	3.5	no	-0.14	10	-0.14	4
Heniochus singularius	Chaetodontidae	iv	3.6	no	-0.45	7	n/a	1
Heniochus varius	Chaetodontidae	iv	3.2	no	0.04	12	-0.24	5
Diodon hystrix	Diodontidae	iv	3.4	yes	-0.86	3	n/a	1
Plectorhinchus chaetodonoides	Haemulidae	iv	3.9	yes	-0.88	4	n/a	1
Plectorhinchus obscurus	Haemulidae	iv	3.8	yes	n/a	1	n/a	0
Plectorhinchus picus	Haemulidae	iv	3.9	yes	n/a	1	n/a	1
Anampses caerulopunctatus	Labridae	iv	3.3	no	0.06	8	0.74	3
Anampses neoguinaicus	Labridae	iv	3.5	no	0.10	9	0.35	3
Anampses twistii	Labridae	iv	3.44	no	-0.10	13	0.18	6
Bodianus anthioides	Labridae	iv	3.5	yes	n/a	2	n/a	2
Bodianus axillaries	Labridae	iv	3.5	yes	0.39	13	0.64	6
Bodianus diana	Labridae	iv	3.5	yes	n/a	1	n/a	0
Bodianus loxozonus	Labridae	iv	3.5	yes	-0.38	13	-0.10	6
Bodianus mesothorax	Labridae	iv	3.2	yes	-0.57	4	n/a	1
Cheilinus chlorourus	Labridae	iv	3.4	yes	0.47	12	0.07	6
Cheilinus fasciatus	Labridae	iv	3.4	yes	0.86	3	n/a	0

Cheilinus oxycephalus	Labridae	iv	3.8	yes	-0.25	4	n/a	1
Cheilinus trilobatus	Labridae	iv	3.5	yes	0.59	10	0.60	5
Cheilinus undulatus	Labridae	iv	4	yes	n/a	2	n/a	1
Coris aygula	Labridae	iv	3.4	yes	-0.65	6	n/a	2
Coris gaimard	Labridae	iv	3.5	yes	0.75	7	n/a	1
Epibulus insidiator	Labridae	pi	3.8	no	-0.32	12	-0.09	5
Gomphosus varius	Labridae	iv	3.6	no	-0.03	13	0.33	6
Halichoeres hortulanus	Labridae	iv	3.4	no	-0.56	13	0.08	6
Halichoeres margaritaceus	Labridae	iv	3.7	no	-0.92	5	n/a	1
Halichoeres marginatus	Labridae	iv	3.3	no	0.30	4	n/a	1
Hemigymnus fasciatus	Labridae	iv	3.2	yes	-0.45	13	0.33	6
Hemigymnus melapterus *	Labridae	iv	3.5	yes	-0.52	10	-0.85	3
Macropharygodon meleagris	Labridae	iv	2.9	no	n/a	1	n/a	0
Oxycheilinus diagrammus *	Labridae	pi	3.7	yes	-0.29	10	-0.74	4
Oxycheilinus unifasciatus	Labridae	iv	4.1	yes	0.32	12	0.66	5
Pseudocheilinus hexataenia	Labridae	iv	3.1	no	n/a	1	n/a	0
Pseudocheilinus octotaenia	Labridae	iv	3.4	no	-0.60	6	n/a	2
Stethojulius bandanensis	Labridae	iv	3.2	no	n/a	2	n/a	1

Thalassoma amblycephalum	Labridae	iv	3.1	no	-0.07	7	-1.00	3
Thalassoma hardwicke	Labridae	iv	3.7	no	-0.02	13	0.67	6
Thalassoma jansenii	Labridae	pi	3.2	no	0.75	3	n/a	1
Thalassoma lutescens	Labridae	iv	3.4	no	-0.05	13	0.34	6
Thalassoma quinquevittatum	Labridae	iv	3.6	no	0.03	7	n/a	2
Gnathodentex aureolineatus	Lethrinidae	iv	3.3	yes	0.05	13	0.80	6
Lethrinus atkinsoni	Lethrinidae	iv	3.8	yes	-0.74	4	n/a	1
Lethrinus erythracanthus	Lethrinidae	iv	3.5	yes	n/a	2	n/a	1
Lethrinus nebulosus	Lethrinidae	iv	4.4	yes	0.98	3	n/a	1
Lethrinus olivaceus	Lethrinidae	iv	4.1	yes	-0.74	4	n/a	0
Monotaxis grandoculis *	Lethrinidae	iv	3.3	yes	-0.34	13	-0.40	6
Aphareus furca	Lutjanidae	pi	4	yes	0.05	12	0.17	6
Aprion virescens	Lutjanidae	iv	4.5	yes	-0.27	4	n/a	1
Lutjanus bohar *	Lutjanidae	pi	3.6	yes	-0.62	11	-0.82	6
Lutjanus fulviflamma	Lutjanidae	pi	3.9	yes	0.24	5	n/a	1
Lutjanus fulvus	Lutjanidae	pi	4.1	yes	0.53	6	n/a	2
Lutjanus gibbus	Lutjanidae	pi	3.5	yes	-0.10	10	-0.34	5
Lutjanus kasmira	Lutjanidae	pi	4	yes	0.03	6	-1.00	3

Lutjanus monostigma *	Lutjanidae	pi	4.3	yes	-0.45	4	-0.60	3
Lutjanus russelli	Lutjanidae	pi	4.3	yes	-0.47	6	n/a	1
Lutjanus semicinctus	Lutjanidae	pi	4.2	yes	n/a	2	n/a	0
Lutjanus vitta	Lutjanidae	pi	4.1	yes	n/a	1	n/a	0
Macolor macularis	Lutjanidae	iv	4	yes	-0.81	6	n/a	2
Macolor niger	Lutjanidae	iv	4	yes	0.12	12	-0.12	6
Aluterus scriptus	Monacanthidae	iv	2.8	yes	0.23	5	n/a	2
Amanses scopas	Monacanthidae	iv	2.8	no	-0.76	4	n/a	2
Cantherhines dumerilii	Monacanthidae	iv	3.1	no	-0.18	6	n/a	1
Cantherhines pardalis	Monacanthidae	iv	3.5	no	-0.59	8	0.68	3
Pervagor melanocephalus	Monacanthidae	iv	2.5	no	n/a	2	n/a	1
Mulloidichthys vanicolensis	Mullidae	iv	3.3	yes	0.37	4	0.49	3
Parupeneus barberinus	Mullidae	iv	3.2	yes	-0.87	3	n/a	0
Parupeneus bifasciatus	Mullidae	iv	3.6	yes	0.30	13	0.35	6
Parupeneus ciliatus	Mullidae	iv	3.5	yes	-0.95	3	n/a	2
Parupeneus cyclostomus	Mullidae	iv	4.2	yes	-0.31	12	-0.15	5
Parupeneus multifasciatus	Mullidae	iv	3.5	yes	0.44	13	-0.36	6
Scolopsis bilineatus	Nemipteridae	iv	4	yes	-0.96	3	n/a	2

Ostracion meleagris	Ostraciidae	iv	2.9	yes	0.52	9	0.87	4
Anyperodon leucogrammicus	Serranidae	pi	4	yes	0.74	3	n/a	0
Cephalopholis argus	Serranidae	pi	4.5	yes	-0.14	13	-0.15	6
Cephalopholis leopardus	Serranidae	pi	4	yes	0.02	6	n/a	2
Cephalopholis urodeta	Serranidae	pi	4.1	yes	-0.12	13	0.60	6
Epinephelus fuscoguttatus	Serranidae	pi	4.1	yes	n/a	1	n/a	0
Epinephelus hexagonatus	Serranidae	pi	4.1	yes	0.54	5	n/a	2
Epinephelus howlandi	Serranidae	pi	4	yes	-0.42	5	n/a	0
Epinephelus maculatus	Serranidae	pi	4	yes	n/a	2	n/a	0
Epinephelus polyphekadion *	Serranidae	pi	4	yes	-0.45	7	-0.86	3
Gracila albomarginata	Serranidae	pi	4.5	yes	n/a	2	n/a	0
Plectropomus areolatus	Serranidae	pi	4.5	yes	n/a	1	n/a	0
Plectropomus laevis *	Serranidae	pi	4.1	yes	-0.31	8	-0.67	4
Plectropomus leopardus	Serranidae	pi	4.5	yes	-0.76	5	n/a	2
Plectropomus maculatus	Serranidae	pi	4.5	yes	n/a	2	n/a	1
Arothron mappa	Tetraodontidae	iv	2.8	no	n/a	1	n/a	1
Arothron nigropunctatus	Tetraodontidae	iv	3.3	yes	0.01	11	0.46	5

Appendix S2 Can predators control starfish dynamics?

The links between exploitation and predator abundance and starfish abundance and reef state are reasonably well understood, however, the link between predation and starfish dynamics is less clear (Birkeland & Lucas 1990). A key issue to examine is whether predatory reef fishes can influence starfish abundance on Fijian reefs and whether starfish exhibit threshold dynamics. Starfish are food limited at high densities, but their dynamics at lower densities are poorly understood (e.g. Bradbury *et al.* 1985). Here we consider three issues, the effects of fishing on potentially predatory species and community predation, whether published predation rates may be sufficient to control starfish and plausible mechanisms for the observed Allee effect.

It has long been suspected that starfish outbreaks are linked to predator removal (Birkeland & Lucas 1990). However, testing this hypothesis has proven difficult, largely because experimental manipulation is not possible at a spatial scale large enough (~0.1-100 km^{-2}) to adequately encompass population dynamics, outbreaks are transient and key aspects of the life cycle may go unobserved, e.g. recruitment or predation events. Also measuring predation events either by direct observation or diet studies may be unreliable or biased. Estimates of predation rates based on dietary data tend to be biased toward underestimation, because of the difficulty of identifying and quantifying stomach contents (Sweatman 1995; Polunin & Pinnegar 2002). We have inferred a predator-starfish link by examining the variation in the combined abundance of piscivorous and invertivorous fishes. Fishes nominally classified as piscivores were included in this study as they are known to occasionally eat large well defended invertebrates (Jennings & Polunin 1997). While we never directly observed fish predation of starfish in Fiji, the families surveyed included species known to feed on the crown-of-thorns starfish and other well-defended prey, such as urchins, at other locations, e.g. wrasses (Labridae), triggerfishes (Balistadae*)* and emperors (Lethrinidae). Fishing has profoundly influenced the predatory capacity of these Fijian fish assemblages. The mean weight of individual fishes halved and the slope of community size spectra steepened in response to exploitation (Dulvy *et al.* 2004). Fish are morphometrically constrained to eat prey smaller than themselves, consequently a removal of larger individuals and a steepening of community size spectra implies a reduction in the predatory capacity of fish communities (Kerr & Dickie 2001). This change in predatory capacity of these Fijian fish communities has been associated with compensatory releases of smaller fishes and epifaunal invertebrates (Dulvy *et al.* 2002; 2004).

A key test of the predatory control hypothesis is whether predation rates are sufficient to cause negative growth of starfish populations. Predation rates of juvenile starfish have been measured only once in the field over 35 days, at one location (Davies reef lagoon) at the Great Barrier Reef, Australia (Sweatman 1995). Predation rates were estimated as 0.13% of individuals per day, this was lower than the theoretical estimate of the predation rate required to prevent outbreaks (1.5%), consequently it was concluded that field predation rates were insufficient to control starfish (Sweatman 1995). These field data are insufficient to rule out the predation control hypothesis for two reasons. First, the theoretical predation rate required to prevent outbreaks may be overestimated. This parameter was calculated using an age-structured model based on a fertility estimate of 1.2-2.4 x 10^7 eggs (McCallum 1987). The best estimates of the fertility of broadcast spawners suggests egg production is 4-5 orders of magnitude greater than recruit production (Myers *et al.* 1999). Assuming this is representative of other broadcast spawners, the predation rate required to prevent a starfish outbreak may also be inflated, possibly by orders of magnitude (McCallum 1987). Second, the use of estimates of predation rates upon juvenile starfish at one small location at one point in time to rule out predation as mechanism controlling starfish densities at ecosystem scale has a high probability of falsely accepting the null hypothesis: predator density is not related to prey density.

The observation of negative per capita population growth in starfish at the lightly exploited islands (Fig. 5b) with high predator densities (Fig. 5c) is consistent with predator regulation of starfish dynamics and a predator saturation Allee effect. Allee effects may be generated by predation and reduced reproductive output (Courchamp *et al.* 1999; Stephens & Sutherland 1999). A predator saturation Allee effect is where the predation rate exceeds the growth rate of prey at low prey densities (Courchamp *et al.* 1999). Reduced reproductive output can occur particularly in sessile or less mobile invertebrates with broadcast spawning (Petersen & Levitan 2001; Gascoigne & Lipcius 2004). The crown-of-thorns starfish exhibits a number of traits consistent with a reproductive Allee effect, including rapidly decaying fertilisation rates with gamete dispersal distance, aggregative spawning behaviour, shallow water migration and synchronisation of spawning behaviour (Babcock *et al.* 1994). The reproductive Allee effect may reinforce another causal factor, such as predation, to form a positive feedback loop (Babcock *et al.* 1994; Scheffer & Carpenter 2003). But it is difficult to see how this mechanism alone can explain the large-scale link between starfish abundance and fishing intensity. The predator saturation Allee effect remains as a possible mechanism for modulating starfish outbreaks. We suggest that taken together that predation is a plausible mechanism for modulating starfish outbreaks.

References

Allen, G.R. (1985). *Snappers of the world. An annotated and illustrated catalogue of lutjanid species known to date*. FAO Fish. Synop. 6(125). Food and Agriculture Organisation, Rome.

Anonymous. (1998). 1996 Fiji census of population and housing: general tables. Suva, Fiji: Parliament of Fiji.

Babcock, R.C., Mundy, C.N. & Whitehead, D. (1994). Sperm diffusion models and in situ confirmation of long-distance fertilization in the free-spawning asteroid *Acanthaster planci*. *Biol. Bull.* 186, 17-28.

Birkeland, C. & Lucas, J.S. (1990). *Acanthaster planci: major management problem of coral reefs*. CRC Press, Florida.

Bradbury, R.H., Hammond, L.S., Moran, P.J. & Reichelt, R.E. (1985). Coral reef communities and the crown-of thorns starfish: evidence for qualitatively stable cycles. *J. Theor. Biol.* 113, 69-81.

Courchamp, F., Clutton-Brock, T. & Grenfell, B. (1999). Inverse density-dependence and the Allee effect. *Trends Ecol. Evol.* 14, 405-410.

Dulvy, N.K., Mitchell, R.E., Watson, D., Sweeting, C. & Polunin, N.V.C. (2002). Scale-dependant control of motile epifaunal community structure along a coral reef fishing gradient. *J. Exp. Mar. Biol. Ecol.* 278, 1-29.

Dulvy, N.K. & Polunin, N.V.C. (2004). Using informal knowledge to infer human-induced rarity of a conspicuous reef fish. *Ani. Conserv.* in press.

Dulvy, N.K., Polunin, N.V.C., Mill, A.C. & Graham, N.A.J. (2004). Size structural change in lightly exploited coral reef fish communities: evidence for weak indirect effects. *Can. J. Fish. Aquat. Sci.* in press.

Gascoigne, J. & Lipcius, R.N. (2004). Allee effects in marine systems. *Mar. Ecol. Prog. Ser.* in press.

Jennings, S. & Polunin, N.V.C. (1995). Comparative size and composition of yield from six Fijian reef fisheries. *J. Fish Biol.* 46, 28-46.

Jennings, S. & Polunin, N.V.C. (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, N.V.C. (1997). Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. *Coral Reefs* 16, 71-82.

Kerr, S.R. & Dickie, L.M. (2001). *The biomass spectrum: a predator-prey theory of aquatic production*. Columbia University Press, New York.

Lieske, E. & Myers, R. (1994). *Coral reef fishes Indo-Pacific and Caribbean*. HarperCollins Publishers, London.

May, R.M. (1977). Thresholds and breakpoints in ecosystems with a multiplicity of stable states. *Nature* 269, 471-477.

McCallum, H.I. (1987). Predator regulation of *Acanthaster planci*. *J. Theor. Biol.* 127, 207-220.

McClanahan, T.R. (1995). Fish predators and scavengers of the sea-urchin *Echinometra mathaei* In Kenyan coral reef marine parks. *Env. Biol. Fishes* 43, 187-193.

McClanahan, T.R. (2000). Recovery of a coral reef keystone predator, *Balistapus undulatus*, in East African marine parks. *Biol. Cons.* 94, 191-198.

Myers, R.A., Brown, K.G. & Barrowman, N.J. (1999). The maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* 56, 2404-2419.

Myers, R.F. (1999). *Micronesian reef fishes*. Coral Graphics, Guam.

Petersen, C.W. & Levitan, D.R. (2001). The Allee effect: a barrier to recovery by exploited species. In: *Conservation of exploited species* (eds. J.D. Reynolds, G.M. Mace, K.H. Redford & J.G. Robinson), Cambridge University Press, Cambridge, pp. 281-300.

Polunin, N.V.C. & Pinnegar, J.K. (2002). Trophic ecology and the structure of marine food webs. In: *Handbook of Fish biology and Fisheries*, vol. 1 (eds. P.J.B. Hart & J.D. Reynolds), Blackwell Science, Oxford, pp. 301-320.

Scheffer, M. & Carpenter, S.R. (2003). Catastrophic regime shifts in ecosystems: linking theory to observation. *Trends Ecol. Evol.* 18, 648-656.

Spalding, M.D., Ravilious, C. & Green, E.P. (2001). *World atlas of coral reefs*. University of California Press, Berkeley.

Stephens, P.A. & Sutherland, W.J. (1999). Consequences of the Allee effect for behaviour, ecology and conservation. *Trends Ecol. Evol.* 14, 401.

Sweatman, H.P.A. (1995). A field study of fish predation on juvenile crown-of-thorns starfish. *Coral Reefs* 14, 47-53.

Woodhall, D. (1984). The geology of the Lau group, Fiji. Fiji: Maps MRD 785-788, Bulletin 9, Marine Resources Department, Suva, Fiji.