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Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management

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Summary

An important principle of environmental science is that changes in single components of systems are likely to have consequences elsewhere in the same systems. In the sea, food web data are one of the few foundations for predicting such indirect effects, whether of fishery exploitation or following recovery in marine protected areas (MPAs). We review the available literature on one type of indirect interaction in benthic marine ecosystems, namely trophic cascades, which involve three or more trophic levels connected by predation. Because many indirect effects have been revealed through fishery exploitation, in some cases we include humans as trophic levels. Our purpose is to establish how widespread cascades might be, and infer how likely they are to affect the properties of communities following the implementation of MPAs or intensive resource exploitation. We review 39 documented cascades (eight of which include humans as a trophic level) from 21 locations around the world; all but two of the cascades are from shallow systems underlain by hard substrata (kelp forests, rocky subtidal, coral reefs and rocky intertidal). We argue that these systems are well represented because they are accessible and also amenable to the type of work that is necessary. Nineteen examples come from the central-eastern and north-eastern Pacific, while no well-substantiated benthic cascades have been reported from the NE, CE or SW Atlantic, the Southern Oceans, E Indian Ocean or NW Pacific. The absence of examples from those zones is probably due to lack of study. Sea urchins are very prominent in the subtidal examples, and gastropods, especially limpets, in the intertidal examples; we suggest that this may reflect their predation by fewer specialist predators than is the case with fishes, but also their conspicuousness to investigators. The variation in ecological resolution amongst studies, and in intensity of study amongst systems and regions, indicates that more cascades will likely be identified in due course. Broadening the concept of cascades to include pathogenic interactions would immediately increase the number of examples. The existing evidence is that cascade effects are to be expected when hard-substratum systems are subject to artisanal resource exploitation, but that the particular problems of macroalgal overgrowth on Caribbean reefs and the expansion of coralline barrens in the Mediterranean rocky-sublittoral will not be readily reversed in MPAs, probably because factors other than predation-based cascades have contributed to them in the first place. More cascade effects are likely to be found in the soft-substratum systems that are crucial to so many large-scale fisheries, when opportunities such as those of MPAs and fishing gradients become available for study of such systems, and the search is widened to less conspicuous focal organisms such as polychaetes and crustaceans.

Keywords: marine protected areas, fishing effects, ecosystems, food webs, management, sea urchins, fish

Introduction

Fishing is the most widespread human exploitative activity in the marine environment (Jennings & Kaiser 1998), and the evidence is that many fisheries around the world are in decline (e.g. Botsford *et al.* 1997). Much of fisheries science continues to focus on single species issues, in spite of the fact that extensive interactions occur between target species and other organisms. Appeals for the greater consideration of non-target species and the food chains on which fish production ultimately depend, have been voiced since as early as 1884 (Botsford *et al.* 1997), and the effects of fishing on marine ecosystem structure and processes have been repeat-

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edly reviewed (Munro *et al.* 1987; Roberts 1995; Jennings & Lock 1996; Jennings & Kaiser 1998; Hall 1999). However, the development of a more holistic approach to marine ecosystem management lags significantly behind management of terrestrial and freshwater systems (Shelton 1992; Sherman 1994).

One of the most widely-expressed concerns about intensive fishing in the marine environment is that it will lead to imbalances in ecosystem function which have ramifications for community structure overall (Jennings & Kaiser 1998). The structure of all communities varies in space and time in response to many physical and biological factors, and the extent to which these different factors influence ecosystem function is one of the fundamental issues of ecology. The understanding of such mechanisms is essential to evaluating community responses to human perturbations including fishing, and there have been several recent syntheses which have attempted to unravel the roles of these processes (e.g. Menge & Sutherland 1987; Power 1992; Strong 1992). In benthic marine systems, community structure is considered to be largely determined by a complex interplay between physical or physiological disturbance, competition, predation and recruitment (Menge & Sutherland 1987). It has often been proposed that the characteristically high levels of recruitment variability that exist in most marine systems can obscure any evidence of underlying processes (Fogarty *et al.* 1991), and there has been much debate arguing whether post-settlement or pre-settlement processes result in the patterns observed in community structure (e.g. Sale 1991). There has also been much debate over whether 'top-down' or 'bottom-up' processes are important in governing these communities (Hunter & Price 1992; Power 1992). On the one hand, predation has been shown to be important in some systems, where competition between plant species or sessile invertebrates has only been observed if their consumers are held at low densities by carnivores (i.e. top-down effects) (Sala *et al.* 1998*a*). Conversely, others have argued that all trophic levels are potentially limited by available food resources and thus any factors affecting plant abundance will cascade up the system and affect population dynamics of herbivores and thus their predators (i.e. bottom-up effects) (Hunter & Price 1992). In reality, 'bottom-up' and 'top-down' forces, as well as variability in recruitment density, probably act on populations and communities simultaneously (Hunter & Price 1992), and we should expect the relative roles of these different ecological factors to vary amongst biological systems depending on environmental heterogeneity. The effects of human perturbation will vary depending on the characteristics of the community concerned; the effects of harvesting in more robust communities, which often experience physical disturbance (e.g. upper rocky shore or shifting fine-grained sediments) may be very different from the effects in environments such as coral reefs that may be more benign (less physically stressful) (Menge & Sutherland 1987).

Fishing may have both direct and indirect effects on benthic community structure (Jennings & Kaiser 1998). The initiation of fishing or harvesting in an unfished system leads to dramatic reductions in the abundance of target stocks and changes in the growth, production and recruitment of the target organism. Over 20% of primary production is required to sustain fisheries in many intensively-fished coastal ecosystems (Pauly & Christensen 1995) and catch can represent a large proportion of the total fish biomass in some seas (Bax 1991). Indirect effects of fishing can be even more consequential for marine ecosystem structure and dynamics than removals of the target organism (Botsford *et al.* 1997), because many fishing gears lead to direct degradation of benthic habitats by physically removing emergent sessile organisms that provide a critical structural habitat, important in recruitment and prey protection (Jennings & Kaiser 1998). Fishery removals may also induce indirect trophic (food web) interactions, of which there are many kinds (Menge 1995).

Trophic cascades are one such indirect effect, the term being described by Hairston *et al.* (1960) and Estes and Palmisano (1974), but first used by Paine (1980) for intertidal communities and Carpenter *et al.* (1985) for North American lakes. Strictly defined (Strauss 1991; Menge 1995), trophic cascades are predatory interactions involving three trophic levels, whereby primary carnivores, by suppressing herbivores, increase plant abundance (Fig. 1), although cascade-type effects have been reported to extend through four or more trophic levels in some instances (Carpenter & Kitchell 1988; Power 1990). In theory, as long as a tri-trophic level interaction is observed, a trophic cascade need not always involve plants or algae at the bottom of food webs. As such, this type of interaction does not involve competition; three-species interactions involving competition include phenomena such as 'keystone predation' (Menge 1995). On the other hand, recruitment of a basal species can be enhanced through predation on a species' consumer, and

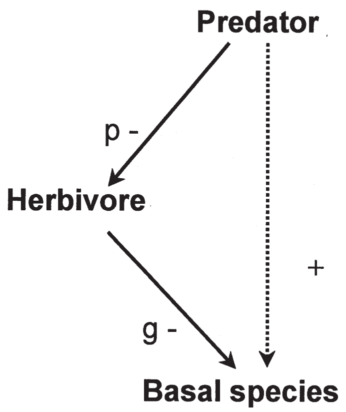

Figure 1 General diagram of a trophic cascade involving a predator which predates (p) and directly controls (–) a herbivore, the herbivore grazes (g) and directly controls a basal species. As a result, the predator has an indirect (dotted line), positive (+) effect on the basal species (after Menge 1995).

Menge (1995) has referred to this situation as an 'expanded trophic cascade'.

There appear to be few, if any, long-term controlled fishing experiments, and consequently, gradients in the intensity of fishing and marine protected areas (MPAs), in which intensive fishing is halted, alone offer valuable opportunities to evaluate specific hypotheses concerning effects of fishing on community structure (Bohnsack 1990; Jones *et al.* 1993; Jennings & Polunin 1997; Russ & Alcala 1998*a*, *b*) in the absence of natural baseline data (Dayton *et al.*1998).

In this paper, our purpose is to summarize what is known of trophic cascades in benthic marine systems, and thus to give those involved in the management of marine areas some idea of how widely these can be expected to occur when marine communities are subject to intensive harvesting, or are allowed to recover from it in MPAs. We focus on trophic cascades exclusively, because large predatory species are the most susceptible to fishing, top-down controls by predation are widely expected, and there is strong expectation that such indirect effects of management are likely (Pace *et al*. 1999). We do this by addressing two general questions. Firstly, in which marine systems/habitats do we find the strongest evidence for trophic cascade effects, and what are the main characteristics of the organisms involved? Secondly, what factors affect the occurrence of these cascades and are there ways in which their importance might be predicted when systems are selectively changed by development or management? For this purpose, we review the available literature both system by system and region by region, and we confine ourselves to benthic cascades involving three or more trophic levels where the interactions are based on predation, not on other processes such as recruitment inhibition or competition. Our benthic focus is warranted by the review of trophic cascades and similar phenomena in pelagic systems by Verity and Smetacek (1996). We have chosen to include humans as one of the trophic levels in cascades, because humans are obviously part of some of the systems which we review, and also because the management with which we are ultimately concerned is focused on the consequences of human interventions. All species names given in this review are in accordance with the authorities of the original reference.

Mediterranean rocky sublittoral

Work concerning possible trophic cascades in the Mediterranean has a relatively short history, but comprises some of the most comprehensive data of any littoral system. Human exploitation of inshore marine resources dates back thousands of years in the Mediterranean and most commercial fish stocks are considered to be greatly over-exploited (Campillo & Bigot 1992; Farrugio *et al.* 1993). It has been suggested that the increased prevalence of barrens of bare substrate and coralline algae in many parts of the western Mediterranean may be one symptom of this long-standing intensive use of the littoral (Sala *et al*. 1998*a*).

Many studies in the Mediterranean rocky littoral have demonstrated that large piscivorous and invertebrate-feeding fish are more abundant within MPAs compared to sites outside (e.g. Bell 1983; Francour 1994; Harmelin *et al.* 1995) and this is often particularly so for the sparid fishes *Diplodus sargus* and *D. vulgaris* (Bell 1983; Harmelin *et al.* 1995). These *Diplodus* species have been implicated (Sala 1997*b*) as major predators of adult sea urchins (particularly *Paracentrotus lividus*), whilst the wrasse *Coris julis* has been suggested to be a major predator on juvenile sea urchins. Although sea urchins are not the main prey of sparid fishes (Sala & Ballesteros 1997), Sala and Zabala (1996) found that within the Medes Islands Marine Reserve, fish (mainly *D. sargus, D. vulgaris* and *C. julis*) accounted for 100% of all urchin predation. Furthermore, at adjacent non-protected sites with a low density of predatory fish, *P. lividus* populations were shown to be 3–4 times higher than at sites in the Medes Reserve (Sala & Zabala 1996).

When at high densities, such as is the case outside MPAs, sea urchins have been shown to remove large erect algae and induce the formation of coralline barrens (Lawrence 1975; Verlaque 1987). Transition from coralline barrens back to erect algal assemblages is possible when sea urchins are eliminated or their populations are strongly reduced as has been shown by both experimental and natural removal (e.g. Kempf 1962; Nédélec 1982). However, the situation becomes greatly complicated by the grazing activity of fishes, mostly *Sarpa salpa* but also *Diplodus* species (Sala & Ballesteros 1997; Sala & Boudouresque 1997). Sala and Boudouresque (1997) demonstrated that where cages excluded fish (and sea urchins), populations of fleshy erect macroalgae developed and dominance by the unpalatable red alga *Asparagopsis armata* was greatly reduced. This coincided with the observation of a seasonal proliferation of *Asparagopsis* and dominance by fine turfs or calcareous algal species in MPAs where grazing fish were more abundant. Sala (1997*a*) found that within fish exclusion cages, most epifaunal groups (e.g. amphipods, gastropods, decapods and ophiuroids) also became more abundant although no difference was detected between MPA and unprotected areas. This Sala (1997*a*) attributed to a combination of reduced predation but also the dynamics of the fleshy erect algae which provide a structural habitat and food for many of the invertebrates considered.

An energy-based simulation of the Mediterranean rocky-sublittoral system has helped to predict how depletion especially of invertebrate-consuming fish such as *Diplodus* spp. might result in dominance by sea urchins, which would dramatically reduce algae, epifauna and gross and net primary production (McClanahan & Sala 1997). The indication is that once a high population of sea urchins has developed, recovery of those fish that eat algae and epifauna might be slowed or even made impossible because their food resources drop below the minimum threshold necessary for in situ population development (McClanahan & Sala 1997). In conclusion therefore, Mediterranean rocky-sublittoral assemblages have been considered to exist in one of two states, namely (1) an overgrazed community with high abundance of sea urchins and low algal biomass i.e. coralline barrens and (2) a 'developed' community with an abundance of fish and dominance by fleshy algae (McClanahan & Sala 1997)(Fig. 2). Sala *et al.* (1998*a*) critically reviewed the literature concerning the effects of fishing on sea-urchin populations and the recent expansion of coralline barrens and concluded that other processes including pollution, diseases, large-scale oceanographic events and availability of refuges from predation, are also likely to be important. This has been somewhat borne out by the findings of Sala *et al.* (1998*b*) who suggested that sea-urchin populations in the Medes Islands exhibit striking short-term fluctuations in abundance in both protected and unprotected sites, such that other factors including recruitment variability may outweigh the effects of fish predation. Thus, Figure 2 is almost certainly overly simplistic in its portrayal of the transition between the two states.

Other circumstantial evidence for fish-mediated trophic cascade effects in the Mediterranean rocky littoral includes the work of Boudouresque *et al.* (1992) in Corsica. Conspicuously lower abundance and species richness of macrozoobenthos (mostly echinoderms and molluscs) were observed within the Scandola MPA (Boudouresque *et al.* 1992), where predators were common compared to sites outside, where the abundance, biomass and diversity of predatory fishes were greatly reduced (Francour 1994). Similarly, within the integral (core) zone of the Ustica MPA (Italy), it was noted (Badalamenti *et al.* 1999; Chemello *et al.* 1999, Milazzo *et al.* in press) that during the spring, abundance and species richness of polychaetes (at 1–15 m depth) and gastropods (1–15 m depth) were significantly higher than at sites where fishing was allowed. This coincided with an observed decrease in the abundance of the small-sized micro-carnivorous fish species (e.g. blenniids, gobiids, tripterygiids and juveniles of several taxonomic groups) and in the same area, an increase of piscivorous and macrocarnivorous fish abundance (e.g. groupers) (Vacchi *et al.* 1998; LaMesa & Vacchi 1999). Macpherson (1994) also observed fewer species and much lower abundances of blenniids inside the Medes Marine Reserve (Spain) compared to sites outside, where potential predators were less abundant. Thus, the different studies carried out in Ustica MPA support a possible tri-trophic level cascade (Fig. 3). However, during the autumn, when the algal coverage at Ustica Island is greatly reduced, polychaetes were not higher within the core of the MPA than outside, and within shallow waters (1–5 m), there were no significant differences in the abundance of gastropods (Badalamenti *et al.* 1999; Chemello *et al.* 1999).

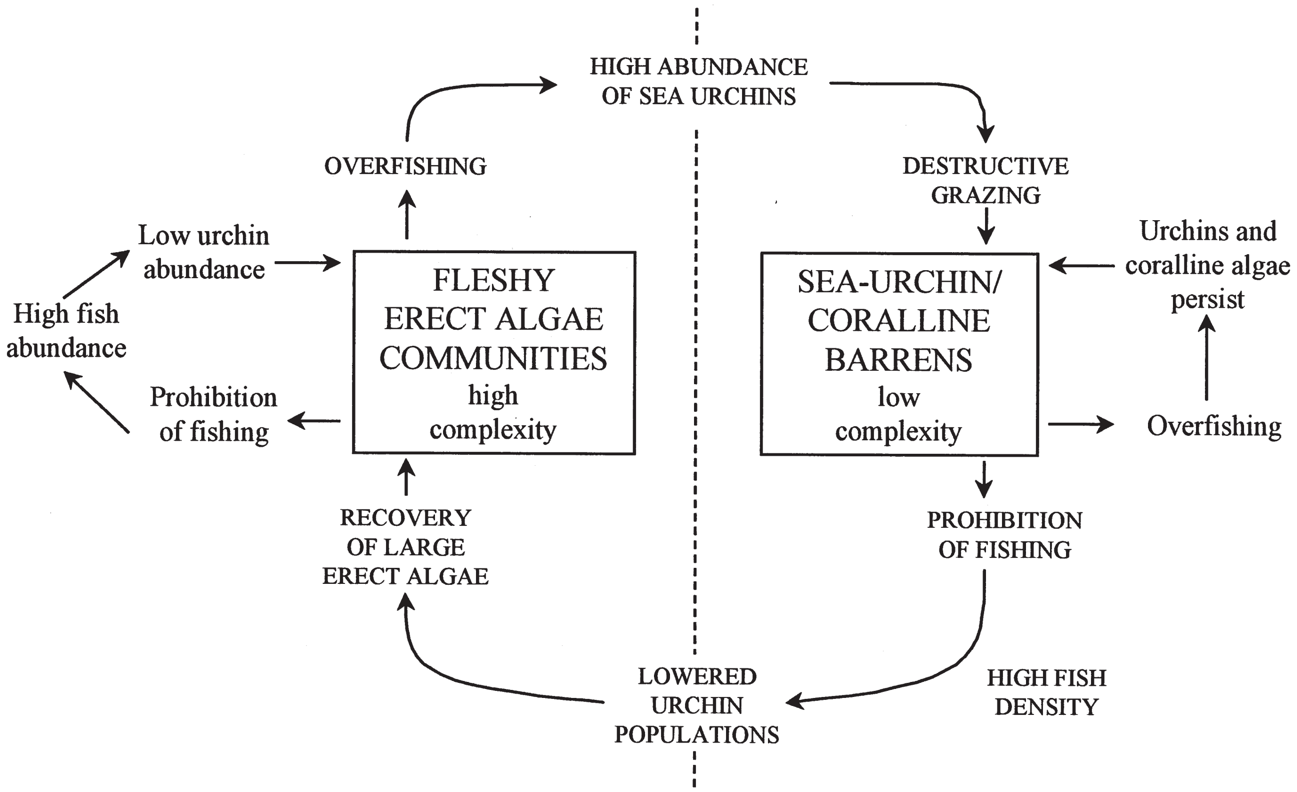

Figure 2 Diagram illustrating two system states in the Mediterranean rocky sublittoral, namely those dominated by (1) fleshy erect algae and (2) coralline algae. Sea-urchin abundance and fishery are indicated as being influential in shifts between these states (after Sala *et al.* 1998*a*, Fig. 1).

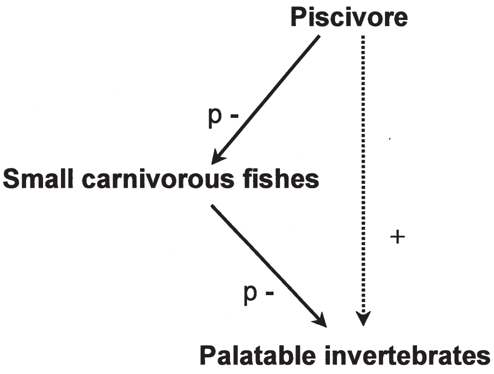

Figure 3 Diagram of the proposed trophic cascade involving piscivorous fishes, small carnivorous fishes and palatable invertebrates such as gastropods and polychaetes, at Ustica Island in the Mediterranean (Badalamenti *et al.* 1999; Chemello *et al.* 1999).

Kelp forests and other rocky-subtidal assemblages

Complex cascade effects have been noted for many years from kelp forests and other subtidal algal assemblages around the world, including the North Western Atlantic, Alaska, California, South Africa, New Zealand and Australia (Schiel & Foster 1986). Almost all of these documented trophic cascades involve a predator, sea urchins and macroalgae/kelp, although the urchin species and predator may vary amongst sites.

In 1968, the rocky floor of St Margarets Bay, Nova Scotia, was almost completely covered by a dense forest of kelp (Mann 1982) and urchin biomass (in this case *Strongylocentrotus droebachiensis*) averaged only 150 g/m^2. However there were several patches where urchin biomass was much higher (1200 g/m^2) and where the kelp had been entirely removed leaving coralline barrens. These, at first relatively small and temporary, became progressively larger and more permanent until they coalesced and most of the kelp beds in some bays were completely destroyed (Breen & Mann 1976). The hypothesis was put forward (Mann & Breen 1972) that the cause of this phenomenon was release of predation pressure on the urchins, caused by overfishing of lobster, *Homarus americanus* (Wharton & Mann 1981). Breen and Mann (1976) showed that the hypothesis was consistent with population dynamics of lobsters and urchins, and that the urchin boom and the demise of the kelp coincided with a rapid decline in lobster landings from the bay. Later it was proven that though urchins were not the preferred prey choice of lobsters, lobsters would nevertheless eat large numbers if they were readily available (Hagen & Mann 1992). The classic lobster-urchin-kelp paradigm (Fig. 4*a*) has been reported for other sites far from the north-western Atlantic.

Bernstein *et al.* (1981) suggested that fish predation might also play an important role in this system, particularly predation by the Atlantic wolf-fish *Anarchias lupus*, and that urchin build-up may require depletion of both lobster and wolf-fish (Fig. 4*a*). Bernstein *et al.* (1983) also advanced a more complicated scenario in which behavioural responses of *S. droebachiensis* to predators triggered the formation of defensive aggregations within kelp beds, leading to locally intensive grazing. This hypothesis was later tested in the field and laboratory by Scheibling and Hamm (1991). Elner and Vadas (1990) reviewed in detail the papers addressing this well-established north-western Atlantic paradigm and showed that with the addition of each new publication, and as more became known about the system, the original tri-trophic level cascade effect became more complicated (Fig. 4*a*). Much of the original work had been based on weak inferences and much of the later work consisted of a series of ad hoc revisions rather than experimentation (Elner & Vadas 1990). Indeed, further and more detailed analysis of feeding rates, stomach contents and biomass of lobsters suggested to Miller (1985) that lobsters could not have controlled sea-

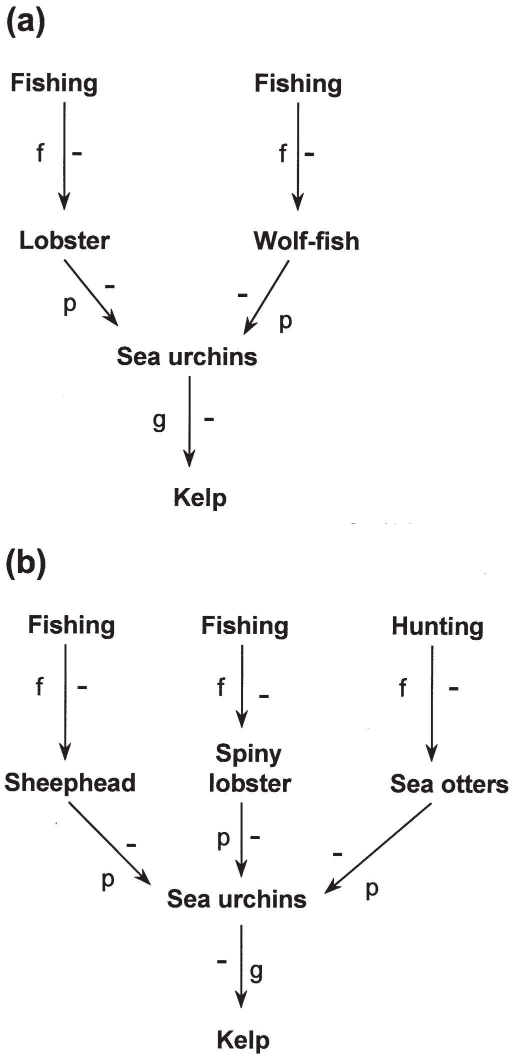

Figure 4 Diagram of proposed trophic cascades involving fishing or hunting (f), (a) in Nova Scotia and (b) Southern California (for other symbols, see Fig. 1).

urchin populations, whilst Hart and Scheibling (1988) have suggested that a large temperature anomaly in June 1960 may have led to intense sea-urchin recruitment and appearance of large adult populations 4–6 years later. Thus, Scheibling (1996) proposed that our understanding of interactions between urchins and their predators is insufficient to support generalizations about the role of predation in regulating populations. Whether or not these criticisms are valid, this body of work did much to provoke experimental research and various ecological techniques were either improved or created to study the phenomenon (Elner & Vadas 1990).

Some of the strongest circumstantial evidence for trophic cascades in the western-north Atlantic exists for the Gulf of Maine (e.g. Steneck 1997), where large predatory groundfish such as cod (*Gadus morhua*) have been fished for over 4000 years. In the 1930s, otter trawls and other technological improvements allowed for the efficient harvesting of coastal spawning stocks, and by the end of the 1940s, inshore groundfish stocks were already becoming heavily depleted (Steneck 1997). This rapid decline in cod stocks (as evinced by changes in the aereal extent of fishing grounds, cod landings and substantial reduction in the average size of fish caught) continued throughout the remainder of the century, such that today, large predatory finfish are functionally absent from regions of the Gulf of Maine (Steneck 1997). This loss of the top trophic level is thought to have fundamentally altered food webs within the Gulf of Maine, and the fish assemblage (and consequently the catch) is now dominated by small-bodied and commercially less important species such as sculpins, dogfishes and skates. Such changes are also thought to have been responsible for significant modification in the abundance of benthic invertebrates in coastal zones, with lobsters, crabs (*Cancer* spp.) and sea urchins all becoming more abundant (Steneck 1997).

Cashes Ledge is a shallow (depths 30–33 m) submarine island 130 km offshore in the Gulf of Maine which appears to have suffered little fishing activity and supports significant populations of large predatory fish such as cod, pollack and wolf-fish (Witman & Sebens 1992). Cashes Ledge has therefore been used as a natural fishery refugium to examine the impacts of large predatory fish on benthic community structure (Vadas & Steneck 1988, 1995; Witman & Sebens 1992; Steneck *et al.* 1995). At similar depths, predation pressure on crabs and other large mobile epibenthos (e.g. brittlestars) was much lower, and crab densities consequently much higher at inshore sites compared to Cashes Ledge (Witman & Sebens 1992). Similarly, at inshore sites, abundances of lobster and sea urchins were significantly higher than at Cashes Ledge (Steneck 1997). Algal abundance, and particularly kelp, was significantly higher at sites dominated by large predatory fish (Cashes Ledge) and this is undoubtedly due to predation on urchins by fish (Steneck *et al.* 1995; Vadas & Steneck 1995). Fish attacks on tethered sea urchins occurred only at sites where large predatory fish were abundant, and urchin abundance seemed to greatly influence kelp abundance (Steneck *et al.* 1995). Furthermore, sea urchins have recently become a targeted species in the Gulf of Maine, and Steneck *et al.* (1995) have been able to show that at inshore sites where urchin harvesting has been intense (e.g. Pemaquid Point), kelp beds have returned.

As early as 1969, population explosions of two sea urchins, *Strongylocentrotus franciscanus* and *S. purpuratus*, and associated degradation of kelp forests, were being recorded along the coasts of southern California (North & Pearse 1969). Initially this was attributed to the almost complete extinction of sea otters (*Enhydra lutris*), an important urchin predator (Fig. 4*b*) (Lowry & Pearse 1973). However, Tegner (1980) reviewed historical evidence and suggested that urchin outbreaks had occurred in southern California long after otters had been absent from the area. Many possible explanations were proposed for the lack of urchin outbreaks in otter-free areas and, following work in Nova Scotia, the spiny lobster (*Panulirus interruptus*) soon became implicated (Tegner & Dayton 1981; Tegner & Levin 1983) along with the sheephead (*Semicossyphus pulcher*) which is a large wrasse (Cowen 1983) (Fig. 4*b*). Although much of this work again relied on inference, it was found that experimental removal of urchins resulted in higher cover of some algal groups (Cowen *et al.* 1982), that spiny lobsters did have impacts on wild urchin populations and were responsible for the bimodal nature of urchin size-frequency distributions, and that lobsters and sheephead promoted cryptic behavioural responses (Tegner & Dayton 1981). Also, experimental removal of sheephead resulted in a 26% increase in urchin numbers and an increase in urchins occupying exposed sites (Cowen 1983). On the other hand, Cowen *et al.* (1982) proposed that the effect of sea urchins on algae might be overshadowed by the effect of physical disturbance associated with storms. A similar position was taken by Foster (1990) who also contended that kelp-forest communities in California (and perhaps the larger North Pacific region generally) are organized by biotic and abiotic processes and that the role of predation had been overemphasized and overgeneralized. Use of exclusion cages has indicated that the removal of spiny lobsters (*P. interruptus*) and other predators such as sheephead (*S. pulcher*) may also impact the communities of the lower intertidal in Southern California and result in the establishment of a distinctive turf of red algae (Robles 1987, 1997; Robles & Robb 1993). It would seem that predators kill juvenile mussels that otherwise overgrow and replace the algae.

Following the early suggestions that sea otters might be important in California, Estes and Palmisano (1974) noted that amongst the Aleutian Islands (Alaska), those islands without sea otters possessed substantially higher sea-urchin (*S. polyacanthus*) densities than those with sea otters, and that only small urchins existed where there was predation by otters. Later Estes *et al.* (1978) showed that on islands where sea otters were absent, fleshy macroalgae were excluded whilst at sites with otters, macroalgae were abundant, and that competition in the plant assemblage was most severe

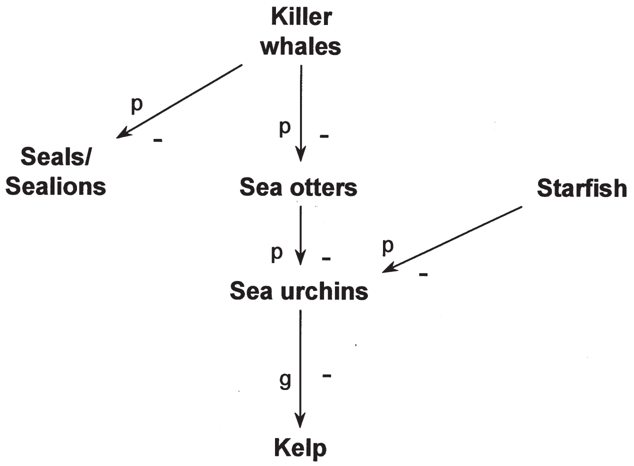

Figure 5 Diagram of proposed trophic cascade in Alaska and Aleutian Island kelp forest (for symbols, see Fig. 1).

in shallow water where sea otters can remove sea urchins more efficiently. Duggins (1983) suggested that for a site on mainland Alaska (Torch Bay), where otters were absent, a mosaic of discrete algal patches existed and that this spatial and temporal pattern was largely the result of the predatory starfish *Pycnopodia helianthoides*, which feeds on urchins but coexists in equilibrium with its prey. Estes and Duggins (1995) showed that kelp and sea-urchin abundance remained largely unchanged at a large number of sites where sea otters were either continually present or continually absent, but that sea-urchin biomass declined by 50% in the Aleutian Islands and nearly 100% in south-east Alaska following the spread of sea otters into previously unoccupied habitat. Differences in the magnitude of response were related to differences in recruitment processes of urchins amongst the two regions (Estes & Duggins 1995).

Recently, however, the cascade effect (Fig. 5) as initially proposed was extended when, after nearly a century of recovery from overhunting, sea otter populations again declined abruptly over large areas of western Alaska (Estes *et al*. 1998). This appeared to coincide with the increased observation of killer whale attacks on sea otters, which had never been observed prior to 1991, but became quite common thereafter. Otter populations have remained stable in lagoons, where they are inaccessible to killer whales, but strikingly rapid changes in the kelp forest ecosystem have occurred in other areas over this period, with great increases in sea-urchin biomass and grazing intensity and an associated drop in total kelp density at some sites, relative to values recorded in 1987 (Estes & Duggins 1995). The recent changes in killer whale behaviour may reflect a collapse in seal and sealion populations along north Pacific coasts attributable to anthropogenic influences including burgeoning fisheries and increased ocean temperature (Estes *et al*. 1998) (Fig. 5).

Two regions in which the predator-urchin-macroalgae paradigm has been most recently investigated are New Zealand and Australia. The dominant urchin of north-eastern New Zealand is *Evechinus chloroticus*, which at sufficient density has again been shown to maintain coralline barrens (Ayling 1981; Andrew & Choat 1982; Choat & Schiel 1982). Andrew and Choat (1982) showed that exclusion of predatory fishes greatly enhanced abundance of juvenile urchins, whilst the removal of echinoids resulted in rapid recruitment of fucoid and laminarian algae. However it was argued that, despite the high densities of predatory fish, some juvenile *E. chloroticus* escape predation and these represent sufficient input into the adult grazing population to maintain the habitat (Andrew & Choat 1982). This interpretation argues against a key role for predators structuring shallow water reef communities in north-eastern New Zealand. Consistent with this, the spiny lobster *Jasus edwardsii* consumed all sizes of urchins in the laboratory, but differing micro-habitat requirements of the two species meant that lobsters are likely to have only minimal impact on *E. chloroticus* populations (Andrew & MacDiarmid 1991). Recently however, Cole and Keuskamp (1998) showed that although there was no clear difference in overall urchin density between a protected and a fished site, higher urchin densities were indeed recorded at sites outside the MPA compared to sites within. Inside the MPA, urchin size structures were also more bimodal, urchins remained crevice-bound up to larger sizes, and transplanted urchins showed higher losses compared with a fished locality (Cole & Keuskamp 1998). Much clearer evidence for a trophic cascade has also emerged from work in the Leigh and Tawharanui MPAs in north-eastern New Zealand (Babcock *et al.* 1999). The abundance of the predatory fish *Pagrus auratus* was at least 5.75 to 8.70 times, and the spiny lobster *J. edwardsii* was 1.6 to 3.7 times, higher inside the MPAs than in adjacent unprotected areas (Babcock *et al.* 1999). Furthermore, in the Leigh Marine Reserve, densities of the sea urchin *E. chloroticus* declined from 4.9 to 1.4 individuals per m^2 since 1978 and urchins were shown to be an important component in the diets of both *P. auratus* and *Parapercis colias* (Babcock *et al.* 1999). Kelp forests were more extensive in the Leigh MPA in 1998 than they were when the Reserve was created in 1975; and in 1998, urchin-dominated barrens occupied only 14% of available reef substratum within the Reserve compared to 40% in adjacent unprotected areas (Babcock *et al.* 1999).

In temperate Australia (New South Wales), the dominant urchin is *Centrostephanus rodgersii*. This species maintains patches of corralline barren habitat around its night-time shelters (Andrew 1993). Here too, experimental manipulation has shown that removal of urchins caused loss of barren habitat and development of an assemblage of foliose algae (Andrew & Underwood 1993), and that the flora and fauna of translocated boulders became progressively similar to that in the surrounding habitats, particularly when algal-covered boulders were moved to barrens. However, Andrew (1994) suggested that *C. rodgersii* has comparatively little impact on kelp abundance outside of barrens.

In the Maria Island MPA in Tasmania (Australia), several changes occurred even within the first year of existence; densities of rock lobsters and sea urchins and the mean sizes of wrasse, leatherjackets, abalone and rock lobsters all increased relative to sites outside (Edgar & Barrett 1997). Over six years, and within several other MPAs, many of these differences were maintained (Edgar & Barrett 1999). Increases in macro-algal species richness have also occurred within the MPAs, although the processes responsible for the transformation of the algal community at Maria Island remain poorly understood (Edgar & Barrett 1999) and strong evidence for trophic cascades in Australian sublittoral systems is generally lacking.

Data on relationships amongst kelp, sea urchins and their predators are also generally lacking on the Pacific coast of South America (Dayton 1985). Dayton (1985) suggested that at some sites (e.g. Golfo de Penag), urchin (*Loxechinus albus*) densities were restricted by the predatory starfish *Meyanaster gelatinosus*, and that this in turn allows kelp communities to develop. Further, the southern king crab (*Lithodes antarctica*) may once have been important but *Lithodes* populations are now much reduced by fishing. Overall though, it was concluded that South American kelp communities do not seem to have the predators capable of controlling urchin populations (Dayton 1985).

A rare example of a trophic cascade not involving urchins (but again involving lobsters) is that of South Africa as described by Barkai and McQuaid (1988)(Fig. 6). In this scenario, rock lobsters (*J. lalandii*) consume settling mussels, thereby preventing the establishment of mussel beds and allowing the dominance of seaweeds which compete with the mussels for space (Barkai & Branch 1988). This is not a true trophic cascade and may be better described as keystone predation (Menge 1995), although where lobsters are excluded by fishing, mussels quickly become established and this can be considered as a trophic cascade with humans as the predator (Fig. 6). The situation becomes confounded by the presence of the whelks (*Burnupena* spp.). These species are a secondary prey of rock lobsters (e.g. at Malgas Island), but where lobsters are absent, their numbers increase ten-fold and they then preclude recolonization by rock lobsters and thus prevent the re-establishment of an algal-dominated system. Lobsters transplanted to whelk-dominated regions (e.g. Marcus Island), are rapidly overwhelmed and killed, thus providing us with a rare example of predator-prey role reversal and of two contrasting stable states within the same ecosystem (Barkai & McQuaid 1988).

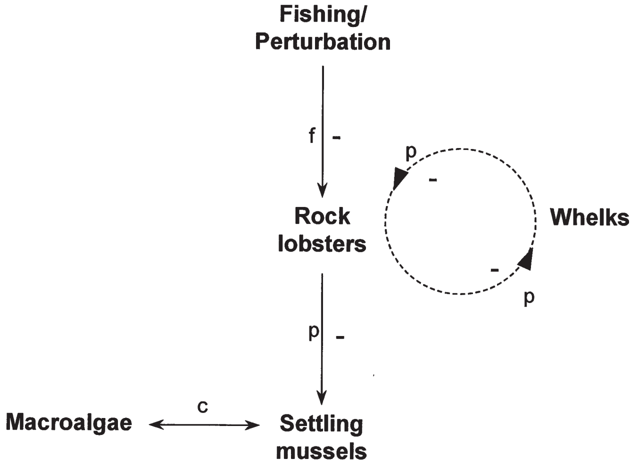

Figure 6 Diagram of a rocky-subtidal system in South Africa, including competition (c) for space between macroalgae and mussels. The circle between lobsters and whelks is symbolic of the prey-predator role reversal which can occur in this system (Barkai & McQuaid 1988) (for symbols, see Figs. 1 & 4).

Coral reefs

Trophic cascades have long been thought to exist and to be important in the structuring of coral reef communities, and evidence of them is strongest for reefs in Kenya and the Caribbean (Jennings & Kaiser 1998). Sea urchins tend to become more abundant as a result of intensive fishing (McClanahan 1992), and feature strongly in the majority of documented coral-reef trophic cascades; comparisons between MPAs and unprotected areas have been very important in the development of this axiom. A preoccupation in the literature has been with reef degradation and the single best documented symptom of this is overgrowth by algae following coral mass mortality. However, the mechanisms, detailed outcomes (Done 1992), and means of reversing algal overgrowth (Done *et al.* 1991) are thought to vary widely and are not fully understood.

On Kenyan reefs, both top-down (McClanahan & Muthiga 1989) and competitive (McClanahan *et al.* 1994) controls on the abundance of sea urchins (*Echinometra mathaei*) are indicated by comparisons primarily of MPAs (notably Malindi, Kisite and Watamu Marine National Parks) with areas unprotected from fishing (McClanahan & Shafir 1990). The triggerfish *Balistapus undulatus* is considered the single most important predator of sea urchins in MPAs and other lightly-fished sites, and probably controls populations of some sea urchins (McClanahan & Muthiga 1989; McClanahan 1995). Where this and other urchin predators are depleted, *E. mathaei* tends to become the dominant grazer, filamentous ('turf') algae become more abundant presumably because they withstand the urchin grazing, and hard corals decline in substratum cover (McClanahan & Shafir 1990) (Fig. 7). Since predation on sea urchins by starfish and gastropods is thought to be of only minor importance in MPAs, the cascade effect is most likely mediated by carnivorous fishes and particularly triggerfish (McClanahan & Muthiga 1989). Other fishes, including large wrasses (*Coris* spp. and *Cheilinus trilobatus*), may be locally more important (e.g. in the more recently created Mombassa MNP) and could potentially replace the triggerfish in their

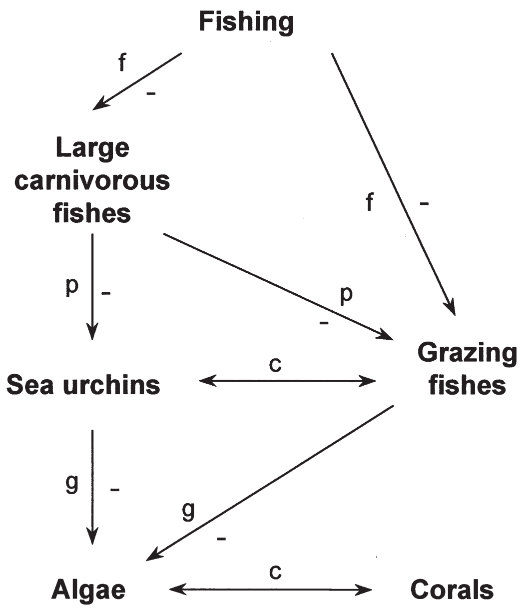

Figure 7 Diagram of a coral reef system similar to that proposed for Caribbean localities such as the north coast of Jamaica, and for Kenya (for symbols, see Figs. 1, 4 & 6).

urchin-predating role (McClanahan 1995). Sea urchins are thought likely to outcompete important grazing fishes such as parrotfishes (McClanahan *et al.* 1994), and increases in urchin abundance probably have important consequences for reef bioerosion to which they contribute significantly (McClanahan & Muthiga 1988). The inference is that where Kenyan reefs are protected from fishing, triggerfish abundance will increase, sea-urchin and turf-algal density on reef flats will decline, and parrotfish abundance and coral cover will increase. However, aside from fishing, sedimentation and nutrient inputs also influence the benthos and may interact in a complex way with grazing processes (McClanahan 1997*b*).

Although predation by invertebrate feeding fish has been shown to be higher in MPAs, McClanahan (1989) suggested that densities of most Kenyan gastropod species were not significantly lower inside MPAs compared to other sites. Lagoons, however, exhibited lower densities than reef flat or edge sites, and this was attributed to greater predation pressure (McClanahan 1990). Within six southern Kenyan lagoons, total gastropod densities were correlated negatively with triggerfish (Balistidae) and total fish densities, and positively with sea-urchin densities. The removal of balistids through fishing appears to lead to co-occuring population increases in gastropod and sea-urchin populations which, in most instances, appear to negate the effect of shell collecting (McClanahan 1990). McClanahan (1994*a*, 1997*a*) indicated that populations of the coral-eating snail *Drupella cornus* greatly increased in Kenyan coral reef lagoons over a period of ten years, and that this increase was greatest on heavily-fished reefs, where triggerfishes have been all but excluded. The increase was less pronounced in unfished, longer established parks, and McClanahan (1997*a*) has given similar results for reefs of the Masoala Peninsula, Madagascar. Rapid increases in *Drupella* population density have been shown to result in substantial coral mortality (Turner 1994). At one reef, however, where the cover of branching corals was lower, the presence of another coral-eating gastropod and potential competitor *Coralliophila neritoidea* seems to exclude *Drupella*. The underlying mechanism promoting outbreaks of corallivorous gastropods remains unclear, although similar increases have been reported for much of East Africa, the Red Sea and western Australia (McClanahan 1994*a*). It has been suggested that enhanced recruitment success during the late 1980s, as a result of improved oceanic conditions, may be responsible for this phenomenon (McClanahan 1994*a*).

A major focus of work in the Caribbean has been on a substantial shift which occurred in the 1980s from hard-coral to macroalgal domination. This shift has been attributed ultimately to fishing, on the basis that fishing reduced the abundance of both predators and grazing fish that are competitors of sea urchins (Hughes 1994). This led to a situation in which grazing came to be exerted almost entirely by a single urchin species, *Diadema antillarum* (Hughes 1994), which is subject to decimation by a pathogen (e.g. Lessios *et al.* 1984). *Echinometra viridis* is an important sea urchin in areas such as Belize and is preyed upon principally by jolthead porgy (*Calamus bajonado*), triggerfish (*Balistes vetula* and *Canthidermis sufflamen*) and hogfish (*Lachnolaimus maximus*), all of which are very susceptible to fishing (McClanahan *et al.* in press). In areas where there is intense fishing, such as Jamaica, sea urchins have thus become more important grazers on reefs (Hay 1984). When a disease-induced mass-mortality of the urchins occurred in the 1980s, macroalgae became greatly dominant (Carpenter 1990) and coral cover declined substantially (Hughes *et al.* 1987), largely because the fast-growing macroalgae evidently outcompeted the corals for space (Hughes 1989). Such changes have had substantial implications for grazing fishes and grazing processes in general, not only because the types of algae that have colonized shallow reefs after *Diadema* mass mortality are relatively unpalatable (Morrison 1988), but also because these fishes evidently competed with the urchin (Robertson 1991). Declines in macroalgae may not necessarily occur in MPAs, however, for a variety of reasons, including eutrophication (Lapointe *et al.* 1997), and naturally low recruitment of predatory and grazing fishes (e.g. Roberts 1997). Other factors, including coral bleaching, coral diseases, and cyclones, have also contributed to the current low abundance of corals on reefs in areas such as Jamaica. Indeed a systematic comparison between MPAs and unprotected areas in five widely separated Caribbean localities indicated no change in the benthos in spite of abundances of many fishery-target fishes being greater in MPAs (Williams & Polunin in press). A further complication is that a lagoonal reef in Belize without obvious pollution or intensive fishing has also been found to have lost much of its coral cover and to have become overgrown by macroalgae (McClanahan & Muthiga 1998).

A cascade similar to that proposed for urchin predators, urchins and algae is likely to exist based on another echinoderm, namely the Crown-of-Thorns starfish, *Acanthaster planci*. When the starfish increases greatly in abundance, its feeding leads to substantial decline in hard-coral cover (Moran 1986; Ormond *et al.* 1990). Ormond *et al.* (1990) noted an inverse relationship between the abundance of Crown-of-Thorns starfish and their fish predators, and suggested that starfish population outbreaks may have resulted from removal of fishes such as emporers (Lethrinidae) and triggerfish that prey on juvenile starfish. Keesing and Halford (1992) documented mortality rates of more than 6% per day for recently settled Crown-of-Thorns starfish and attributed this to predation, however Sweatman (1995) studied predation on juvenile starfish on the Great Barrier Reef and concluded that at this site, predation rates would be too low to regulate starfish populations. Consequently, there is only weak inference that removal of predators is responsible for outbreaks of Crown-of-Thorns starfish and a cascade leading to loss of coral cover.

Predation is widely considered intensive on undisturbed reefs (e.g. Arias-Gonzalez *et al.* 1997), but much of the information on reef fishes contrasts with that on urchins. Some comparisons between MPAs and fished areas have indicated greater abundances of certain species in exploited sites. Thus in the Red Sea, grazing surgeonfishes (Roberts & Polunin 1992), and in Kenya, diodontids and small-bodied wrasses and damselfishes (McClanahan 1994*b*) are more abundant at sites where predators are depleted. However, in the two cases where a gradient of fishing pressures has been studied, no evidence of fish-prey release has been found. Depletion of predators occurs along gradients of increasing fishing pressure on reefs in Fiji and the Seychelles, but prey fishes, however characterized (e.g. by family, species or trophic category), have not been found to increase in abundance (Jennings *et al.* 1995; Jennings & Polunin 1997; Polunin & Jennings 1998). Similar conclusions emerged from the work of Russ and Alcala (1998*a*, *b*) at sites in the Philippines, where there was little evidence for changes in abundance of prey fishes in response to increased fishing or to protection.

Intertidal

In his review of indirect effects in 23 documented intertidal communities, Menge (1995) suggested that true trophic cascades are a relatively rare phenomenon, occurring 37 times but in only five webs and representing only 6.5% of the indirect interactions observed. This was contrasted with 'keystone predation' which was by far the most frequent type of indirect effect in intertidal communities, occurring in 19 webs and representing 34.7% of the observed indirect interactions (Menge 1995). The cascades reviewed by Menge (1995) include the high intertidal of Boiler Bay (Oregon, USA), the mid-intertidal Cape Banks (Sydney, Australia), the high and low intertidal of Taboguilla Island (Panama) and the high and low intertidal of Washington State (USA). Because of the evaluation and analysis of these situations by Menge (1995), we will give only a few details here (Table 1).

One of the earliest intertidal webs to be studied is that of the Washington State coast, north-western USA (reviewed by Paine 1984). Paine (1966) showed that removal of the predatory starfish *Pisaster orchraceus* resulted in the extension of mussel (*Mytilus californianus*) beds to lower in the intertidal, excluding the dominant algal species *Hedophyllum sessile* and *Alaria nama* (Paine 1966, 1974). This in itself is not a trophic cascade effect, but another example of 'keystone predation' (Menge 1995). However, were it not for *Pisaster* creating space for the algal assemblage to develop, another trophic cascade (again involving urchins) would not be possible. Paine and Vadas (1969) showed that when urchins were removed from intertidal pools previously dominated by coralline algae (whether the removal was experimental or by the predatory sunstar, *Pycnopodia helianthoides*), there was rapid growth of fleshy macroalgae. This was later confirmed by Dayton (1975), who showed similar algal blooms and suggested that although the actual consumption of urchins by *Pycnopodia* is insufficient to have an overwhelming effect on urchin densities, their presence causes a stampede of urchins away from the predator thus leaving vacant areas. The effect of *Pycnopodia* on urchin populations is compounded by the fact that many of the fleeing urchins are caught and consumed by the green anemone, *Anthopleura xanthogrammica* (Dayton 1975). Thus, these papers together give a very early account of an intertidal cascade effect involving three trophic levels (Fig. 8). Molluscan herbivores were not observed to make any measurable impact on the recruitment or survival of algae, and it was suggested that this may be due to predation by the starfish *P. orchraceus* and *Leptasterias hexactis,* which in some areas totally exclude herbivorous gastropods from the lower intertidal algal zone. However, Paine (1992) has suggested that the chiton *Katharina tunicata* might also be important, although no significant effect was shown by Dayton (1975).

Recently, the urchin-based cascade has been extended by Wootton (1995), who showed that by excluding birds (*Larus*

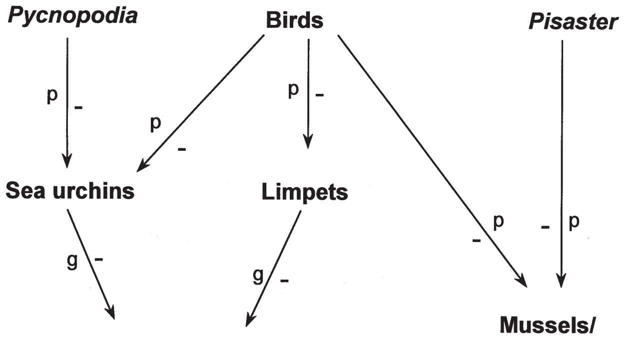

Figure 8 Diagram of a rocky intertidal system in Washington State (USA), involving two starfish (*Pycnopodia* and *Pisaster*) and birds (for symbols, see Fig. 1).

glaucescens, Haematopus bachmani and *Corvus caurinus*) using wire cages, urchin abundance increased by 45–59% and that by reducing urchin grazing, birds indirectly increased algal cover 24-fold. Birds have also been shown to greatly reduce the biomass of limpets (*Lottia digitalis* and *L. pelta*) in the upper intertidal (Wootton 1992), particularly where there is very little shelter. This, together with reduction of space competition (birds also consume the barnacle *Pollicipes polymerus*; Wootton 1994), has been shown to enhance the abundance of algae 26-fold. Thus, at least three trophic cascades have been identified for the shores of Washington State (Fig. 8).

Lindberg *et al.* (1998) proposed a three trophic level cascade amongst American oystercatchers (*Haematopus bachmani*), limpets (*Lottia* spp.) and fleshy algae in rocky intertidal communities of central and southern California. Experimental removal of the large territorial limpet *Lottia gigantea* resulted in increased cover of erect algae, although substrates were gradually re-colonized by increased numbers of smaller limpets. Removal of the small limpets also resulted in increased algal cover, thus demonstrating that both large and small limpets had similar inhibitory effects on plant populations (Lindberg *et al.* 1998). Where oystercatchers were common, mortality of limpets on horizontal surfaces was high and limpets tended only to inhabit vertical surfaces. Shorelines frequented by humans typically lacked oystercatchers, however humans also exploit *L. gigantea* and reduced populations to low densities (Lindberg *et al.* 1998). An almost identical trophic cascade was described for islands off the south-western Cape of South Africa (Hockey & Branch 1984), whereby the density of the principal midshore grazing gastropod *Patella granularis* has been reduced through predation by African black oystercatchers (*H. moquini*) to a level where the remaining limpet population was no longer able to control algal growth at the sporeling stage, and persistent beds of macroalgae developed. These beds were largely absent on the nearby mainland where the density of oystercatchers, and hence predation pressure on the limpets was much less (Hockey & Branch 1984). Algal growth rates on island shores were further enhanced by the enrichment of intertidal and nearshore waters by seabird guano (Bosman *et al.* 1986); seabird rookeries do not occur on the adjacent mainland.

A similar situation involving humans as the predator was observed by Moreno *et al.* (1984) (reviewed by Castilla 1999) for the mid-intertidal in southern Chile. When harvesting by humans was excluded from a 600 m^2 MPA near Mehuin, it resulted in increased abundance of keyhole limpets (*Fissurella* spp.) coupled with a dramatic decline in the abundance of macroalgae, principally *Iridaea boryana*. By contrast, where limpets had been experimentally removed (Moreno & Jaramillo 1983), macroalgal cover increased to near 100%, which coincided with the observation that adjacent to large fishing villages, where harvesting was most severe, *I. boryana* was particularly abundant (Moreno *et al.* 1984). Godoy and Moreno (1989) demonstrated that removal of *Fissurella picta*, whether by human gatherers or experimentally, also resulted in increased fecundity (by ~38%) of a second species of herbivorous limpet, *Siphonaria lessoni,* which competes with *F. picta* for food.

Within the same system, the carnivorous muricid gastropod *Concholepas concholepas* (Castilla 1999) is harvested by subsistence food-gatherers. Human exclusion from a stretch of coast resulted in a substantial increase in *C. concholepas,* followed by a dramatic decline in the cover of its prey, the dominant intertidal mussel *Perumytilus purpuratus* (Castilla & Duran 1985; Moreno *et al.* 1986). Outside the MPA a monoculture of *P. purpuratus* remained present (Botsford *et al.* 1997). These results together suggest that humans can regulate predatory efficiency and/or selectivity, and thereby manage, enhance, reduce, conserve or preserve species or communities (Castilla 1999).

On rocky intertidal shores of warm temperate New South Wales (Australia), bivalves, urchins and predatory starfish are scarce in comparison with sites elsewhere in the world (Fairweather & Underwood 1991). In the midshore assemblage, the whelk, *Morula marginalba*, is the dominant predator and a substantial body of literature exists concerning the effects of *Morula* on populations of its prey (mostly limpets and barnacles). These studies have utilized a wide variety of experimental methods including exclusion fences (Underwood *et al.* 1983), manual removal of individuals (Fairweather *et al.* 1984), the cementing up of *Morula* shelters (Fairweather *et al.* 1984) and the deployment of exclusion cages (Fairweather & Underwood 1991). In general, it would appear that where whelks were excluded, prey densities, including grazing gastropod molluscs, were significantly higher (Fairweather & Underwood 1991). Underwood (1980) and Jernakoff (1983) demonstrated that where limpet grazers (*Patelloida latistrigata* and *Cellana tramoserica*) were excluded there was rapid colonization of macroalgal sporelings (mostly *Ulva lactuca*). Consequently although this body of literature is rather diffuse, a trophic cascade involving predatory whelks, grazing gastropods and macroalgae is inferred, and this is one of the trophic cascades highlighted in the synthesis of Menge (1995).

Soft bottoms

In relation to other benthic marine systems, there is comparatively little evidence for trophic cascade effects amongst soft bottom communities. Fishery-target populations may recover in terms of numerical abundance and biomass after a cessation of fishing activities (Saeger 1981; Yamasaki & Kuwahara 1990; Pipitone *et al.* 2000), but there has been little regard for potential indirect effects on prey species. Caging experiments in soft bottom communities have showed that the exclusion of predators generally results in large increases in density and diversity of infaunal species (Virnstein 1977). However, because trawls and dredges may inflict considerable physical damage on infauna populations (Kaiser &

Spencer 1996*a*, *b*; Prena *et al.* 1999), the effects of predation and thus observation of any potential trophic cascades may be obscured (see review by Jennings & Kaiser 1998); populations may even show increases in numerical abundance and biomass after cessation of trawling, despite increases in their predators.

Pipitone *et al.* (in press) reported an eight-fold increase in fish biomass over the four years following a trawling ban in the Gulf of Castellammare (NW Sicily, Italy). Biomasses of certain target species such as *Mullus barbatus* increased 33-fold with respect to data collected prior to the closure (Riggio 1988, 1989), however the biomass of cephalopods (excluding *Octopus vulgaris*) generally declined. This accords with the findings of Pauly (1985, 1988) for the Gulf of Thailand, that where predators of squid pre-recruits were common, squid were less common, but as fishing intensified and indeed rays and sawfish virtually disappeared, cephalopods became more important. Similar trends were predicted by Christensen (1998) using a simulation model, where increased fishing pressure resulted in declines of most demersal groups like rays, crabs, lobsters and large piscivorous fish, and, indirectly, increases in some of their potential prey such as cephalopods, scads and shrimp. These 'prey-release' predictions also agreed with an observed increase in shrimp recruitment for the Gulf of Thailand by Pauly (1982) following the increase in fishing pressure and an observed decrease in total shrimp production in Indonesia following a trawl ban (Garcia 1986).

There is evidence from the coasts of north-west and west Africa (Caddy 1983; Gulland & Garcia 1984) that domination by cephalopods, and particularly squid, may be a general feature of intensively fished soft-bottom demersal systems. A 90% increase in the catch of cephalopods occurred between 1960 and the early 1970s (Gulland & Garcia 1984) and similar patterns were observed by Caddy (1983) off the Mauritanian coast. These increases corresponded with a dramatic decline in the sparid fishery of this region (Caddy 1983), although the mechanisms responsible for such changes remain unclear (Caddy 1983; Hall 1999) and thus it is not possible to say whether these data imply a true trophic cascade or not.

In certain soft-bottom communities, ophiuroid beds persist because predatory fish are absent (Aronson & Harms 1985; Aronson 1992). At sites on the south-west coast of Great Britain, ophiuroids have experienced considerable changes in abundance over the past century (Holme 1984). Aronson (1989) demonstrated that predation pressure on ophiuroids was significantly lower where fishes and portunid crabs were rare amongst soft bottoms, in comparison with adjacent sites on rocky reefs where potential predators (e.g. fish, crabs and starfish) were relatively abundant. Overfishing along UK and Irish coasts has severely depleted teleost predators, and it has been suggested that this has resulted in a system dominated by echinoderms and crustaceans (Aronson 1989, 1990, 1992).

Synthesis and discussion

We have reviewed evidence for 49 different documented cascades in benthic marine systems from 26 locations around the world (Table 1). We acknowledge that the quality of the evidence varies greatly, and some of the cascades which we have listed may be more speculative than most of the literature has indicated, for example those in kelp/macroalgal systems involving sea otters and sea urchins (Hart & Scheibling 1988; Strong 1992), and fish and sea urchins (Sala *et al.* 1998*a*). Consequently we have tried to distinguish cascades which appear to be well supported by data (numbered entries in Table 1) from those where the underlying evidence is more circumstantial (in parenthesis only in Table 1). If we omit the latter cases, the best-substantiated examples of cascades are 39 in number, and come from 21 locations (Table 1).

What are the limitations in the data?

Before discussing any potential patterns in this information, it is worth considering how different the number of cases listed in Table 1 might have been had we characterized the literature and the underlying evidence in ways other than we did. To begin with, only instances which are predominantly benthic were included; for marine systems as a whole (pelagic as well as benthic), the list of Table 1 would be longer (Verity & Smetacek 1996). Although we suspect we have cropped all of the best-substantiated benthic instances from the literature, we accept that, particularly towards the 'circumstantial' end of the range, our list is probably not exhaustive. To extend it further with respect to poorly-substantiated examples, however, would risk our appearing to propagate the expectation that top-down controls must be prevalent in systems such as reefs (e.g. Roberts 1995), whereas some of the best data indicate they may not be (Keough *et al.* 1993; Jennings & Polunin 1997; Polunin & Jennings 1998). There is nevertheless an area in-between the extremes, where substantiation or otherwise relies somewhat on subjective criteria. For example, we have included amongst the best-documented cascades those that include humans; without these, the list (Table 1) would have been shorter by eight, given the strict requirement that three or more trophic levels characterize cascades. We included instances involving humans at the risk of entering a debate about whether humans are or are not a natural part of the systems concerned, because human impacts are increasingly evident (e.g. Kitchell & Carpenter 1993) and our ultimate purpose here is to understand the consequences of cascades and recovery of systems from such impacts, given the widespread attention they have received (e.g. Botsford *et al.* 1997; Jennings & Kaiser 1998).

We also included separately those cases where detailed study has revealed a number of very similar cascades in the same system, as in the Taboguilla Islands of Panama (e.g. Menge 1995), whereas in other cases some of the substantia-

Table 1 Details of documented cascade effects, listed by system type: numbered cascade outlines are based on the best-substantiated examples, while those in parenthesis are those based on more circumstantial evidence. Of the intertidal webs reviewed by Menge (1995), those involving recruitment inhibition have been omitted as being outside the definition of trophic cascade *sensu stricto*.

Location	*System*	*Cascade outline*
Nova Scotia & Newfoundland (Canada)	Kelp forest	(1) Lobster–urchin–kelp (2) Wolf fish–urchin–kelp
Southern California (USA)	Kelp forest	(3) Spiny lobster–urchin–kelp (4) Fish-urchin–kelp (Sea otter–urchin–kelp)
Alaska & Aleutian Is. (USA)	Kelp forest	(5) Sea otter–urchin–kelp (6) Starfish–urchin–kelp (7) Killer whale–sea otter–urchin–kelp
New Zealand/Australia	Kelp forest	(8) Fish/lobster–urchin–kelp
Southern Chile	Kelp forest	(9) Starfish–urchin–kelp (King crab–urchin–kelp)
South Africa	Rocky subtidal	(10) Humans–rock lobster–mussel
Medes Is. (Spain)	Rocky subtidal	(11) Fish–urchin–algae (Humans–herbivorous fish–algae)
Scandola, Corsica (France)	Rocky subtidal	(12) Humans–fish–macroinvertebrate
Ustica Is., Sicily (Italy)	Rocky subtidal	(13) Grouper–small fish–amphipod/polychaete
Gulf of Maine	Rocky subtidal	(14) Humans–cod/wolf fish–mobile epibenthos (15) Predatory fish–urchin–kelp
Kenya	Coral reef	(16) Fish–urchin–algae (17) Fish–*Drupella*–coral (Humans–piscivore–diodontid/wrasse/damselfish)
Caribbean	Coral reef	(18) Fish–urchin–algae (Humans–herbivorous fish–algae)
Pacific (including Great Barrier Reef)	Coral reef	(19) Fish–corallivorous starfish–coral
Red Sea (Egypt)	Coral reef	(Humans–piscivore–surgeon fish)
Central & Southern California (USA)	Intertidal	(20) Oystercatcher–limpet–algae (21) Humans–limpet–algae (Humans–spiny lobster–mussel)
Southern Chile	Intertidal	(22) Humans–limpet–algae (23) Humans–muricid gastropod–mussel
Washington State (USA)	Intertidal	(24) Starfish–chiton–algae–limpet–starfish (25) Starfish–urchin–algae–limpet–starfish (26) Starfish–urchin–algae–limpet–buccinid gastropod (27) Bird–urchin–algae (28) Bird–limpet–algae
New South Wales (Australia)	Intertidal	(29) Buccinid gastropod–grazing gastropod–algae
Taboguilla Is. (Panama)	Intertidal	(30) Puffer fish–muricid gastropod–herbivorous gastropod (31) Puffer fish–muricid gastropod–barnacle (32) Fish–limpet–algae (33–35) Muricid gastropod–limpet–algae
Boiler Bay, Oregon (USA)	Intertidal	(36) Bird–limpet–algae
South Africa	Intertidal	(37) Oystercatcher–limpet–algae
Gulf of Castellammare, Sicily (Italy)	Soft bottom	(38) Humans–fish–cephalopod
Gulf of Thailand	Soft bottom	(39) Humans–large fish–scad/shrimp/cephalopod
NW Africa	Soft bottom	(Humans–fish–cephalopod)
Irish Sea & English Channel	Soft bottom	(Humans–fish–ophiuroid)
Chesapeake Bay (USA)	Soft bottom	(Humans–fish–infauna)

tion which we have accepted (Table 1), for example the relationships between fish and sea urchins, and urchins and algae, in the Caribbean are poorly resolved at the species level. Future studies comparable in intensity to those conducted in Panama may yet identify separate cascades within the same system (T.R. McClanahan, personal communication 1998). The scope for direct comparisons amongst examples of cascades derived from such a variety of methodologies, and spatial and temporal scales is clearly limited. It is notable that most of the documented cascades (Table 1) rely on bringing together information from different sources and types of study (e.g. Sala & Zabala 1996;

Sala 1997*b*). If we had confined ourselves only to large-scale observations, for example of areas subject to different levels of exploitation, then the inventory of studies in Table 1 would have been shorter than it is. Such data, however, are typically weak, in their lack of controls for example, while small-scale controlled manipulations offer a more rigorous basis for inferring the existence of cascades and are not necessarily without inferences at large spatial scales.

It is likely that a change occurring at any point in a food web will often be propagated out from that point, but progressively decrease in amplitude with each step, so that changes down food webs, as in cascades, are likely to be highly diffuse (Strong 1992). This will be particularly so if influences such as recruitment accumulate with each step. In ecosystems, species are interconnected by different types of direct and indirect linkage (Menge 1995), the effects of which become intermingled, thus clouding any trophic cascade effects (Strong 1992; Steneck 1998; Sala *et al.* 1998*a*). It follows that the inventory in Table 1 must be a small part of the cascades that actually exist; they are probably those which have the largest effects detectable in some of the most conspicuous of organisms.

Are there ecological and geographical patterns in the prevalence of cascades?

Some contrasts are evident in the distribution of the examples (Table 1). Four main systems are represented in the best-documented cascades, namely those of subtidal algal beds (including those of kelp and other macroalgae) (14 in number), coral reefs (4), rocky intertidal (17) and soft bottoms (2) (Table 1). The systems from which nearly all these benthic cascades have been reported, have a number of characteristics in common; these include shallowness, accessibility to investigators, and underlying hard substratum. Shallowness has consequences for accessibility to human investigation, but so also does substratum hardness; for example, many organisms are sessile or strongly site-attached, and are more amenable to experimentation and repeated detailed observation than on soft substrata. If factors such as shallowness and accessibility are important in the preponderance of cascades observed in littoral systems, however, they do not alone explain an apparent absence of reports of cascades from other shallow-water systems such as seagrass beds. In the case of soft sediments generally, it may be that the likelihood of cascades being detected is small because of the difficulty of assessing the abundance of mobile predators and absence of conspicuous primary producers such as macroalgae, the abundance of which could be easily measured.

The distribution of the published examples is also geographically uneven, for example when the fisheries regions of the Food and Agriculture Organization of the United Nations (FAO) are considered (Table 2). The majority of examples of trophic cascades come from the Americas, especially North America, where many of the underlying ecosystem concepts originated (e.g. Paine 1980) and study of shallow-water systems appropriate for detecting indirect interactions has been most intensive (e.g. Menge 1995). Conversely, we could find no reports of cascades from the north-eastern Atlantic, eastern-central Atlantic, south-western Atlantic, Southern Ocean, eastern Indian Ocean, or north-western Pacific (Table 2). For the Southern Ocean, there has been much interest in the effects of removing marine mammals such as whales on their prey populations (Beverton 1985; Croxall 1992; Kock 1994), and increases in species such as penguins (Sladen 1964) and seals (Payne 1977) have been attributed to increases in krill abundance following decline of the baleen whale stocks. However, this example is principally pelagic, and therefore outside of the scope of the present review, while re-examination of such cascades has also suggested that many of the early reports and analyses for the Southern Ocean cascades were in error (Beddington & de la Mare 1985; Cooke 1985) or not as convincing as first thought (Jennings & Kaiser 1998). Similarly, a largely pelagic trophic cascade has been proposed (van der Elst 1979) for Natal (South Africa), whereby gill netting reduced the number of large sharks which in turn allowed a population boom of small sharks (their prey), which consequently depressed the abundance of fin fish in the region.

Table 2 Distribution by FAO fisheries region of the best-substantiated reports of cascade effects.

Region	*FAO code*	*Number of cascades reported*
NW Atlantic	Area 21	4
NE Atlantic	Area 27	0
WC Atlantic	Area 31	1
EC Atlantic	Area 34	0
SW Atlantic	Area 41	0
Mediterranean and Black Sea	Area 37	4
SE Atlantic	Area 47	2
Southern Ocean	Areas 48, 58, 80	0
W Indian Ocean	Area 51	2
E Indian Ocean	Area 57	0
WC Pacific	Area 71	2
NW Pacific	Area 61	0
NE Pacific	Area 67	9
EC Pacific	Area 77	10
SW Pacific	Area 81	2
SE Pacific	Area 87	3

The apparent absence of reports of trophic cascades from the north-eastern Atlantic (Table 2) is surprising, given for example a long history of work in countries like Britain on the rocky intertidal, a system which elsewhere has produced several examples of cascades (Table 1). There have been experiments at large scales; for example sea-urchin removals have demonstrated short-term control of macroalgae in British waters (e.g. Kitching & Ebling 1961), but cascade effects have not apparently been demonstrated there. The apparent absence of reports of cascade-type effects from the north-western Pacific is also unexpected in relation to long-standing human exploitation of shallow rocky systems in countries like Japan, but the lack of examples from the eastern-central Atlantic, south-western Atlantic, and eastern Indian Ocean, is explicable in terms of the paucity of detailed scientific studies in the littorals of these regions.

If physical and physiological environmental stresses on organisms are significantly reduced in subtidal environments, and such low stress is conducive to top-down controls in benthic systems (Menge & Sutherland 1987), then this may help explain the large number of cascades reported from subtidal systems. However, according to Menge and Sutherland (1987), the intertidal may typically be more stressful, yet, as noted, many cascades have been reported from these systems as well (Table 1). One possibility is that recruitment does not control population sizes as extensively in stressful intertidal habitats as often supposed. At less stressful intertidal sites, predation may be more important (Menge & Sutherland 1987) both on and by focal animals such as limpets (Table 1). Since Menge (1995) points out that cascades are in fact relatively infrequent amongst indirect interactions in the intertidal however, it is possible that the relatively large number of examples identified is related to the comparatively intensive study to which the intertidal has been subjected.

What are the underlying structures and mechanisms?

A general point is the focal role played by gastropods and sea urchins in systems with hard substrata (Table 1). The low number of substantiated cascades which we have identified from the literature contrasts with the expectation of some observers (e.g. Roberts 1995; Pace *et al.* 1999), but could be explicable by generalized predation acting across many trophic levels, as in the 'multichannel omnivory' of Polis and Strong (1996). On the other hand, the repeated prominence of urchins and gastropods in documented trophic cascades could be related to the fact that only a few specialists can overcome the body armour, such as spines and thick shells, which these grazers have (e.g. Branch 1981; McClanahan 1995; Sala 1997*b*); prominent amongst these predators are fishes, lobsters and birds. We suggest that food webs in which specialist predators control ecologically-important prey, such as sea urchins, are more susceptible to perturbation because if, for example, one predator is reduced in density, there is little to replace it; and consequently if not controlled by other factors, prey will therefore increase.

Fish predation as a whole is considered very substantial in many marine food webs (e.g. Bax 1991), but this does not always mean that abundances of prey species are controlled or regulated by predators; spatial and temporal variations in processes such as those that contribute to recruitment could in fact often be determining differences in adult abundance of prey species (Jennings & Kaiser 1998). We suggest that much predation by fishes is of a generalist nature, such that there is great overlap in diet, and great scope for species to replace one another in ecological terms. Many fish prey are likely to be subject to a greater range of predators than are armoured prey such as sea urchins, and under these circumstances there may need to be extensive reductions across predator species, before increases in prey densities are likely to occur (Polunin & Jennings 1998). At the same time, if more species can fulfil similar predatory roles, then the magnitude of predation on certain species, or functional groups, should be greater per individual than where specialist predators are involved, assuming recruitment and other controls on predator populations are similar. This indicates that top-down controls by generalist predators should exist, but that maybe these will occur more often at aggregate levels such as those of functional groups, rather than at the level of single species.

In addressing the predominance of gastropods and echinoids in documented cascades, we have not highlighted the possibility that this predominance is largely an artefact of the relative conspicuousness of sea urchins compared to other organisms. The fact is that the resolution (on visual and taxonomic grounds) of existing studies is very poor, and polychaete worms, decapod crustaceans and ophiuroids are a few of the potentially interesting candidates for future study (e.g. Badalamenti *et al.* 1999).

Up to this point, we have also tended to assume that predation refers only to consumers that are large enough to eat other species in food webs, but there is much evidence that if the outline definition had been extended to parasitism and pathogens, the number of cascades in Table 1 would have been greater, increasing the number of documented cases from regions such as the NW Pacific (Pearse & Hines 1987), NW Atlantic (Scheibling & Stephenson 1984), SW Pacific (Andrew 1991) and WC Atlantic (e.g. Carpenter 1990) (Table 2), from which sea-urchin mass mortalities and system consequences have been reported. Menge (1995) allows for the inclusion of parasites and pathogens in his definition of trophic cascades. Such cascades have been demonstrated for cold-water streams in Michigan (Strong 1992; Kohler & Wiley 1997) and potential cascades involving parasites have also been proposed by Huxham and Raffaelli (1995) for the Ythan estuary and Loch Leven in Scotland.

What are the implications for ecosystem management?

In spite of the interest expressed in ecosystem management of fisheries (e.g. Botsford *et al.* 1997), it appears that information for predicting the occurrence of an important class of indirect effects mediated by food webs, namely trophic cascades, is not as strong as the strength of the cascade paradigm would lead us to expect. The information we have reviewed supports the existence of cascades at small spatial and temporal scales. It would however be premature to suppose that such interactions would invariably be found at large scale if they were looked for (Martinez & Dunne 1998). Nearly all of the evidence comes from hard-bottom habitats which are unsuitable for gears such as trawls, and this means that any inferences we can make will be almost exclusively with respect to recreational angling, subsistence gathering, pot fishing and other artisanal fishing activities which these habitats accommodate. We can thus expect cascade effects of exploitation in shallow subtidal hard-bottom systems including coral reefs, kelp forests and other macroalgal beds, where the exploitation is intensive. This may have profound effects on the immediate ecosystems and on occasion on adjacent ecosystems, as indicated for example by the study of McClanahan and Muthiga (1988), where fishing has evidently increased bioerosion of the reef by sea urchins. Because this is likely to reduce the protective role of the fringing reef as a barrier to wave energy, erosion and transportation of sand further inshore, away from Kenyan beaches, is almost certainly being enhanced, and consequently this may result in an increasingly important effect on coastal tourism.

In the Mediterranean, fish can potentially control sea-urchin populations and the cover of crustose algae (McClanahan & Sala 1997), but recruitment, human predation and other influences may intervene (Sala & Zabala 1996; Sala *et al*. 1998*a*, *b*). For example, the recovery of fleshy algae may occur only when sea urchins are totally removed (Benedetti-Cecchi *et al*. 1998). Also, predatory interactions between urchin predators (Sala 1997*b*) mean that some urchin predators are likely to become less abundant in MPAs, while others increase in density (Francour 1994). Non-linear response of algae, high variability of sea-urchin recruitment, and predation on juvenile sea urchins by fishes associated with their crevice-dwelling behaviour, are probably the main explanations for non-reversal of coralline barrens in MPAs.

In the Caribbean, there is, as yet, very little, if any evidence, that MPAs will reverse the widespread macroalgal overgrowth (Williams & Polunin in press). This is not surprising; the grazing dominance of sea urchins is attributable ultimately to intense fishing, but the proximate cause of the overgrowth is the urchin mass mortality of the early 1980s, caused by a pathogen and subsequent slow recruitment (Hughes 1994). Sea-urchin abundance is generally increasing, and appears to be limited by recruitment, although densities in MPAs might ultimately be lower if urchin predators increase with local fishing closures (W. Hunte, personal communication 1998). At small scale, however, managers might artificially increase urchin densities in enclosures (J.L. Munro, personal communication 1997). Grazing fishes might increase in MPAs, but the evidence for this happening is very weak (Polunin & Roberts 1993; Williams & Polunin in press). At large scale, however, there is circumstantial evidence from a negative correlation between grazer biomass and macroalgal cover that increase in grazer abundance could substantially reverse macroalgal overgrowth (Williams & Polunin in press). Herbivory by fish might also prove to be more important in the Mediterranean than previously presumed for temperate waters, raising the possibility that if sea-urchin density could not easily be controlled, the density of grazing fishes might also be enhanced by MPA management where fishing has substantially depleted it. However, for the moment, there is no evidence that extensive coralline barrens in the Mediterranean have been reversed in any MPA.

Systems underlain by soft substrata are very important to large-scale fisheries (e.g. FAO 1997), but we can find very little evidence of cascades reported from them in the literature (Table 1). For hard substrata, MPAs have played a central role, ultimately it seems because the reef-type systems concerned are foci of recreational diving and are not suitable for industrial gears. The artisanal fisheries which predominate in hard-bottom systems have also proved amenable to study in some regions, in a way that industrial fisheries have not (e.g. Jennings & Kaiser 1998). In contrast, the opportunity to compare areas subject to different levels of management (involving MPAs of whatever kind) or fishing pressure (fishing gradients) has scarcely been available for the industrial fisheries which predominate in many systems with soft substrata. Where the opportunity does arise in future, we suspect that cascade effects will be found, although the methods of study and organisms targeted will likely be different.

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References

Andrew, N.L. (1991) Changes in subtidal habitat following mass mortality of sea-urchins in Botany Bay, New South Wales. *Australian Journal of Ecology* **16**: 353–62.

Andrew, N.L. (1993) Spatial heterogeneity, sea urchin grazing, and habitat structure on reefs in temperate Australia. *Ecology* **74**: 292–302.

Andrew, N.L. (1994) Survival of kelp adjacent to areas grazed by sea-urchins in New South Wales, Australia. *Australian Journal of Ecology* **19**: 466–72.

Andrew, N.L. & Choat, J.H. (1982) The influence of predation and conspecific adults on the abundance of juvenile *Evechinus chlorotilus*. *Oecologia* **54**: 80–7.

Andrew, N.L. & MacDiarmid, A.B. (1991) Interrelations between sea-urchins and spiny lobsters in northeastern New Zealand. *Marine Ecology Progress Series* **70**: 211–22.

Andrew, N.L. & Underwood, A.J. (1993) Density dependent foraging in the sea urchin *Centrostephanus rodgerii* on shallow subtidal reefs in New South Wales, Australia. *Marine Ecology Progress Series* **99**: 89–98.

Arias-Gonzalez, J.E., Delesalle, B., Salvat, B. & Galzin, R. (1997)

Trophic functioning of the Tiahura reef sector, Moorea Island, French Polynesia. *Coral Reefs* **16**: 231–46.

Aronson, R.B. (1989) Brittlestar beds: low predation anachronisms in the British Isles. *Ecology* **70**: 856–65.

Aronson, R.B. (1990) Onshore-offshore patterns of human fishing activity. *Palaios* **5**: 88–93.

Aronson, R.B. (1992) Biology of a scale-independent predator-prey interaction. *Marine Ecology Progress Series* **89**: 1–13.

Aronson, R.B. & Harms, C.A. (1985) Ophiuroids in a Bahamian saltwater lake: the ecology of a paleozoic-like community. *Ecology* **66**: 1472–83.

Ayling, A.M. (1981) The role of biological disturbance in temperate subtidal encrusting communities. *Ecology* **62**: 830–47.

Babcock, R.C., Kelly, S., Shears, N.T., Walker, J.W. & Willis, T.J. (1999) Changes in community structure in temperate marine reserves. *Marine Ecology Progress Series* **189**: 125–34.

Badalamenti, F., Cantone, G., Domina, R., Di Pietro, N., Catalano, D., Mollica, E. & D'Anna, G. (1999) Primi dati sulla fauna a policheti di substrato duro dell'infralitorale fotofilo superiore dell'Isola di Ustica. *Biologia Marina Mediterranea* **6**: 230–6

Barkai, A. & Branch, G.M. (1988) Contrasts between the benthic communities of subtidal hard substrata at Marcus and Malgas Islands, a case of alternative stable states. *South African Journal of Marine Science* **7**: 117–37.

Barkai, A. & McQuaid, C. (1988) Predator-prey role reversal in a marine benthic ecosystem. *Science* **242**: 62–4.

Bax, N.J. (1991) A comparison of the fish biomass flow to fish, fisheries, and mammals in six marine ecosystems. *ICES Marine Science Symposia* **193**: 217–24.

Beddington, J.R. & de la Mare, W.K. (1985) Marine mammal fishery interactions: modelling and the Southern Ocean. In: *Marine Mammals and Fisheries*, ed. J.R. Beddington, R.J.H. Beverton & D.M. Lavigne, pp. 94–105. London: George Allen & Unwin.

Bell, J.D. (1983) Effects of depth and marine reserve fishing restrictions on the structure of a rocky reef fish assemblage in the north-western Mediterranean Sea. *Journal of Applied Ecology* **20**: 357–69.

Benedetti-Cecchi, L., Bulleri, F. & Cinelli, F. (1998) Density dependent foraging of sea urchins in shallow subtidal reefs on the west coast of Italy (western Mediterranean). *Marine Ecology Progress Series* **163**: 203–11.

Bernstein, B.B., Williams, B.E. & Mann, K.H. (1981) The role of behavioural response to predators in modifying urchins' (*Strongylocentrotus droebachiensis*) destructive grazing and seasonal foraging patterns. *Marine Biology* **63**: 39–49.

Bernstein, B.B., Schroeter, S.C. & Mann, K.H. (1983) Sea urchin (*Strongylocentrotus droebachiensis*) aggregating behaviour investigated by a subtidal multifactoral experiment. *Canadian Journal of Fisheries and Aquatic Sciences* **40**: 1975–86.

Beverton, R.J.H. (1985) Analysis of marine-mammal-fisheries interactions. In: *Marine Mammals and Fisheries*, ed. J.R. Beddington, R.J.H. Beverton & D.M. Lavigne, pp. 3–33. London: George Allen & Unwin.

Bohnsack, J.A. (1990) The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic: Miami. NOAA (National Oceanic and Atmospheric Administration) Technical Memorandum NMFS-SEFC-261: 40 pp.

Bosman, A.L., Du Toit, J.T., Hockey, P.A.R. & Branch, G.M. (1986) A field experiment demonstrating the influence of seabird guano on intertidal primary production. *Estuarine, Coastal and Shelf Science* **23**: 283–94.

Botsford, L.W., Castilla, J.C. & Peterson, C.H. (1997) The management of fisheries and marine ecosystems. *Science* **277**: 509–15.

Boudouresque, C.F., Caltagirone, A., Lefevre, J.R., Rico, V. & Semroud, R. (1992) Macrozoobenthos de la réserve naturelle de Scandola (Corse, Méditerranée nord-occidentale). Analyse pluriannuelle de l'effet réserve. *MEDPAN News* **3**: 15–20.

Branch, G.M. (1981) The biology of limpets: physical factors, energy flow and ecological interactions. *Oceanography and Marine Biology Annual Review* **19**: 235–380.

Breen, P.A. & Mann, K.H. (1976) Changing lobster abundance and the destruction of kelp beds by sea urchins. *Marine Biology* **34**: 137–42.

Caddy, J.F. (1983) The cephalopods: factors relevant to their population dynamics and to the management of stocks. *FAO Fisheries Technical Paper* **231**: 416–52.

Campillo, A. & Bigot, J.L. (1992) Les pêcheries françaises de Méditerranée. Synthèse des connaissances. IFREMER-CEE (Institut Français de Recherche pour l'Exploration de la Mer), 92/1211625/TF: 206 pp.

Carpenter, R.C. (1990) Mass mortality of *Diadema antillarum* I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. *Marine Biology* **104**: 67–77.

Carpenter, S.R. & Kitchell, J.F. (1988) Consumer control of lake productivity. *BioScience* **38**: 764–9.

Carpenter, S.R., Kitchell, J.F. & Hodgson, J.R. (1985) Cascading trophic interactions and lake productivity. *BioScience* **35**: 634–9.

Castilla, J.C. (1999) Coastal marine communities: trends and perspectives from human-exclusion experiments. *Trends in Ecology and Evolution* **14**: 280–3.

Castilla, J.C. & Duran, L.R. (1985) Human exclusion from the rocky intertidal zone of central Chile: the effects on *Concholepas concholepas* (Gastropoda). *Oikos* **45**: 391–9.

Chemello, R., Milazzo, M., Nasta, E. & Riggio, S. (1999) Studio della malacofauna associata ad alghe fotofile nella riserva marina Isola di Ustica. *Biologia Marina Mediterranea* **6**: 247–9.

Choat, J.H. & Schiel, D.R. (1982) Patterns of distribution and abundance of large brown algae and invertebrate herbivores in subtidal regions of nothern New Zealand. *Journal of Experimental Marine Biology and Ecology* **60**: 129–62.

Christensen, V. (1998) Fishery-induced changes in a marine ecosystem: insight from models of the Gulf of Thailand. *Journal of Fish Biology* **53** (Suppl. A): 128–42.

Cole, R.G. & Keuskamp, D. (1998) Indirect effects of protection from exploitation: patterns from populations of *Evechinus chloroticus* (Echinoidea) in northeastern New Zealand. *Marine Ecology Progress Series* **173**: 215–26.

Cooke, J.G. (1985) Has the age at sexual maturity of southern hemisphere minke whales declined? *Report of the International Whaling Commission* **32**: 633–42.

Cowen, R.K. (1983) The effect of sheephead (*Semicossyphus pulcher*) predation on Red Sea urchin (*Strongylocentrotus franciscanus*) populations: an experimental analysis. *Oecologia* **58**: 249–55.

Cowen, R.K., Agegian, C.R. & Foster, M.S. (1982) The maintenance of community structure in a central California giant kelp forest. *Journal of Experimental Marine Biology and Ecology* **64**: 189–201.

Croxall, J.P. (1992) Southern ocean environmental changes, effects on seabird, seal and whale populations. *Philosophical Transactions of the Royal Society of London B* **338**: 319–28.

Dayton, P.K. (1975) Experimental evaluations of ecological dominance in a rocky intertidal community. *Ecological Monographs* **45**: 137–59.

Dayton, P.K. (1985) The structure and regulation of some South American kelp communities. *Ecological Monographs* **55**: 447–68.

Dayton, P.K., Tegner, M.J., Edwards, P.B. & Riser, K.L. (1998) Sliding baselines, ghosts and reduced expectations in kelp forest communities. *Ecological Applications* **8**: 309–22.

Done, T.J. (1992) Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia* **247**: 121–32.

Done, T.J., Dayton, P.K., Dayton, A.E. & Steger, R. (1991) Regional and local variability in recovery of shallow coral communities: Moorea, French Polynesia and central Great Barrier Reef. *Coral Reefs* **9**: 183–92.

Duggins, D.O. (1983) Starfish predation and the creation of mosaic patterns in a kelp-dominated community. *Ecology* **64**: 1610–19.

Edgar, G.J. & Barrett, N.S. (1997) Short term monitoring of biotic change in Tasmanian marine reserves. *Journal of Experimental Marine Biology and Ecology* **213**: 261–79.

Edgar, G.J. & Barrett, N.S. (1999) Effects of the declaration of marine reserves on Tasmanian reef fishes, invertebrates and plants. *Journal of Experimental Marine Biology and Ecology* **242**: 107–44.

Elner, R.W. & Vadas, S.R.L. (1990) Inference in ecology: the sea urchin phenomenon in the northwestern Atlantic. *The American Naturalist* **136**: 108–25.

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

Estes, J.A. & Palmisano, J.F. (1974) Sea otters: their role in structuring nearshore communities. *Science* **185**: 1058–60.

Estes, J.A., Smith, N.S. & Palmisano, J.F. (1978) Sea otter predation and community organization in the western Aleutian Islands, Alaska. *Ecology* **59**: 822–33.

Estes, J.A., Tinker, M.T., Williams, T.M. & Doak, D.F. (1998) Killer whale predation on sea otters linking oceanic and nearshore ecosystems. *Science* **282**: 473–6.

Fairweather, P.G. & Underwood, A.J. (1991) Experimental removals of a rocky intertidal predator: variations within two habitats in the effects of prey. *Journal of Experimental Marine Biology and Ecology* **154**: 29–75.

Fairweather, P.G., Underwood, A.J. & Moran, M.J. (1984) Preliminary investigations of predation by the whelk *Morula marginalba*. *Marine Ecology Progress Series* **17**: 143–56.

FAO (1997) *Review of the State of the World Fishery Resources: Marine Fisheries*. FAO Fisheries Circular 920: 173 pp.

Farrugio, H., Oliver, P. & Biagi, F. (1993) An overview of the history, knowledge, recent and future research trends in Mediterranean fisheries. *Scientia Marina* **57**: 105–19.

Fogarty, M.J., Sissenwine, M.P. & Cohen, E.B. (1991) Recruitment variability and the dynamics of exploited marine populations. *Trends in Ecology and Evolution* **6**: 241–6.

Foster, M.S. (1990) Organization of macroalgal assemblages in the northeast Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia* **192**: 21–33.

Francour, P. (1994) Pluriannual analysis of the reserve effect on ichthyofauna in the Scandola natural reserve (Corsica, Northwestern Mediterranean). *Oceanologica Acta* **17**: 309–17.

Garcìa, S. (1986) Seasonal trawling bans can be very successful in heavily overfished areas: the "Cyprus effect". *Fishbyte* **4**: 7–12.

Godoy, C. & Moreno, C.A. (1989) Indirect effects of human exclusion from the rocky intertidal in southern Chile: a case of cross-linkage between herbivores. *Oikos* **54**: 101–106.

Gulland, J.A. & Garcìa, S. (1984) Observed patterns in multispecies fisheries. In: *Exploitation of Marine Communities*, ed. R.M. May, pp. 155–90. Berlin: Springer-Verlag.

Hagen, N.T. & Mann, K.H. (1992) Functional response of the predators American lobster *Homarus americanus* and Atlantic wolffish *Anarhichas lupus* to increasing numbers of the green urchin *Strongylocentrotus droebachiensis*. *Journal of Experimental Marine Biology and Ecology* **159**: 89–112.

Hairston, N.G., Smith, F.E. & Slodbodkin, L.B. (1960) Community structure, population control and competition. *American Naturalist* **94**: 421–5.

Hall, S.J. (1999) *The Effects of Fishing on Marine Ecosystems and Communities*. Oxford: Blackwell Science: 274 pp.

Harmelin, J.G., Bachet, F. & Garcia, F. (1995) Mediterranean marine reserves: fish indices as tests of protection efficiency. *PSZNI Marine Ecology* **16**: 233–50.

Hart, M.W. & Scheibling, R.E. (1988) Heat waves, baby booms, and the destruction of kelp beds by sea urchins. *Marine Biology* **99**: 167–76.

Hay, M.E. (1984) Patterns of fish and urchin grazing on Caribbean coral reefs: are previous results typical? *Ecology* **65**: 446–54.

Hockey, P.A.R. & Branch, G.M. (1984) Oystercatchers and limpets: impact and implications. A preliminary assessment. *Ardea* **72**: 199–206.

Holme, N.A. (1984) Fluctuations of *Ophiothrix fragilis* in the western English Channel. *Journal of the Marine Biological Association of the United Kingdom* **64**: 351–78.

Hughes, T.P. (1989) Community structure and diversity of coral reefs: the role of history. *Ecology* **70**: 275–9.

Hughes, T.P. (1994) Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science* **265**: 1547–51.

Hughes, T.P., Reed, D.C. & Boyle, M.J. (1987) Herbivory on coral reefs: community structure following mass mortalities of sea urchins. *Journal of Experimental Marine Biology and Ecology* **113**: 39–59.

Hunter, M.D. & Price, P.W. (1992) Playing chutes and ladders: heterogeneity and the relative roles of bottom up and top-down forces in natural communities. *Ecology* **73**: 724–32.

Hurlbert, S.H., Zedler, J. & Fairbanks, D. (1992) Ecosystem alteration by mosquitofish (*Gambusia affinis*) predation. *Science* **175**: 639–41.

Huxham, M. & Raffaelli, D. (1995) Parasites and food-web patterns. *Journal of Animal Ecology* **64**: 168–76.

Jennings, S. & Kaiser, M.J. (1998) The effects of fishing on marine ecosystems. *Advances in Marine Biology* **34**: 201–352.

Jennings, S. & Lock, J.M. (1996) Population and ecosystem effects of fishing. In: *Reef Fisheries*, ed. N.V.C. Polunin & C.M. Roberts, pp. 193–218. London: Chapman and Hall.

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* **14**: 71–82.

Jennings, S., Grandcourt, E.M. & Polunin, N.V.C. (1995) The effects of fishing on the diversity, biomass and trophic structure of Seychelles' reef fish communities. *Coral Reefs* **14**: 225–35.

Jernakoff, P. (1983) Factors affecting the recruitment of algae in a midshore region dominated by barnacles. *Journal of Experimental Marine Biology and Ecology* **67**: 17–31.

Jones, G.P., Cole, R.C. & Battershill, C.N. (1993) Marine reserves: do they work? In: *Proceedings of the Second International Temperate*

Reef Symposium, 7–10 January 1992, Auckland, New Zealand, ed. C.N. Battershill, D.R. Schiel, G.P. Jones, R.G. Crease & A. MacDiarmid, pp. 29–45. Wellington, New Zealand: National Institute of Water and Atmospheric Research (NIWA) Marine Publications.

Kaiser, M.J. & Spencer, B.E. (1996*a*) The behavioural response of scavengers to beam-trawl disturbance. In: *Aquatic Predators and their Prey*, ed. S.P.R. Greenstreet & M.L. Tasker, pp. 117–23. Oxford: Blackwell Scientific Publications.

Kaiser, M.J. & Spencer, B.E. (1996*b*) The effects of beam-trawl disturbance on infaunal communities in different habitats. *Journal of Animal Ecology* **65**: 348–58.

Keesing, J.K. & Halford, A.R. (1992) Field measurements of survival rates of juvenile *Acanthaster planci* – techniques and preliminary results. *Marine Ecology Progress Series* **85**: 107–14.

Kempf, M. (1962) Recherches d'écologie comparée sur *Paracentrotus lividus* (Lmk.) et *Arbacia lixula* (L.). *Receuil des Travaux Station Marine d' Endoume* **25**: 47–116.

Keough, M.J., Quin, G.P. & King. A. (1993) Correlations between human collecting and intertidal mollusc populations on rocky shores. *Conservation Biology* **7**: 378–90.

Kitchell, J.F. & Carpenter, S.R. (1993) Synthesis and new directions. In: *The Trophic Cascade in Lakes*, ed. S.R. Carpenter & J.F. Kitchell, pp. 332–50. Cambridge: Cambridge University Press.

Kitching, J.A. & Ebling, F.J. (1961) The ecology of Lough Ine. XI. The control of algae by *Paracentrotus lividus* (Echinoidea). *Journal of Animal Ecology* **30**: 373–82.

Kock, K.H. (1994) Fishing and conservation in southern waters. *Polar Record* **30**: 3–22.

Kohler, S.L. & Wiley, M.J. (1997) Pathogen outbreaks reveal large-scale effects of competition in stream communities. *Ecology* **78**: 2164–76.

LaMesa, G. & Vacchi, M. (1999) An analysis of the coastal fish assemblage of the Ustica Island marine reserve (Mediterranean Sea) *PZNI Marine Ecology* **20**: 147–65.

Lapointe, B.E., Littler, M.M. & Littler, D.S. (1997) Macroalgal overgrowth of fringing coral reefs at Discovery Bay, Jamaica: bottom-up versus top-down control. *Proceedings of the 8th International Coral Reef Symposium* **1**: 927–32.

Lawrence, J.M. (1975) On the relationships between marine plants and sea urchins. *Oceanography and Marine Biology: an Annual Review* **13**: 213–86.

Lessios, H.A., Robertson, D.R. & Cubit, J.D. (1984) Spread of *Diadema* mass mortality through the Caribbean. *Science* **226**: 335–7.

Lindberg, D.R., Estes, J.A. & Warheit, K.I. (1998) Human influences on trophic cascades along rocky shores. *Ecological Applications* **8**: 880–90.

Lowry, L.F. & Pearse, J.S. (1973) Abalones and sea urchins in an area inhabited by sea otters. *Marine Biology* **23**: 213–19.

Macpherson, E. (1994) Substrate utilisation in a Mediterranean littoral fish community. *Marine Ecology Progress Series* **114**: 211–18.

Mann, K.H. (1982) Kelp, sea urchins and predators: a review of strong interactions in rocky subtidal systems of eastern Canada 1970–1980. *Netherlands Journal of Sea Research* **16**: 414–23.

Mann, K.H. & Breen, P.A. (1972) The relation between lobster abundance, sea urchins, and kelp beds. *Journal of the Fisheries Research Board of Canada* **29**: 603–605.

Martinez, N.D. & Dunne, J.A. (1998) Time, space, and beyond: scale issues in food-web research. In: *Ecological Scale. Theory and Applications*, ed. D.L. Peterson & V.T. Parker, pp. 207–26. New York, NY: Columbia University Press.

McClanahan, T.R. (1989) Kenyan coral reef-associated gastropod fauna: a comparison between protected and unprotected reefs. *Marine Ecology Progress Series* **53**: 11–20.

McClanahan, T.R. (1990) Kenyan coral reef-associated gastropod assemblages: distribution and diversity patterns. *Coral Reefs* **9**: 63–74.

McClanahan, T.R. (1992) Resource utilization, competition and predation: a model and example from coral reef grazers. *Ecological Modelling* **61**: 195–215.

McClanahan, T.R. (1994*a*) Coral-eating snail *Drupella cornus* population increases in Kenyan coral reef lagoons. *Marine Ecology Progress Series* **155**: 131–7.

McClanahan, T.R. (1994*b*) Kenyan coral reef lagoon fish: effects of fishing, substrate complexity, and sea urchins. *Coral Reefs* **13**: 231–41.

McClanahan, T.R. (1995) Fish predators and scavengers of the sea urchin *Echinometra mathaei* in Kenyan coral-reef marine parks. *Environmental Biology of Fishes* **43**: 187–93.

McClanahan, T.R. (1997*a*). Dynamics of *Drupella cornus* populations on Kenyan coral reefs. *Proceedings of the 8th Coral Reef Symposium, Panama* **1**: 633–8.

McClanahan, T.R. (1997*b*) Primary succession of coral-reef algae: differing patterns on fished versus unfished reefs. *Journal of Experimental Marine Biology and Ecology* **218**: 77–102.

McClanahan, T.R. & Muthiga, N.A. (1988) Changes in Kenyan coral reef community structure and function due to exploitation. *Hydrobiologia* **166**: 269–76.

McClanahan, T.R. & Muthiga, N.A. (1989) Patterns of predation on a sea urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs. *Journal of Experimental Marine Biology and Ecology* **126**: 77–94.

McClanahan, T.R. & Muthiga, N.A. (1998) An ecological shift in a remote coral atoll of Belize over 25 years. *Environmental Conservation* **25**: 122–30.

McClanahan, T.R. & Sala, E. (1997) A Mediterranean rocky-bottom ecosystem fisheries model. *Ecological Modelling* **104**: 145–64.

McClanahan, T.R. & Shafir, S.H. (1990) Causes and consequences of sea urchin abundance and diversity in Kenyan coral reef lagoons. *Oecologia* **83**: 362–70.

McClanahan, T.R., Nugues, M. & Mwachireya, S. (1994) Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: the role of reef management. *Journal of Experimental Marine Biology and Ecology* **184**: 237–54.

McClanahan, T.R., Done, T.J. & Polunin, N.V.C. (in press) Resiliency of coral reefs. In: *Resilience and Behaviour of Large-Scale Ecosystems*, ed. L. Gunderson, B.O. Jansson, C. Folke & C.S. Holling. Scientific Committee on Problems of the Environment (SCOPE).

Menge, B.A. (1995) Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs* **65**: 21–74.

Menge, B.A. & Sutherland, J.P. (1987) Community regulation: variation in disturbance, competition, and predation in relation to environmental stress and recruitment. *The American Naturalist* **130**: 730–57.

Milazzo, M., Chemello, R., Badalamenti, F. & Riggio, S. (in press) Molluscan assemblages associated with photophilic algae in the marine reserve of Ustica Island (southern Tyrrhenian Sea, Italy). *Italian Journal of Zoology*.

Miller, R.J. (1985) Seaweeds, sea urchins and lobsters: a reappraisal. *Canadian Journal of Fisheries and Aquatic Sciences* **42**: 2061–72.

Moran, P.J. (1986) The *Acanthaster* phenomenon. *Oceanography and Marine Biology Annual Review* **24**: 379–480.

Moreno, C.A. & Jaramillo, E. (1983) The role of grazers in the zonation of intertidal macroalgae of the Chilean coast. *Oikos* **41**: 73–6.

Moreno, C.A., Sutherland, J.P. & Jara, H.F. (1984) Man as a predator in the intertidal zone of southern Chile. *Oikos* **42**: 155–60.

Moreno, C.A., Lunecke, K.M. & Lepez, M.I. (1986) The response of an intertidal *Concholepas concholepas* (Gastropoda) population to protection from man in southern Chile and the effects on benthic sessile assemblages. *Oikos* **46**: 359–64.

Morrison, D. (1988) Comparing fish and urchin grazing in shallow and deeper coral reef algal communities. *Ecology* **69**: 1367–82.

Munro, J.L., Parrish, J.D. & Talbot, F.H. (1987) The biological effects of intensive fishing upon reef fish communities. In: *Human Impacts on Coral Reefs: Facts and Recommendations*, ed. B. Salvat, pp. 41–9. French Polynesia: Antenne Museum E.P.H.E.

Nédélec, H. (1982) Ethologie alimentaire de *Paracentrotus lividus* dans la baie Galeria (Corse) et son impact sur les peuplements phytobenthiques. Doctoral thesis, Université Pierre et Marie Curie and Université Aix-Marseille II, Marseille: 162 pp.

North, W.J. & Pearse, J.S. (1969) Sea urchin population explosion in southern California coastal waters. *Science* **167**: 209.

Ormond, R.F.G., Bradbury, R., Bainbridge, S., Fabricus, K., Keesing, J., De Vantier, L., Medley, P. & Steven, A. (1990) Test of a model regulation of Crown-of-Thorns starfish by fish predators. In: *Acanthaster and the Coral Reef: a Theoretical Perspective*, ed. R. Bradbury, pp. 189–207. Berlin: Springer-Verlag.

Pace, M.L., Cole, J.J., Carpenter, S.R. & Kitchell, J.F. (1999) Trophic cascades revealed in diverse ecosystems. *Trends in Ecology and Evolution* **14**: 483–8

Paine, R.T. (1966) Food web complexity and species diversity. *American Naturalist* **100**: 65–75.

Paine, R.T. (1974) Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia* **15**: 93–120.

Paine, R.T. (1980) Food webs: linkage, interaction strength and community infrastructure. *Journal of Animal Ecology* **49**: 667–85.

Paine, R.T. (1984) Ecological determinism in the competition for space. *Ecology* **65**: 1339–48.

Paine, R.T. (1992) Food-web analysis through field measurement of per capita interaction strength. *Nature* **355**: 73–5.

Paine, R.T. & Vadas, R.L. (1969) The effects of grazing by sea urchins, *Strongylocentrotus* spp., on benthic algal populations. *Limnology & Oceanography* **14**: 710–19.

Pauly, D (1982) A method to estimate the stock-recruitment relationship of shrimps. *Transaction of the American Fisheries Society* **111**: 13–20.

Pauly, D. (1985) The population dynamics of short-lived species, with emphasis on squids. *NAFO Scientific Council Studies* **9**: 143–54.

Pauly, D. (1988) Fisheries research and the demersal fisheries of Southeast Asia. In: *Fish Population Dynamics*, 2nd edn, ed. J.A. Gulland, pp. 329–48. Chichester: John Wiley & Sons.

Pauly, D. & Christensen, V. (1995) Primary production required to sustain global fisheries. *Nature* **374**: 255–7.

Payne, M.R. (1977) Growth of a fur seal population. *Philosophical Transactions of the Royal Society* **B279**: 67–79.

Pearse, J.S. & Hines, H.A. (1987) Long-term population dynamics of sea urchins in a central California kelp forest: rare recruitment and rapid decline. *Marine Ecology Progress Series* **39**: 275–83.

Pipitone, C., Badalamenti, F., D'Anna, G. & Patti, B. (in press) Fish biomass increase after a four-year trawl ban in the Gulf of Castellammare (NW Sicily, Mediterranean Sea). *Fisheries Research*.

Polis, G.A. & Strong, D.R. (1996) Food web complexity and community dynamics. *The American Naturalist* **147**: 813–46.

Polunin, N.V.C. & Jennings, S. (1998) Differential effects of small-scale fishing on predatory and prey fishes on Fijian reefs. In: *Dynamics of Tropical Communities*, ed. D.M. Newbery, H.H.T. Prins & N.D. Brown, pp. 95–124. Oxford: Blackwell Science.

Polunin, N.V.C. & Roberts, C.M. (1993) Greater biomass and value of target coral-reef fishes in two small Caribbean marine reserves. *Marine Ecology Progress Series* **100**: 167–76.

Power, M.E. (1990) Effects of fish in river food webs. *Science* **250**: 811–14.

Power, M.E. (1992) Top down and bottom up forces in food webs: do plants have primacy? *Ecology* **73**: 733–46.

Prena, J., Schwinghamer, P., Rowell, T., Gordon, Jr, D.C., Gilkinson, K.D., Vass, W.P. & McKeown, D.L. (1999) Experimental otter trawling on a sandy bottom ecosystem of the Grand Banks of Newfoundland: analysis of trawl bycatch and effects on epifauna. *Marine Ecology Progress Series* **181**: 107–24.

Riggio, S. (1988) Valutazione delle risorse demersali nell'area compresa tra Capo Gallo e Capo S. Vito (U.O. 11). Relazione triennale conclusiva. Unpublished report, Università di Palermo: 26 pp.

Riggio, S. (1989) Valutazione delle risorse demersali nell'area compresa tra Capo Gallo e Capo S. Vito (U.O. 11). Relazione "Anno di prosecuzione maggio '87 – aprile '88". Unpublished report, Università di Palermo: 15 pp.

Roberts, C.M. (1995) The effects of fishing on the ecosystem structure of coral reefs. *Conservation Biology* **9**: 988–95.

Roberts, C.M. (1997) Connectivity and management of Caribbean coral reefs. *Science* **278**: 1454–7.

Roberts, C.M. & Polunin, N.V.C. (1992) Effects of marine reserve protection on northern Red Sea fish populations. In: *Proceedings of the 7th International Coral Reef Symposium*, vol. 2, pp. 969–77. Mangilao, Guam, Micronesia: University of Guam Press.

Robertson, D.R. (1991) Increases in surgeonfish populations after mass mortality of the sea urchin *Diadema antillarum* in Panamá indicate food limitation. *Marine Biology* **111**: 437–44.

Robles, C. (1987) Predator foraging characteristics and prey populations structure on a sheltered shore. *Ecology* **68**: 1502–14.

Robles, C.D. (1997) Changing recruitment in constant species assemblages: implications for predation theory in intertidal communities. *Ecology* **78**: 1400–14.

Robles, C. & Robb, J. (1993) Varied carnivore effects and the prevalence of intertidal algal turfs. *Journal of Experimental Marine Biology and Ecology* **166**: 65–91.

Russ, G.R. & Alcala, A.C. (1998*a*) Natural fishing experiments in marine reserves 1983–1993: community and trophic responses. *Coral Reefs* **17**: 383–97.

Russ, G.R. & Alcala, A.C. (1998*b*) Natural fishing experiments in marine reserves 1983–1993: roles of life history and fishing intensity in family responses. *Coral Reefs* **17**: 399–416.

Saeger, J. (1981) Do trawling bans work in tropical waters? *ICLARM Newsletter* **4**: 3–4.

Sala, E. (1996) The role of fishes in the organization of a Mediterranean subtidal community. Doctoral thesis, Université d'Aix-Marseille II, France: 180 pp.

Sala, E. (1997*a*) The role of fishes in the organization of a Mediterranean sublittoral community II: epifaunal communities. *Journal of Experimental Marine Biology and Ecology* **212**: 45–60.

Sala, E. (1997*b*) Fish predators and scavengers of the sea urchin *Paracentrotus lividus* in protected areas of the north-west Mediterranean Sea. *Marine Biology* **129**: 531–9.

Sala, E. & Ballesteros, E. (1997) Partitioning of space and food resources by three fish of the genus *Diplodus* (Sparidae) in a Mediterranean rocky infralittoral ecosystem. *Marine Ecology Progress Series* **152**: 273–83.

Sala, E. & Boudouresque, C.F. (1997) The role of fishes in the organization of a Mediterranean sublittoral community. I. Algal communities. *Journal of Experimental Marine Biology and Ecology* **212**: 25–44.

Sala, E. & Zabala, M. (1996) Fish predation and the structure of the sea urchin *Paracentrotus lividus* populations in the NW Mediterranean. *Marine Ecology Progress Series* **140**: 71–81.

Sala, E., Boudouresque, C.F. & Harmelin-Vivien, M. (1998*a*) Fishing, trophic cascades, and the structure of algal assemblages: evaluation of an old but untested paradigm. *Oikos* **82**: 425–39.

Sala, E., Ribes, M., Hereu, B., Zabala, M., Alva, V., Coma, R. & Garrabou, J. (1998*b*) Temporal variability in abundance of the sea urchins *Paracentrotus lividus* and *Arbacia lixula* in the northwestern Mediterranean: comparison between a marine reserve and an unprotected area. *Marine Ecology Progress Series* **168**: 135–45.

Sale, P.F. (1991) Reef fish communities: open nonequilibrial systems. In: *The Ecology of Fishes on Coral Reefs*, ed. P.F. Sale, pp. 564–98. San Diego: Academic.

Scheibling, R.E. (1996) The role of predation in regulating sea urchin populations in eastern Canada. *Oceanologica Acta* **19**: 421–30.

Scheibling, R.E. & Hamm, J. (1991) Interactions between sea urchins (*Strongylocentrotus droebachiensis*) and their predators in field and laboratory experiments. *Marine Biology* **110**: 105–16.

Scheibling, R.E. & Stephenson, R.L. (1984) Mass mortality of *Strongylocentrotus droebachiensis* (Echinodermata: Echinoidea) off Nova Scotia, Canada. *Marine Biology* **78**: 153–64.

Schiel, D.R. & Foster, M.S. (1986) The structure of subtidal algal stands in temperate waters. *Oceanography and Marine Biology Annual Review* **24**: 265–307.

Shelton, P.A. (1992) Detecting and incorporating multispecies effects into fisheries management in the North-West and South-East Atlantic. *South African Journal of Marine Science* **12**: 723–37.

Sherman, K. (1994) Sustainability, biomass yields, and health of coastal ecosystems – an ecological perspective. *Marine Ecology Progress Series* **112**: 277–301.

Sladen, W.J.L. (1964) The distribution of the Adelie and Chinstrap penguins. In: *Biologie Antarctique*, ed. R. Carrick, M.W. Holgate & J. Prevost, pp. 359–65. Paris: Hermann.

Steneck, R.S. (1997) Fisheries-induced biological changes to the structure and function of the Gulf of Maine ecosystem. Plenary paper. In: *Proceedings of the Gulf of Maine Ecosystem Dynamics Scientific Symposium and Workshop*, ed. G.T. Wallace & E.F. Braasch, pp. 151–65. Hanover, NH: Regional Association for Research on the Gulf of Maine.

Steneck, R.S. (1998) Human influences on coastal ecosystems: does overfishing create trophic cascade? *Trends in Ecology and Evolution* **13**: 429–30.

Steneck, R.S., McNaught, D. & Zimsen, S. (1995) Spatial and temporal patterns in sea urchin populations, herbivory and algal community structure in the Gulf of Maine. In: *1994 Workshop on the Management and Biology of the Green Sea Urchin* (*Strongylocentrotus droebachiensis*), pp. 34–73. Massachusetts Department of Natural Resources.

Strauss, S.Y. (1991) Indirect effects in community ecology: their definition, study and importance. *Trends in Ecology and Evolution* **6**: 206–10.

Strong, D.R. (1992) Are trophic cascades all wet? Differentiation and donor-control in species ecosystems. *Ecology* **73**: 747–54.

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

Tegner, M.J. (1980) Multispecies considerations of resource management in southern California kelp beds. *Canadian Technical Report of Fisheries and Aquatic Sciences* **954**: 125–43.

Tegner, M.J. & Dayton, P.K. (1981) Population structure, recruitment and mortality of two sea urchins (*Strongylocentrotus franciscanus* and *S. purpuratus*) in a kelp forest. *Marine Ecology Progress Series* **5**: 255–68.

Tegner, M.J. & Levin, L.A. (1983) Spiny lobsters and sea urchins: analysis of a predator-prey interaction. *Journal of Experimental Marine Biology and Ecology* **73**: 125–50.

Turner, S.J. (1994) The biology and population outbreaks of the corallivorous gastropod *Drupella* on Indo-Pacific reefs. *Oceanography and Marine Biology Annual Review* **32**: 461–530.

Underwood, A.J. (1980) The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. *Oecologia* **46**: 201–13.

Underwood, A.J., Denley, E.J. & Moran, M.J. (1983) Experimental analysis of the structure and dynamics of midshore rocky intertidal communities in New South Wales. *Oecologia* **56**: 202–19.

Vacchi, M., Bussotti, S., Guidetti, P. & La Mesa, G. (1998) Study of the coastal fish assemblage in the marine reserve of the Ustica Island (southern Tyrrhenian Sea). *Italian Journal of Zoology* **65**: 281–6.

Vadas, R.L. & Steneck, R.S. (1988) Zonation of deep water benthic algae in the Gulf of Maine. *Journal of Phycology* **24**: 338–46.

Vadas, R.L. & Steneck, R.S. (1995) Overfishing and inferences in kelp-sea urchin interactions. In: *Ecology of Fjords and Coastal Waters*, ed. H.R. Hopkins, C. Erikstad & H.R. Leinaas, pp. 509–24. Amsterdam: Elsevier Science.

van der Elst, R.P. (1979) A proliferation of small sharks in the shore-based Natal sport fishery. *Environmental Biology of Fishes* **4**: 349–62.

Verity, P.G. & Smetacek, V. (1996) Organism life cycles, predation, and the structure of marine pelagic ecosystems. *Marine Ecology Progress Series* **130**: 277–93.

Verlaque, M. (1987) Relations entre *Paracentrotus lividus* (Lamark) et le phytobenthos de Méditerranée occidentale. In: *Colloque Internationale sur Paracentrotus Lividus et les Oursins Comestibles*, ed. C.F. Boudouresque, pp. 5–36. Marseille: GIS Posidonie Publications.

Virnstein, R.W. (1977) The importance of predation by crabs and fishes on benthic fauna in Chesapeake Bay. *Ecology* **58**: 1199–217.

Wharton, W.G. & Mann, K.H. (1981) Relationship between destructive grazing by the sea urchin, *Strongylocentrotus droebachiensis*, and the abundance of American lobster *Homarus* *americanus,* on the Atlantic coast of Nova Scotia. *Canadian Journal of Fisheries and Aquatic Sciences* **38**: 1339–49.

Williams, I.D. & Polunin, N.V.C. (in press) Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs*.

Witman, J.P. & Sebens, K.P. (1992) Regional variation in fish predation intensity: a historical perspective in the Gulf of Maine. *Oecologia* **90**: 305–15.

Wootton, J.T. (1992) Indirect effects, prey susceptibility, and habitat selection: impacts of birds on limpets and algae. *Ecology* **73**: 981–91.

Wootton, J.T. (1994) Predicting direct and indirect effects: an integrated approach using experiments and path analysis. *Ecology* **75**: 151–65.

Wootton, J.T. (1995) Effects of birds on sea urchins and algae: a lower-intertidal trophic cascade. *Ecoscience* **2**: 321–8.

Yamasaki, A. & Kuwahara, A. (1990) Preserved area to effect recovery of overfished Zuwai crab stocks off Kyoto prefecture. In: *Proceedings of the International Symposium on King & Tanner Crabs. Anchorage, Alaska*, pp. 575–85. Alaska Sea Grant College Program, University of Alaska, Fairbanks, Alaska.