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REVIEW AND SYNTHESIS

Patterns and ecosystem consequences of shark declines in the ocean

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Abstract

Whereas many land predators disappeared before their ecological roles were studied, the decline of marine apex predators is still unfolding. Large sharks in particular have experienced rapid declines over the last decades. In this study, we review the documented changes in exploited elasmobranch communities in coastal, demersal, and pelagic habitats, and synthesize the effects of sharks on their prey and wider communities. We show that the high natural diversity and abundance of sharks is vulnerable to even light fishing pressure. The decline of large predatory sharks reduces natural mortality in a range of prey, contributing to changes in abundance, distribution, and behaviour of small elasmobranchs, marine mammals, and sea turtles that have few other predators. Through direct predation and behavioural modifications, top-down effects of sharks have led to cascading changes in some coastal ecosystems. In demersal and pelagic communities, there is increasing evidence of mesopredator release, but cascading effects are more hypothetical. Here, fishing pressure on mesopredators may mask or even reverse some ecosystem effects. In conclusion, large sharks can exert strong top-down forces with the potential to shape marine communities over large spatial and temporal scales. Yet more empirical evidence is needed to test the generality of these effects throughout the ocean.

Keywords

Connectivity, ecological role, ecosystem, effects of fishing, evolution, mesopredator release, predation, risk effects, top-down effects, trophic cascades, sharks.

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INTRODUCTION

Ecologists have long been intrigued by the often strong effects of predation on community structure (Paine 1966; Schmitz *et al.* 2004; Knight *et al.* 2005; Ritchie & Johnson 2009). Predator effects, however, do vary considerably among different species and ecosystems. For example, a meta-analysis of 102 field experiments indicated strong cascading effects, on average, in lakes and marine benthos and weaker effects in marine plankton and terrestrial food webs (Shurin *et al.* 2002). Classic work on the effects of predation often concerns relatively small-bodied, slow-moving predators such as starfish (Paine 1969) or spiders (Schmitz *et al.* 2004), that are easily manipulated and controlled. Recent studies on large-bodied and highly mobile terrestrial predators (e.g. wolves, *Canis lupus*; Ripple & Beschta 2007) suggest that they exert similar or even more powerful effects; yet large marine predators have been much less studied, mainly for logistical reasons (Heithaus *et al.* 2008a; Baum & Worm 2009).

Here, we attempt to synthesize what is known about the ecological role of sharks, which are among the largest and most wide-ranging predators in the ocean. This topic has received urgent attention over the past decade, as studies have indicated rapid and widespread declines, particularly of large sharks, because of the direct and indirect effects of fishing (Baum *et al.* 2003; Dulvy *et al.* 2008; Ferretti *et al.* 2008). This has prompted questions about the nature and scale of the ecological consequences. In this context, marine biologists have debated the patterns of decline for different species, the apparent community changes, and whether sharks do play a unique and fundamental role (Stevens *et al.* 2000; Kitchell *et al.* 2002; Baum *et al.* 2005; Burgess *et al.* 2005; Myers *et al.* 2007; Heithaus *et al.* 2008a). While sharks have distinct ecological features that could lead to strong structuring roles in marine environments, such effects are not necessarily ubiquitous because other marine predators may potentially take sharks' place when functionally removed by fishing (e.g. Kitchell *et al.* 2002). Also there is considerable diversity in body sizes and trophic interactions among sharks and other elasmobranchs, hence some variation in ecological roles might be expected.

In this study, we begin by briefly reviewing the ecological features of sharks, highlighting differences from other marine predators. We then analyse the current state and history of shark exploitation, searching for general patterns of community change in coastal, demersal, and pelagic ecosystems. Finally, we synthesize the expected and observed effects of sharks on marine ecosystems from experimental, empirical, and modeling studies. In the conclusion, we attempt to explain under which conditions sharks are expected to play a unique role, and how that role may depend on the ecosystem context. This study is largely based on all major peer-reviewed papers published on this topic over the past decade, but also includes important earlier work.

ECOLOGICAL FEATURES

Primordial predators

Sharks comprise about half of all contemporary chondrichthyans (492 sharks, 621 batoids, 46 chimeras, http://www.catalogueoflife.org), a monophyletic group of predatory fishes that originated about 423 million years ago (Fig. 1), before any other extant vertebrate predators.

Evolving initially as small coastal consumers, over evolutionary time, selection favoured larger body sizes, continuous growth, delayed age at maturity, and the ability to colonize deeper oceanic waters (Grogan & Lund 2004). The group acquired ecological niches previously occupied by now extinct predatory vertebrates (Walker & Brett 2002), and have influenced the diversification and distribution of prey and competitor species (Lindberg & Pyenson 2006). One spectacular example is the extinct *Carcharodon megalodon*, the largest predatory fish ever recorded, which may have caused substantial changes in the evolutionary history of marine mammals, its preferred prey (Lindberg & Pyenson 2006). Compared with other marine vertebrates, the

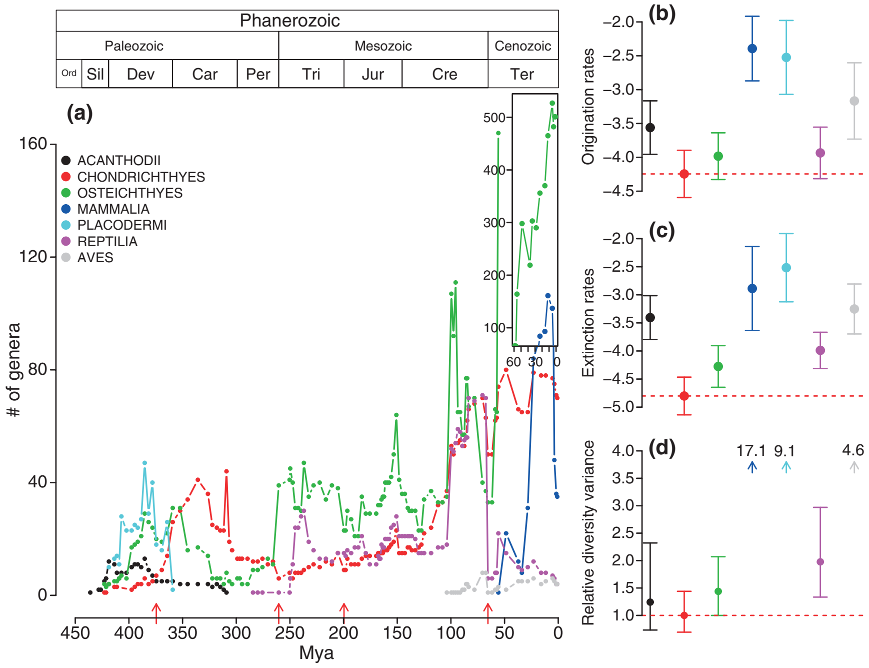

Figure 1 Diversification of chondrichthyans and other marine vertebrates. (a) Time trend in genus diversity from the fossil record; geological eras and periods are indicated at the top; red arrows indicate major mass extinction events. (b) Origination and (c) extinction rates are expressed as $y = \log(x/z)$, where x is the number of genus extinctions or originations in each geological era, and y is the contemporary genus richness. Bars represent 95% confidence intervals. The relative diversity variance (d) for each taxon was obtained by detrending each time series in panel (a) with a moving average of the order 1, and calculating the variance of the residuals. We tested the null-hypothesis that the ratio between the variance in genus richness of chondrichthyans and other taxa was equal to 1. Symbols represent the ratio between the variance of a given taxon and that of chondrichthyans. Confidence intervals were off-scale for mammals (8.11–50.28), placoderms (4.74–21.71) and marine birds (2.73–8.78). Data from Sepkoski (2002) compiled in http://geology.isu.edu/FossilPlot/.

trajectory of chondrichthyan evolution appears steadier, with lower origination and extinction rates (Fig. 1). This resilience has been related to a high evolutionary adaptability and ecological generalism (Grogan & Lund 2004; Kriwet *et al.* 2009).

Contemporary sharks inhabit coastal, demersal, and pelagic habitats in all oceans (Compagno 1990). While most species are limited to the continental shelves, there is a small number of fully oceanic species (e.g. blue, oceanic whitetip, mako), and a larger count that migrates between coastal and oceanic waters (e.g. hammerhead, silky, tiger, white). Sharks are carnivores with body sizes from 0.2 to > 20 m (fishbase.org) and feeding types ranging from filter-feeding (basking, whale shark) to suction crushing (carpet sharks) and effective raptorial mechanisms (white, tiger sharks) (Compagno *et al.* 1990). While most larger species (> 3 m total length) function as top predators, there is a high diversity of mesopredatory elasmobranchs (typically < 1.5 m total length) that are prey to larger sharks. Many sharks are generalists, feeding on a wide variety of prey items. This explains the high connectivity of sharks seen in food-web models (Bascompte *et al.* 2005), and the likely limited effects on any particular prey species (Ellis & Musick 2007).

Sharks feeding is not gape-limited as in bony fish; the hyostylic suspension of their jaw, a consequent powerful bite, and efficient cutting dentition allow sharks to cut large prey into chunks (Wilga *et al.* 2007) and thus to attack larger prey than bony fishes of the same size. For this reason, large megafauna, including marine reptiles, mammals, and elasmobranchs often have large sharks as their major or exclusive predators. These species often show strong behavioural responses to the risk of shark predation that could result in lower population sizes through non-consumptive mechanisms (Heithaus *et al.* 2008a). Finally, through their high mobility large sharks may connect widely spaced food webs (Musick *et al.* 2004).

Vulnerability to fishing

Most chondrichthyans are characterized by low growth rates, late sexual maturity, and low fecundity compared to bony fish (Frisk *et al.* 2001; Myers & Worm 2005), which makes them vulnerable to fishing mortality. A comparison of 26 shark and 151 bony fish populations found that sharks show twice the fishing extinction risk of bony fishes (Myers & Worm 2005). Also their ability to recover after depletion is low on average: rebound potential of 26 shark populations ranged between 14% (*Mustelus californicus*) and 1.7% (*Squalus acanthias*) per year (Smith *et al.* 1998) with variability explained by a combined effect of size and preferred habitat. In fact, it was highest for small coastal sharks, intermediate for pelagic and minimal for large coastal species (Smith *et al.* 1998). Deep-water sharks may be among the most vulnerable to fishing, with population growth rates 40–60% lower compared with pelagic, and 55–63% lower compared with coastal species (García *et al.* 2008).

As a life history trade-off, most elasmobranchs invest more into juvenile survival and growth (Frisk *et al.* 2001) rather than fecundity (Cortés 2002). Elasticity analyses show that changes in juvenile and adult survival and age at maturity have the highest contributions to population growth rate (Cortés 2002; Frisk *et al.* 2005). This explains why elasmobranch populations generally respond strongly to changes in both predation and fishing. While exploitation often leads to decreased ages at maturity and increased fecundities in teleosts (Jorgensen *et al.* 2007), there is little evidence for such compensating responses in elasmobranchs (Frisk *et al.* 2005).

Finally, while life history determines the level of mortality sharks can sustain, their vulnerability depends on the combination of life history, sensitivity to habitat loss (Heupel *et al.* 2007) and exposure to perturbations such as catchability and availability to fisheries. The latter relates to many factors including geographic range (Dulvy & Reynolds 2002; Shepherd & Myers 2005), habitat use (García et al. 2008), behaviour (Ward & Myers 2005; Gilman *et al.* 2008), and body size (Dulvy *et al.* 2003; Field *et al.* 2009).

PATTERNS OF CHANGE

Global fisheries and conservation status

Historically, many sharks had low commercial value, and were not regularly recorded in fisheries statistics. Thus, detailed catch or survey data are often lacking (Dulvy & Reynolds 2002; Clarke *et al.* 2006), and population changes for many species have not been well documented until recently (Stevens *et al.* 2000; Graham *et al.* 2001; Myers & Worm 2005; Dulvy *et al.* 2008; Ferretti *et al.* 2008). On a global scale, elasmobranch landings reported to the United Nations Food and Agriculture Organization (FAO) are often aggregated. Only 15% are reported at the species level, the rest as larger taxonomic groups (e.g. dogfishes, skates) or more often 'sharks and rays' (Clarke *et al.* 2006; Dulvy *et al.* 2008). Reliability and resolution of these data vary among nations (Watson & Pauly 2001), and underreporting is probably severe for many shark species (Clarke *et al.* 2006). Nonetheless, some interesting patterns emerge.

In general, industrial fisheries commenced in the NW Pacific, NE Atlantic and Mediterranean before the 1950s. These three areas, in decreasing order, recorded the highest initial catches per unit shelf area (Fig. 2). Over time, these fisheries expanded to other regions (Myers & Worm 2003; Pauly *et al.* 2005), and elasmobranch catches increased in many areas (Fig. 2). However, individual shark fisheries

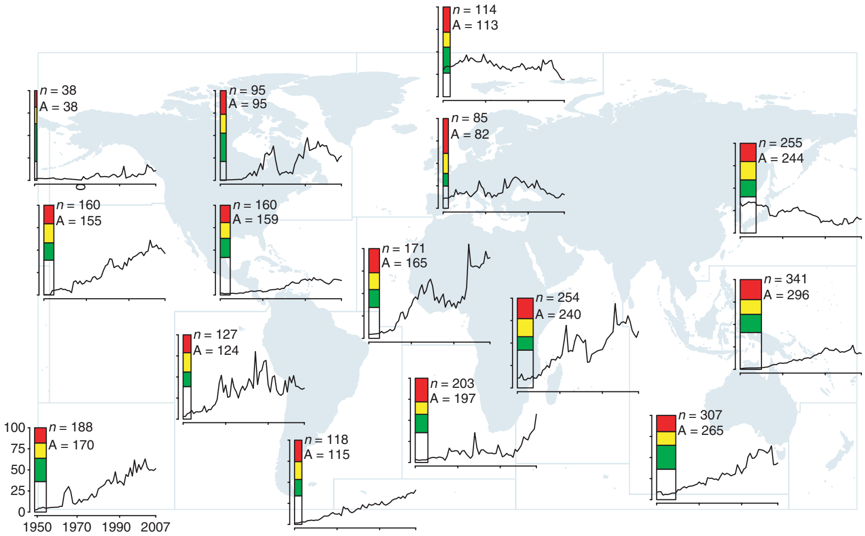

Figure 2 Global fisheries trends and conservation status of chondrichthyans. Time series refer to landings of sharks, rays and chimeras in thousands of metric tonnes km^{-2} of shelf area since 1950, as reported to the United Nations Food and Agriculture Organization (FAO). Stacked bars represent the global conservation status of all chondrichthyans assessed by the International Union for the Conservation of Nature (IUCN) Shark Specialist Group (Appendix S1, Camhi *et al.* 2009, http://www.redlist.org). Red indicates the percentage of species that occur in a particular FAO area and that are globally assessed as critically endangered (CR), endangered (EN), and vulnerable (VU); yellow indicates near threatened (NT) status and green the percentage of species assessed as least concern (LC). Transparent bars refer to species that are assessed data deficient (DD) or that have not been assessed yet. FAO assessment areas are outlined in light blue on the background map. A list of chondrichthyans occurring in each FAO area was derived from FishBase (http://www.fishbase.org). N, total number of species occurring in that area; A, number of species assessed by IUCN.

have often been depleted within a few decades after their onset (Hurley 1998; Stevens *et al.* 2000). Thus, the increase in total catches may mask local population depletions, changes in species composition, and fisheries expansions into newly exploited regions and deeper waters.

Different catch trajectories may reflect local histories of exploitation. The NW Pacific shows a steady decline in elasmobranch catches since 1950. Here, landings have been driven by Japan with some of the largest elasmobranch fisheries (Stevens *et al.* 2000). Japan was already trading shark fins with China > 200 years ago and had well-developed trawl fisheries with signs of overexploitation before World War II (Nakano 1999). Thus, in the NW Pacific elasmobranch exploitation may have peaked at or before the 1950s. The NE Atlantic and Mediterranean have also experienced long exploitation histories (Lotze *et al.* 2006). Both show fluctuating landing trajectories with recent downward trends and relatively low catch per unit shelf area today (Fig. 2). Independent data suggest that these areas have experienced exceptional elasmobranch population depletions (Ferretti *et al.* 2008; see Appendix S1).

Only over the past 5–10 years has the conservation status of many elasmobranchs been systematically evaluated by the International Union for the Conservation of Nature (IUCN). Its shark specialist groups concluded that elasmobranchs are primarily threatened by fishing (96.1%) including directed commercial (31.7%), by-catch (57.9%), recreational (0.7%) and artisanal/subsistence fishing (5.8%), followed by habitat destruction (2.9%) and pollution (0.4%, http://www.redlist.org). Of the 1159 chondrichthyans known, 881 species have been evaluated globally with 42.8% listed as data deficient (DD), 25.7% least concern (LC), 13.9% near threatened (NT), 11.2% vulnerable (VU), 4.1% endangered (EN) and 2.4% critically endangered (CR, http://www.redlist.org). Status varies by region, with the highest proportion of threatened (VU, EN, CR) species in the Mediterranean and NE Atlantic (Fig. 2), while in the NW Pacific the situation appears less critical. However, there is considerable uncertainty as many species are listed as data deficient or not yet assessed (Fig. 2). Three regional IUCN assessments further highlight the critical situation in the Mediterranean and NE Atlantic, while providing a more optimistic assessment for Australia (Appendix S1).

Coastal ecosystems

Coastal ecosystems have been exploited throughout history and few have remained unaffected by human activities (Lotze *et al.* 2006). Hence, reconstructing pre-exploitation abundances and historical changes of coastal sharks is difficult (Ferretti *et al.* 2008). However, spatial gradients of human impacts can be used to gain insight into the structure of near-pristine ecosystems and their response to human disturbance. DeMartini *et al.* (2008) surveyed the fish assemblage in the remote Northern Line Islands (Fig. 3a). On uninhabited Kingman Reef, the bulk of fish biomass was composed by predators, 74% of which were reef sharks (*Triaenodon obesus*, *Carcharhinus amblyrhinchos*, *C. limbatus*). The proportion and biomass of sharks gradually declined with increasing human presence on neighbouring atolls (Fig. 3a). Similarly, the proportion of sharks (*T. obesus*, *C. amblyrhinchos*, *C. galapagensis*) to total fish biomass in the protected North Western Hawaiian Islands (NWHI) was 13% compared to almost zero in the densely populated Main Hawaiian Islands (MHI) (Fig. 3b, Friedlander & DeMartini 2002). On the Great Barrier Reef, no-entry marine reserves had higher shark densities (*T. obesus*, *C. amblyrhinchos)* than a near-pristine control site (Cocos Island), while sharks were greatly depleted in fished and even unfished areas where people were allowed to enter (Fig. 3c, Robbins *et al.* 2006). Interestingly, there was a sharp difference in overall shark abundance across these case studies. Shark biomass in Kingman Reef was an order of magnitude higher than in NWHI, which had variable fishing regulations over time (Friedlander & DeMartini 2002). Yet NWHI had still twice the sharks than the most protected portions of the Great Barrier Reef (Fig. 3), around which commercial fishing for sharks occurs (Robbins *et al.* 2006). These results suggest that the overall human footprint, including historical and current fishing in surrounding areas, may affect the structure of even protected ecosystems; yet differences in environmental factors or sampling methods may also have played a role (Ward-Paige 2010).

Another valuable source of data on coastal ecosystems comes from shark netting programs, which were developed in South Africa and Australia to protect swimmers. These programs provide long-term time series of shark catches-per-unit-effort (CPUE) in a region. They often pre-dated commercial exploitation and revealed high initial diversity and abundance of large sharks in inshore areas. At least 14 species were caught in netting programs in South Africa (Dudley & Simpfendorfer 2006), 25 in New South Wales (Reid & Krogh 1992) and 11 in Queensland, Australia (Appendix S2). Most species were coastal carcharhinids such as bull (*Carcharhinus leucas*) and blacktip sharks (*C. limbatus*). Soon after netting programs began, shark CPUE dropped dramatically. In New South Wales, 10 years after the first nets were installed in the late 1930s, catch rates had declined

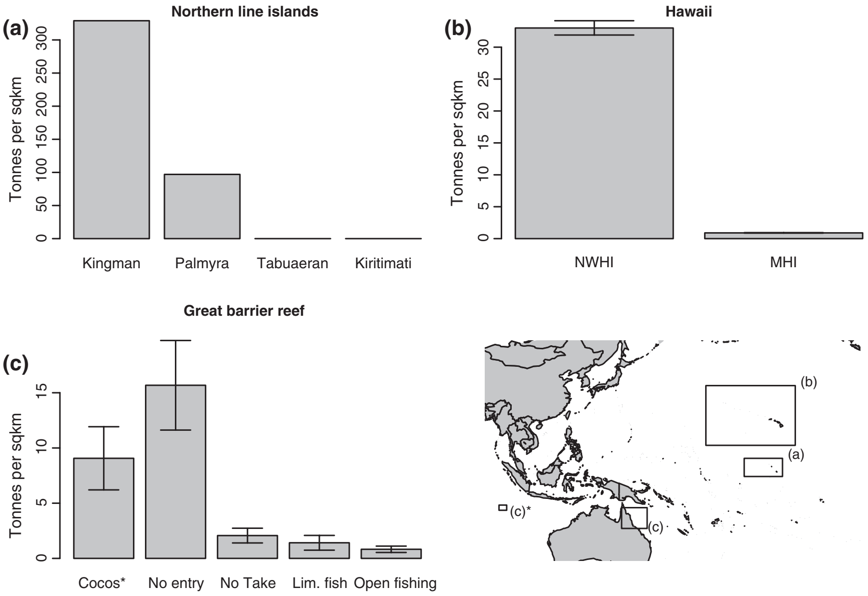

Figure 3 Estimates of shark biomass on tropical reefs across gradients of human impacts. These were derived from dive transect surveys in the (a) Northern Line islands (DeMartini *et al.* 2008), (b) Northwest Hawaiian (NWHI) and Main Hawaiian (MHI) Islands (Friedlander & DeMartini 2002), and (c) different management zones on the Great Barrier Reef and Cocos Island (Robbins *et al.* 2006). Sample areas are outlined by black boxes on the map. To obtain indices of abundance from (Robbins *et al.* 2006) comparable to the other studies, we transformed abundance from number per m^2 to weight per km^2. Using information on survival and fecundity provided in the study, we first estimated a stable age distribution for the recorded species. Then, we used species-specific parameters of the von Bertanlaffy growth function (http://www.fishbase.org) to estimate a frequency distribution of lengths at age. From this, we calculated the average length of the population and, using published length-weight relationships (http://www.fishbase.org), estimated the mean weight of the population.

by 94% (Reid & Krogh 1992). In South Africa, shark netting started in the early 1950s. From 1961 to 1972 species-specific catch rates declined between 27% and > 99% (Fig. 4, Appendix S3), yet anecdotal information suggested that severe declines had already occurred before systematic data collection (Holden 1977). Queensland developed its program in the 1960s, and catches decreased by 85% over 45 years (Appendix S2). Generally, the nets were only installed on a fraction of the shoreline. South Africa had a maximum of 32 km of nets along 267 km of coastline in 1975. Yet, this was sufficient to affect large sharks across the whole region (van der Elst 1979). In Queensland, newly installed nets recorded similarly low CPUEs as established ones (Appendix S2), indicating that shark declines were not just localized phenomena.

These studies suggest that even light fishing pressure by artisanal and subsistence fishing on remote islands or shark-netting programs along continental shores can be sufficient to cause dramatic declines in populations of large coastal sharks. This would explain why such populations are now rare or absent in more impacted systems such as the Gulf of Mexico, Caribbean, and Mediterranean Sea (Shepherd & Myers 2005; Ferretti *et al.* 2008; Ward-Paige 2010). Moreover, shark-netting data suggest some patterns of ecological reorganisation. As large coastal sharks declined, catch rates of more fecund and wide-ranging species such as

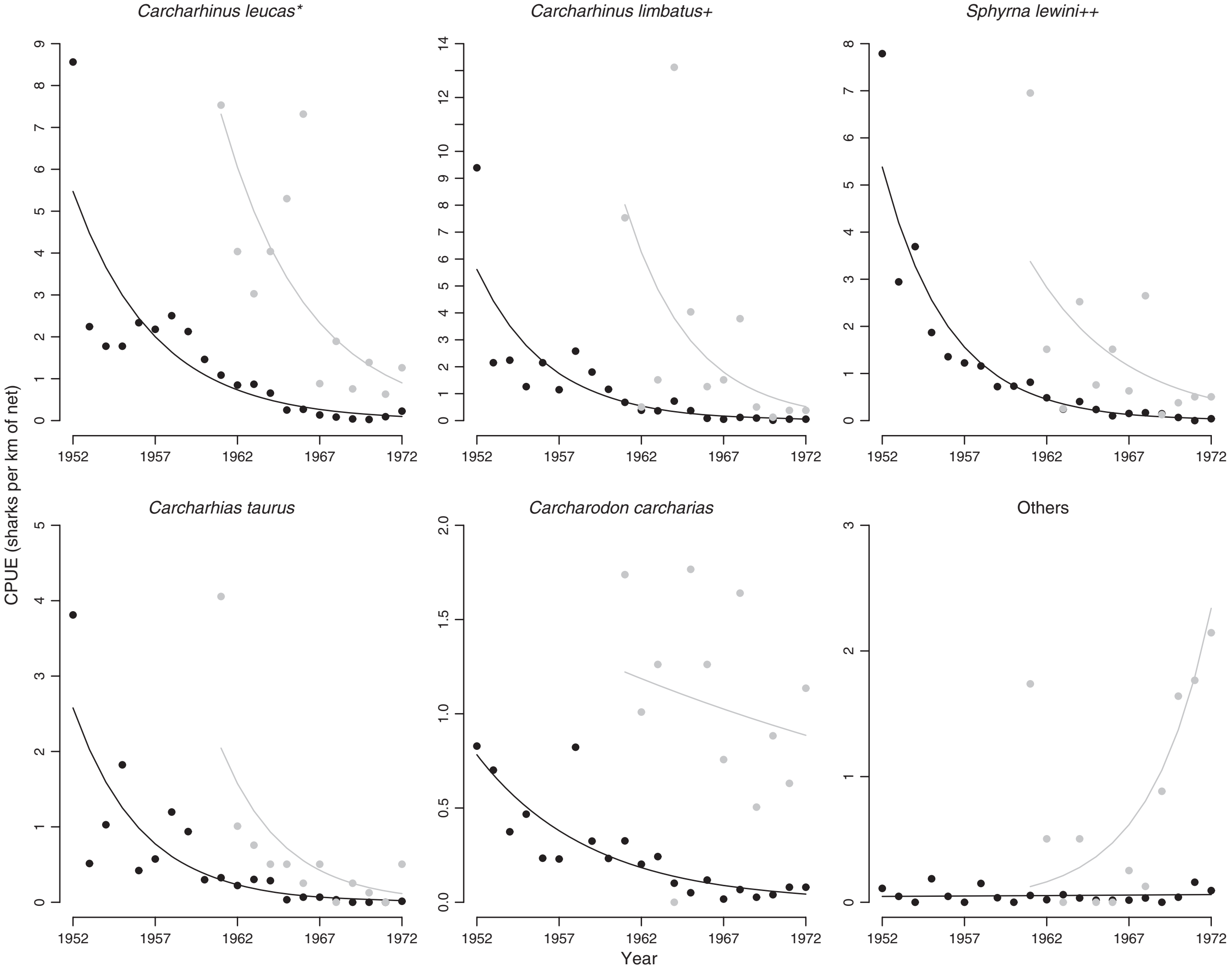

Figure 4 Depletion of large coastal sharks. Shown are catches per unit effort (CPUE) of sharks caught by the shark netting program in Main Beach (1952–1972, black symbols) and Brighton Beach (1961–1972, grey symbols) near Durban, South Africa. Data were extracted from Holden (1977). Generalized linear models were fit to the data assuming a Poisson distribution and a log link. Fishing effort in terms of meters of nets per location was treated as an offset variable. Species names refer to the most common species; *few *C. obscurus*; $^{+}$some *S. tudes*; $^{++}$some *C. brevipinna*. Parameter estimates of the models are reported in Appendix S3. 'Others' were mainly pelagic species such as shortfin mako (*Isurus oxyrinchus*), blue shark (*Prionace glauca*) and tiger shark (*Galeocerdo cuvier*).

tiger (*Galeocerdo cuvier*) or hammerhead sharks (*Sphyrna* spp.) increased, at least temporarily, in shark nets in New South Wales (Reid & Krogh 1992), South Africa (Dudley & Simpfendorfer 2006), and Queensland (Paterson 1990, Appendix S2), However, it is unclear at this point to which extent these reflect changes in abundance, distribution, or behaviour (Simpfendorfer 1992).

Demersal ecosystems

More than 90% of elasmobranch species worldwide inhabit demersal ecosystems on continental shelves and slopes (Compagno 1990), which makes them vulnerable to trawl fishing (Shepherd & Myers 2005). When trawling begins, catches of elasmobranchs are usually abundant and diverse including both small and large species despite the lower catchability of the latter. For example, scientific trawl surveys in recently exploited shelf regions off South Africa, detected four species of large predatory sharks and 51 small elasmobranchs in 1986–1990 (Compagno *et al.* 1991). On a small shallow bank in eastern South Africa, six large coastal sharks and 21 small elasmobranchs were recorded in 1989–1992, as by-catch in a prawn fishery that developed in the late 1970s (Fennessy 1994). Similarly, in the Gulf of Carpentaria, another recently exploited region of Australia, prawn trawl surveys recorded 10 large coastal sharks and 46 small elasmobranchs in 1990–1998 (Stobutzki *et al.* 2002).

As fishing proceeds, this initial diversity and abundance can be eroded very quickly. Large sharks often disappear from catches, and the community becomes dominated by smaller elasmobranch mesopredators (e.g. in the NE Atlantic, Ellis *et al.* 2005). Moreover, major restructuring of elasmobranch communities can occur through differential vulnerabilities to fishing gears, variation in spatial occurrence relative to fishing areas, and release from predation and competition. Scientific trawl surveys in the Gulf of Mexico in 1972–2002 revealed substantial changes in the relative abundance of 31 elasmobranch species that are by-catch in the US shrimp fishery (Shepherd & Myers 2005). Catch rates of shallow-water species such as *Dasyatis say* and *Gymnura micrura* declined by 60% and 99% respectively, whereas those of deeper-water species declined less or even increased, from 6- (*Squatina dumeril*) to 13-fold (*Mustelus canis*). For deeper-water species, shrimp fishing in depths < 20 m was less detrimental (Shepherd & Myers 2005). In the Tyrrhenian Sea, trawl surveys in 1974–2005 indicated strong declines in most sharks (e.g. *Scyliorhinus stellaris* 99%, *Squalus acanthias* 89%, *Galeus melastomus* 73%), while bathoids were less affected; again catch rates of deeper-water species declined less or even increased (Ferretti *et al.* 2005).

Over time, trawl fisheries often expand towards further offshore and deeper grounds (Aldebert 1997; Klaer 2001) where elasmobranch communities are composed of less resilient species (García et al. 2008). In SE Australia, offshore trawling developed in the 1970s, and elasmobranchs made up almost 50% of total fish biomass. After 20 years, elasmobranch catch rates were reduced by 80% (90% if *Squalus megalops* is excluded, Graham *et al.* 2001).

At this stage, domains of developed trawl fisheries often exceed the habitat and dispersal range of many elasmobranch species (Dulvy & Reynolds 2002), leaving no spatial refuges. This is the case of the Mediterranean, where a century of trawl fishing led to the loss of 16 of 31 recorded elasmobranch species in the Tyrrhenian Sea, six of 33 species in the Adriatic Sea (Appendix S4) and half of the elasmobranch species recorded in trawl fisheries in the Gulf of Lion since the 1950s (Aldebert 1997, Appendix S4). Similarly, in the North Sea, a diverse elasmobranch assemblage changed to one dominated by few small, highly productive species such as small spotted cat sharks (*Scyliorhinus canicula*) and little skates (*Raja naevus*, *R. montaguy*, Rogers & Ellis 2000).

Pelagic ecosystems

Industrial fisheries in the open ocean started in the 1950s (Ward *et al.* 2000) primarily to catch tuna and swordfish on the high seas. Fisheries statistics and scientific surveys were available from the beginning, and early catch rates essentially reflect unexploited fish communities (Myers & Worm 2003; Baum & Myers 2004; Ward & Myers 2005). Sharks constituted a substantial by-catch (Ward *et al.* 2000), and often a nuisance in causing damage to hooked target fish (Myers & Worm 2003; Baum & Myers 2004). In the Gulf of Mexico and Pacific Ocean, longliners caught about one shark for every two yellowfin tuna (*Thunnus albacares*, Baum & Myers 2004; Ward & Myers 2005) and in the Atlantic, 2–3 sharks for every swordfish (Brodie & Beck 1983). This led to rapid declines in shark catches over the last 50 years. In the Pacific, standardized catch rates of *Carcharhinus falciformis* decreased by 91.7%, while in the Gulf of Mexico those of *C. longimanus* were reduced by > 99% (Baum & Myers 2004). In the NW Atlantic, 18 coastal and pelagic sharks showed declines in catch rates of 49–89% in < 15 years (Baum *et al.* 2003, Fig. 5).

We note here that trend estimates depend on accurate interpretation of commercial longline CPUE data, which can be prone to both hyperdepletion (CPUE declines faster than the population) or hyperstability (population declines faster than CPUE) (Harley *et al.* 2001). These problems can be alleviated by standardizing for changes in fishing practises, area covered, and other factors. Also using different statistical frameworks can bias trend estimates in different ways (Minami *et al.* 2007). However, substantial uncertainties remain in some cases, and are the source of

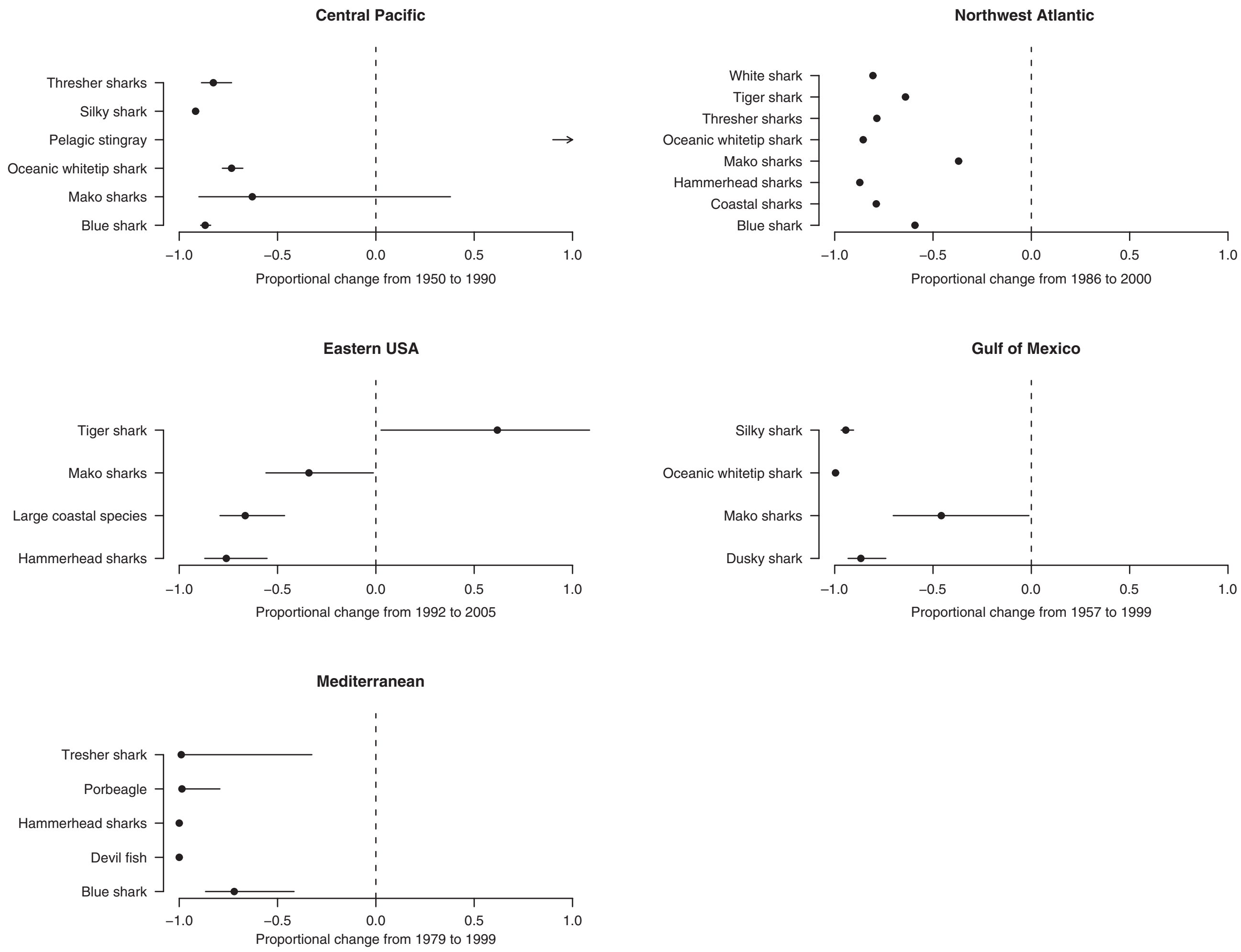

Figure 5 Relative changes in population abundance of pelagic sharks in the Central Pacific (Ward & Myers 2005), Northwest Atlantic (Baum *et al.* 2003), Eastern USA (Myers *et al.* 2007), Gulf of Mexico (Baum & Myers 2004), and the Mediterranean (Ferretti *et al.* 2008, using the analyses of the Ionian Sea pelagic fishery).

considerable debate (Baum *et al.* 2005; Burgess *et al.* 2005; Aires-da-Silva *et al.* 2008).

At the community level, declines are not uniform across species. Less resilient carcharhinids usually declined first potentially benefiting more prolific species such as blue and mako sharks (*Isurus oxyrinchus*). From 1977 to 1994, pelagic fisheries landings in Brazil revealed the disappearance of 14 species of carcharhinids (dominated by *C. signatus*), and a concomitant increase of mako and blue sharks (Amorim *et al.* 1998). Likewise, in the North Pacific, blue shark biomass is estimated to have increased by 20% relative to the 1970s (Sibert *et al.* 2006), and this species is now considered the most abundant shark in pelagic ecosystems (Dulvy *et al.* 2008). Mako sharks appear to have declined less than other large species in the Gulf of Mexico, Central Pacific and NW Atlantic (Fig. 5). However, when intense exploitation continues, all large sharks can be virtually eliminated such as in the Mediterranean Sea (Ferretti *et al.* 2008).

Approximately 21 oceanic elasmobranch species are commonly caught in high seas fisheries; these are broad-ranging species with circumglobal distribution (Dulvy *et al.* 2008). Although there are no documented cases of local species extinctions, 58% of pelagic species are considered threatened by IUCN, more than any other listed group of chondrichthyans (Dulvy *et al.* 2008). The high demand for shark fins in Asian markets (Schindler *et al.* 2002) is an important factor in the decline of pelagic species, which are often highly priced for their fins. This has motivated new shark fisheries and prompted others to switch from bony fish to sharks (Amorim *et al.* 1998; Aires-da-Silva *et al.* 2008). Pelagic sharks range across extensive, poorly monitored areas (Gilman *et al.* 2008); thus the amount of sharks taken globally for their fins is estimated to be four times higher than that reported to FAO (Clarke *et al.* 2006).

In summary, sharks have been increasingly threatened by the direct and indirect effects of fishing worldwide. This has caused marked declines in shark populations, particularly larger and less resilient species such as carcharhinids. These declines have coincided with substantial reorganisation of elasmobranch communities, including the rise of smaller sharks and rays in some regions. Next, we examine possible mechanisms that can lead to ecological reorganisation while evaluating the wider ecosystem consequences of shark declines.

ECOSYSTEM CONSEQUENCES

We are just beginning to understand the potential ecological consequences of shark declines, largely because of the difficulties in studying sharks and their prey in their natural environments. Ecosystem models predict that in some situations sharks will exert considerable top-down impacts on their prey, while not in others (Stevens *et al.* 2000; Kitchell *et al.* 2002; Okey *et al.* 2004). Unfortunately, a paucity of empircal studies makes it difficult to draw strong conclusions from some of these predictions. For example, we found little data on the effects of shark removals on teleosts and cephalopods, which comprise a large portion of their diets. This likely stems from the difficulties in studying population responses of these prey to variation in shark abundances, but it is also possible (and expected based on models decribed below) that these taxa would be less impacted by shark predation (Jennings & Kaiser 1998; Stevens *et al.* 2000). Larger-bodied and longer-lived prey species, however, are more likely to respond behaviourally and numerically to shark predation (Heithaus *et al.* 2008a). Indeed, both theoretical and empirical studies indicate that the decline of large sharks in particular can contribute to observed increases in the abundance of elsasmobranch mesopredators, marine mammals and reptiles and that this can induce cascading effects in some ecosystems. Similar to terrestrial predators (Creel & Christianson 2008), these effects are driven by both consumptive (direct predation) and non-consumptive (behavioural or 'risk') mechanisms (Heithaus *et al.* 2008a). Therein, risk effects act on the entire population, can be at least as influential as consumptive effects, and may be substantial even for prey that are rarely consumed (Creel & Christianson 2008; Heithaus *et al.* 2008a). In general, risk effects are expected to be greater when prey are in good body condition and in long-lived species that might invest more in predator avoidance than short-lived ones (Heithaus *et al.* 2008a). In the following, we are first documenting the theoretical, then the empirical evidence for the ecosystem effects of sharks and their respective mechanisms.

Insights from food-web models

Partly because of a scarcity of empirical data on community changes caused by fishing, food-web models based on diet data have been employed to explore possible effects of shark declines on food-web structure. For example, Bascompte *et al.* (2005) compiled data on trophic interactions of 249 species or trophic groups in the Caribbean, including 10 shark species, and analysed the occurrence of strong and weak interactions in the resulting food web. Sharks were represented in 48% of the trophic chains with strong interactions, and 31% of these were characterized by some degree of omnivory. Bioenergetic models showed that the removal of sharks could induce trophic cascades and make communities more prone to perturbations by reducing the degree of omnivory (Bascompte *et al.* 2005). The authors hypothesized that overfishing of sharks could have indirectly contributed to an observed shift from coral- to seaweed-dominated reefs, via an increase of fish consumers, which depressed herbivore density. However, others have suggested that predation on groupers and herbivorous parrotfish would occur simultaneously and therefore weaken the indirect effects of sharks on coral reef ecosystems (Mumby *et al.* 2006).

Mass-balance trophodynamic models (Ecopath with Ecosim, EwE) have been widely used to explore the potential effects of shark declines (Stevens *et al.* 2000). These models have sometimes been controversial, mainly because current applications do not adequately address uncertainty in data inputs and model structure (Plagányi and Butterworth 2004). Yet they allow us to frame hypotheses about the potential ecosystem effects of fishing. Regarding sharks, EwE models have suggested that effects of shark removal depend on the species involved and the ecosystem context (Stevens *et al.* 2000). Strong effects were seen particularly for large sharks in coastal environments. For example, in French Frigate Shoals (NW Hawaiian Islands), a simulated decline of tiger sharks caused increases in a range of prey species, including seabirds, turtles, monk seals and reef sharks, which in turn led to rapid declines of tuna and jacks. In contrast, removing reef sharks from the same ecosystem model had little effect (Stevens *et al.* 2000). One possible explanation is that reef sharks feed on fish and invertebrates that have relatively high turnover rates, as compared to the birds, turtles, seals, and sharks consumed by tiger sharks. Moreover, jacks and other predatory fish may functionally replace reef sharks that feed on similar species, whereas tiger sharks are the only major predator on turtles, for example. In a similar model of Floreana Island (Galapagos), the loss of all sharks led to increased abundance in toothed cetaceans, sea lions, and non-commercial reef predators, which forced decreases in a number of commercial reef fishes, and an increase in small invertebrates via a four-level trophic cascade (Okey *et al.* 2004). While the increase in marine mammals and decrease in commercial fishes is similar to what was seen in the Hawaiian model, it is unfortunate that the effects of larger sharks (mostly *Carcharhinus galapagensis*) and reef sharks could not be separated.

With respect to demersal systems, on the NE Venezuelan shelf, the simulated removal of smaller demersal sharks (mesopredators feeding on fish and invertebrates) caused complex and persistent changes in the abundance of many species groups, some of which had weak trophic interactions with sharks (Stevens *et al.* 2000). However, it is unclear which mechanisms caused those complex effects. Less strong and persistent effects were seen in pelagic systems. In the Alaska Gyre, the modeled depletion of pelagic blue and salmon sharks (*Lamna ditropis*) had mostly transient effects on pinnipeds and large fish (Stevens *et al.* 2000). Similarly, in the Central North Pacific, Kitchell *et al.* (2002) did not identify sharks as keystone predators of the pelagic community. In their model, the effect of pelagic sharks on the fish community was limited because of sharks' restricted diets and low consumption rates. Predatory fishes such as tuna and billfishes, characterized by faster biomass turnover, could substitute sharks without significantly affecting the dynamics of other species (Kitchell *et al.* 2002). Thus, based on these trophodynamic models we would predict that the effects of shark declines should be more pronounced in coastal and demersal than pelagic systems. We also would expect larger effects in sharks that feed on long-lived prey species.

Behaviourally-explicit models suggest that the risk of shark predation could also be important in driving community dynamics. For example in Prince William Sound, Alaska, harbour seals (*Phoca vitulina richardsi*) are preyed upon by killer whales (*Orcinus orca*) near the surface and sleeper sharks (*Somnius pacificus*) in deeper waters. Seal prey resources are segregated in the water column as well; Pacific herring (*Clupea pallasi*) occur towards the surface while walleye pollock (*Theragra chalcogramma*) overlap with sleeper shark distribution at depth. Modelling shark, orca, seal and prey depth distribution from fisheries data and tagging experiments, Frid *et al.* (2007) predicted that both orcas and sharks influenced seals' diving behaviour and resource use. However, sharks elicited a stronger behavioural response than killer whales, even although seals were only a minor portion of their diets (Frid *et al.* 2007). In the presence of sharks, seals reduced foraging on abundant pollock, unless herring was scarce or seals were in poor energy condition (Frid *et al.* 2007).

Effects on elasmobranch mesopredators

Large sharks are important, and sometimes the only consumers of smaller elasmobranchs (Wetherbee & Cortés 2004 and references therein). An increase in these species following declines of large sharks has been documented in several coastal and demersal habitats, but rarely in pelagic ecosystems. Above we discussed the increases in small demersal sharks and rays in the Gulf of Mexico and Mediterranean (Ferretti *et al.* 2005; Shepherd & Myers 2005). Likewise, along the eastern United States, catch rates of 14 small elasmobranch species in research surveys increased from 1.2% to 25.6% per year from 1959 to 2005, possibly in response to large predatory shark declines (Myers *et al.* 2007). Similarly, on the US west coast, from California to Canada, seven small chondrichthyans species increased from 1977 to 2001 (Levin *et al.* 2006).

Dogfishes (*Squalus* spp.) in particular have shown strong increases in many regions. *S. acanthias* increased 20- and 17-fold in the Gulf of Alaska and Prince William Sound, respectively (Fowler *et al.* 2004), and *S. megalops* increased 5-fold in SE Australia from 1976 to 1997 (Graham *et al.* 2001). Dogfishes and other small demersal elasmobranchs also increased sharply in New England in the 1970s to 1990s (Rago *et al.* 1998), a trend that coincided with the overfishing of groundfish (Fogarty & Murawski 1998) and the depletion of large sharks (Hurley 1998; Baum *et al.* 2003). They are now the most abundant demersal sharks on the shelf and upper slope of New Zealand (Beentjes *et al.* 2002) and South Africa (Kroese & Sauer 1998). In contrast, dogfishes have been driven to very low levels in the NE Atlantic because of intense target exploitation, and a similar overfishing trend has been seen where directed fisheries developed in the NW Atlantic (Rago *et al.* 1998; Fowler *et al.* 2004). These observations suggest that small elasmobranchs show widespread increases which could be partly linked to predator release. However, such increases can be reversed quickly by fishing, because of the high sensitivity of elasmobranchs to any changes in survival (Shepherd & Myers 2005). Note that most examples of local extinctions in Appendix S4 also concern smaller mesopredatory elasmobranchs.

In pelagic ecosystems, information about mesopredator changes is more limited, probably because those species have little commercial value, are not recorded, or are not susceptible to longline gear. Scientific survey and observer data from the Central Pacific (Ward & Myers 2005), however, do suggest large increases in pelagic stingray (*Pteroplatytrygon violacea*) and small teleosts, e.g. slender sunfish (*Ranzania laevis*) and pomfrets (Bramidae), from 1950s to 1990s. In addition to changing population size, increases may also be due to changes in habitat use; the removal of large sharks may allow small species to move into sunlit epipelagic waters during the day, which once were the domain of large predators (Ward & Myers 2005). Because sharks and other predatory fish such as tuna and billfish declined at the same time, the apparent increase in mesopredators cannot be attributed to sharks alone.

Effects on marine mammals and sea turtles

A number of large sharks commonly prey on marine mammals and reptiles, exerting both direct predation and risk effects (Heithaus 2001; Heithaus *et al.* 2008b). The preferential distribution of predatory sharks in tropical and temperate latitudes is thought to be one of the limiting factors for the expansion of pinnipeds and pursue-diving birds in these regions (Cairns *et al.* 2008). For example, tiger sharks are primary predators of some sirenians, dolphins, sea turtles, sea snakes and cormorants (Heithaus 2001, Heithaus *et al.* 2008b). Detailed studies in Shark Bay, Australia have shown how seasonal occurrence of tiger sharks influences the distribution, habitat use, and feeding behaviour of multiple preys (*Chelonia mydas*, *Dugong dugong*, *Tursiops aduncus*) with population and ecosystem-level consequences (Heithaus *et al.* 2008a, and references therein). Tiger sharks increase in abundance in warmer months yet almost disappear in the cold season. Their preference for productive shallow habitats causes even infrequent prey such as dolphins and dugongs to give up foraging opportunities to enhance safety. Not all individuals, however, abandon profitable but dangerous foraging locations. For example, green turtles in poor energetic condition are more frequently observed in the interior of seagrass beds, where the highest-quality plants are found, despite increased predation risk (Heithaus *et al.* 2007).

Relaxation of shark predation may have partially contributed to the recovery of some megafauna populations. In the NW Atlantic, the recovering grey seal (*Halichoerus grypus*) population on Sable Island experienced an increase in pup production of 12.6% per year in 1962–1982. Reduced shark predation on juveniles has been proposed as a contributing factor (Brodie & Beck 1983), because large-scale declines of predatory sharks have occurred since the 1960s (Brodie & Beck 1983; Hurley 1998; Baum *et al.* 2003). Likewise, the harbour seal population increased by 6% per year throughout the 1980s (Lucas & Stobo 2000; Bowen *et al.* 2003), but strongly declined in the 1990s due to increased mortality (Lucas & Stobo 2000; Bowen *et al.* 2003). Bite morphologies suggested Greenland sharks (*Somniosus microcephalus*) as possible predators (Z. Lucas, unpublished work), and it was suggested that a water temperature decline caused these cold-water sharks to expand to Sable Island (Bowen *et al.* 2003). Grey seals were also preyed upon, but seemed less affected because of their high abundance. This likely contributed to the decline of the harbour seal population through increased competition (Lucas & Stobo 2000; Bowen *et al.* 2003). A conservative estimate suggests that sharks might have contributed to ~50% of the harbour seal decline (Lucas and Stobo 2000).

Finally, the endangered Hawaiian monk seal (*Monachus schauinslandi*) is preyed upon by both tiger and Galapagos sharks. Monk seal populations at French Frigate Shoals experienced sudden increases in juvenile mortality in the early 1990s enhancing ongoing population declines (Antonelis *et al.* 2006). An experimental removal of 10 Galapagos sharks from pupping beaches reduced annual shark-inflicted pup mortality from 28 in 1997 to three in 2003 (Antonelis *et al.* 2006), suggesting that sharks could play an important role in seal population dynamics.

Empirical evidence of trophic cascades

Several recent studies support the idea that changes in large shark abundance can induce trophic cascades through changes in prey abundance or behaviour. Data from 17 research surveys from Florida to Maine revealed increases of 12 small sharks, skates and rays that coincided with declines in large sharks from 1970 to 2005 (Myers *et al.* 2007). One ray, *Rhinoptera bonasus*, strongly increased in abundance and in turn reduced its prey, the bay scallop *Agropecten irradians*, in North Carolina (Myers *et al.* 2007). While the effects of rays on scallops were confirmed by exclusion experiments (Myers *et al.* 2007), the effect of sharks on rays is less well documented. There is an active debate concerning the magnitude of predation release and possible mechanisms. For example, some increases in catch rates of small elasmobranchs may not only reflect changes in population size but also changes in migration patterns, range shifts, or habitat expansions.

The 50-year shark netting program along the Kwala-Zulu Natal shore in South Africa provides another good example of possible cascading effects (Fig. 6). In 1956–1976, while large shark CPUE declined in netting programs (Fig. 6a) recreational fishing tournaments revealed a proliferation of smaller elasmobranchs in inshore waters and a decline of bony fish (Fig. 6b–d; van der Elst 1979). The increase in smaller sharks was dominated by two species: juvenile *Carcharhinus obscurus* and *Rhizoprionodon acutus*. These were only lightly affected by shark nets, but preyed upon by larger sharks. Although *C. obscurus* can grow to large size (maximum length 4.2 m), it uses those inshore waters as nursery areas (van der Elst 1979) and the reduced presence of large predatory sharks may have benefited its pup survival. Van der Elst (1979) proposed that the increase in these mesopredators contributed to observed declines of bony fish, which constitute a large portion of their diet. Independent projections estimated that between 419 000 and 2.8 million small sharks, and ~5000 dolphins would have escaped shark predation in the period 1956–1976 (van der Elst 1979; Dudley & Cliff 1993). Data collected after 1977 from the same fisheries provide an intriguing temporal contrast. Since the 1990s, *C. obscurus* and *R. acutus* (representing 69% of elasmobranch catches) showed an overall decline (Fig. 6f). Angling pressure for these species

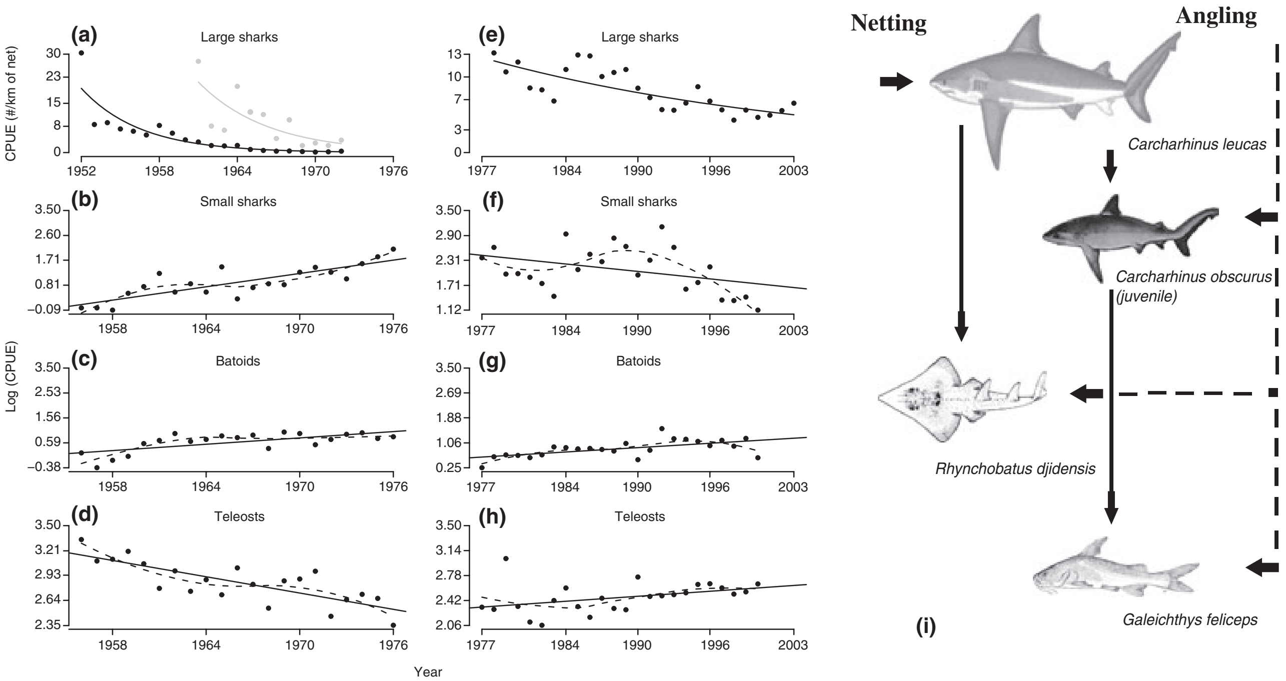

Figure 6 A possible trophic cascade in the inshore waters of Kwa-Zulu Natal, South Africa. Two periods are contrasted: 1952–1977 and 1978–2003. (a, e) Large sharks caught in shark netting programs (black: Main Beach, grey: Brighton Beach); data were derived from aggregated catches of large sharks species reported in Holden (1977) and Dudley & Simpfendorfer (2006). To be consistent between time periods, the species included in this group in both panels (a, e) are those reported by Holden (1977). Regression lines are: (a) generalized linear models as specified in Fig. 4, and (e) linear models of log(CPUE)~year. Panels (b–d) and (f–h) are time series of log CPUE of small sharks (mostly juvenile dusky sharks), batoids (skates and rays) and teleost fishes from the recreational fishery, as reported by van der Elst (1979) and Pradervand *et al.* (2007). As the fraction of teleosts was not explicitly reported in Pradervand *et al.* (2007), we estimated it by subtracting the elasmobranchs from the total number of fish caught. Solid lines depict linear regressions fitted to log transformed data. Dashed lines represent local regressions (LOESS). The diagram shows common species caught by shark nets and recreational angling, respectively, as well as their trophic relationships. The initial increase of small sharks was thought to be due to predatory release, and their later decline because of increased angling pressure.

was elevated (Pradervand *et al.* 2007) and likely overcompensated for the previous decrease in natural mortality. At the same time, catches of rays and bony fish increased (Fig. 6g,h), likely benefitting from reduced predation and competition from sharks. Pradervand *et al.* (2007) cautioned that these trends may have been influenced by changes in fishing technology or attitude, yet clear evidence for these mechanisms is missing.

Risk effects can also initiate trophic cascades. For example, green turtles and dugongs affect the spatial distribution and species composition of seagrass beds through foraging and excavation (Preen 1995; Aragones 2000). In Shark Bay, Australia, the spatial patterns of seagrass nutrient composition suggest that tiger shark-induced shifts in foraging locations and behaviours of green turtles and dugongs cascade to seagrasses (Heithaus *et al.* 2007, 2008a). Recent studies in other areas, where tiger shark populations have declined but green turtles have begun to recover, also suggest indirect effects of sharks on seagrass, mediated by the release of large grazers (Murdoch *et al.* 2007; Heithaus *et al.* 2008b).

It seems likely that trophic cascades driven by the depletion of large sharks may play out in other parts of the world, but have so far remained undocumented because of a lack of data on non-commercial species (Myers *et al.* 2007) or missing connections between separate studies that involve many species and broad temporal and spatial scales. Clearly, there is a need to find out whether the above examples represent isolated cases or common patterns that shape contemporary marine ecosystems.

CONCLUSIONS

Our overview shows that in natural, unexploited systems, sharks often exhibit high abundance and diversity. Yet even light fishing pressure is sufficient to cause strong population declines in vulnerable species, particularly large sharks. Such trends have been shown for artisanal and subsistence fishing

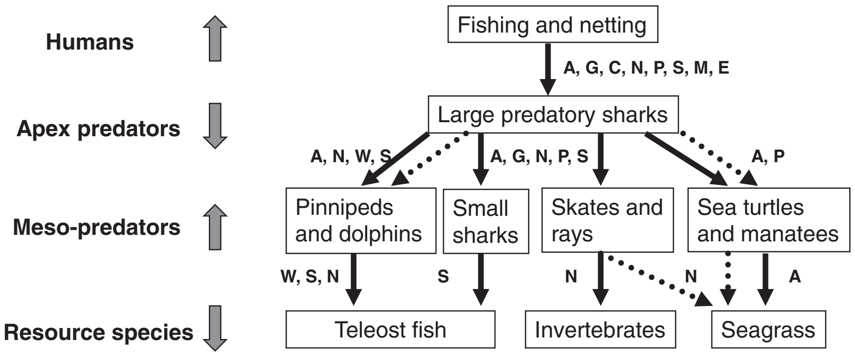

Figure 7 Documented ecosystem effects of fishing large sharks. Depicted are trophic (solid arrows) and behavioural (dotted arrows) interactions between humans, large and mesopredator elasmobranchs and their prey species. Block arrows represent overall population trends of the various functional groups. Regions in which particular interactions have been documented (see text) are indicated by letters (A, Australia; C, Caribbean; E, Europe; G, Gulf of Mexico; M, Mediterranean Sea; N, North American East Coast; P, Central Pacific; S, South Africa; W, North American West Coast). Note that few studies have documented effects on teleost and cephalopod prey.

on remote islands, shark netting programs, and in trawl and long-line fisheries in many regions, resulting in community shifts from large- to small-bodied species. Population declines of large species often exceeded one, sometimes two orders of magnitude with some local extinctions. Yet some more resilient species have not declined as drastically or have even increased, possibly via reduced competition or predation. Larger shark populations are still seen in some remote or protected areas, particularly in the Pacific, and may provide valuable opportunities to further understand the ecological role of sharks. Yet, reported catches of sharks and other elasmobranchs are still increasing in most regions, possibly indicating that more fisheries target sharks where they have not been historically exploited, a trend partially driven by the rising demand for highly prized shark fins on Asian markets.

Our brief review of shark evolution and life history suggests that sharks have been a relatively stable force in ocean ecosystems over evolutionary time, and possess a unique combination of ecological traits. They are morphologically and phylogenetically related to bony fish, but their life-histories may be more comparable to marine mammals, specifically with respect to their large size, low rate of reproduction, and late maturity. This renders sharks highly sensitive to changes in survival, either through predation or fishing. Many large sharks are the sole predators of smaller elasmobranchs and other marine megafauna, and the depletion of large sharks has likely contributed to considerable increases in these species in some regions. With their wide-ranging distribution and predatory role, large sharks in particular can spread their impacts across different ecosystems. Such spatial connectivity has also been shown to be important in freshwater and terrestrial ecosystems (Knight *et al.* 2005), and may increase the connectivity and stability of ocean food webs.

Ecosystem models predict that the loss of sharks should result in complex community changes, including trophic cascades, mesopredator release, and consequent declines in some commercial fish. The strength and persistence of these effects, however, appear to decrease from coastal and reef to demersal and pelagic environments. Observational studies suggest the presence of strong species interactions in some regions, mediated by direct consumption and risk effects, sometimes leading to trophic cascades. Fig. 7 attempts to conceptualize observed top-down links, and broad abundance trends across coastal and demersal ecosystems in different regions: as fishing and netting effort has increased, declines in large apex-predatory sharks have coincided with widely documented increases in smaller sharks and rays, as well as mammals and turtles. These mesopredator increases may be partly explained by decreased predation mortality and risk effects, and have in some cases led to increased pressure on prey species, such as invertebrates and teleost fishes or even seagrasses (Fig. 7). We must caution that many of the interactions displayed in Figure 7 are supported by limited empirical evidence. We are only beginning to study the complex ecological roles that large-bodied, wide-ranging predators such as sharks play. An important consideration for further research is the context-dependence of these interactions, which undoubtedly are mediated by a number of factors. These may include, among others:

(1) Food web properties: the diversity of available prey species will determine whether sharks can easily switch to alternative prey, and could limit the effects on any particular species. Furthermore, the presence and strength of intraguild predation in which sharks are involved could affect their role as a group (Kitchell *et al.* 2002; Kondoh 2008). Finally, whether particular prey species of sharks have other predators (such as billfish

or tuna in pelagic systems), and whether these prey are strong interactors themselves (such as large-bodied grazers in coastal systems), will affect the propagation of shark predatory effects through the food web.

(2) The life-history attributes of mesopredator and prey species: long-lived species and those which cannot compensate for increased mortality through growth or reproduction should be most affected by shark predation and risk effects. Also, the scope for effective anti-predator behaviour varies among species and individuals (Heithaus *et al.* 2008a). Separating direct predation and risk effects and understanding their potential interactions for different prey species poses a fascinating challenge for the study of large mobile predators.

(3) The interplay of fishing and predation: fishing affects not just sharks, but a wide range of target and bycatch species, and continues to change the nature of top-down regulation in the ocean (Heithaus *et al.* 2008a; Baum & Worm 2009). Any assessment of the effects of sharks needs to take into account changes in both natural (predation and environmental factors) and fishing mortality. While ecologists tend to focus on natural mortality, fisheries and conservation biologists tend to concentrate on human-related threats. In reality, however, natural and fishing mortality interact such that they both drive observed changes. For example, the decrease in both human and shark-inflicted mortality may have affected the rapid increase in grey seals in Eastern Canada (Brodie & Beck 1983), whereas both fishing and increased natural mortality from cownose rays may have contributed to the collapse of bay scallops in North Carolina (Myers *et al.* 2007). We suggest that these drivers, along with their direct, indirect and interactive effects should pose a ripe challenge for theoretical and empirical research. The objective would be to quantify and visualize spatially and temporally dynamic landscapes of risk and mortality, integrating the complex effects of human and non-human predators.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 IUCN regional conservation status of chondrichthyans.
Appendix S2 Queensland shark netting catch series.
Appendix S3 Parameter estimates of shark netting trends in South Africa.
Appendix S4 List of elasmobranch local extinctions.
Appendix S5 Parameter estimates of linear models in Fig. 6b–d.
Appendix S6 Parameter estimates of linear models in Fig. 6f–h.

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