

Extinction, survival or recovery of large predatory fishes

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Large predatory fishes have long played an important role in marine ecosystems and fisheries. Over-exploitation, however, is gradually diminishing this role. Recent estimates indicate that exploitation has depleted large predatory fish communities worldwide by at least 90% over the past 50–100 years. We demonstrate that these declines are general, independent of methodology, and even higher for sensitive species such as sharks. We also attempt to predict the future prospects of large predatory fishes. (i) An analysis of maximum reproductive rates predicts the collapse and extinction of sensitive species under current levels of fishing mortality. Sensitive species occur in marine habitats worldwide and have to be considered in most management situations. (ii) We show that to ensure the survival of sensitive species in the northwest Atlantic fishing mortality has to be reduced by 40–80%. (iii) We show that rapid recovery of community biomass and diversity usually occurs when fishing mortality is reduced. However, recovery is more variable for single species, often because of the influence of species interactions. We conclude that management of multi-species fisheries needs to be tailored to the most sensitive, rather than the more robust species. This requires reductions in fishing effort, reduction in bycatch mortality and protection of key areas to initiate recovery of severely depleted communities.

Keywords: conservation; extinction risk; fisheries management; global overfishing; marine biodiversity; meta-analysis

1. INTRODUCTION

Throughout human history, global fisheries have relied, significantly, on large predatory fishes. Similarly, on land, human hunters have often concentrated on large vertebrates, causing extinction waves of terrestrial megafauna (Alroy 2001). Although fishing pressure on large marine predators, such as sharks, tuna, billfish, large groundfish, etc. is high, it has long been assumed that these species are largely extinction-proof. The main reasons behind this idea were the seemingly inexhaustible abundance of marine life, the remoteness of many marine habitats and the perceived high fecundity of marine fish populations. All of these arguments have been shown to be wrong. By the turn of the millennium, more than two-thirds of global fisheries had been categorized as fully exploited, overexploited or depleted (Botsford *et al.* 1997). Recent studies suggest that even those numbers may be overly optimistic, as historical declines have often been overlooked or forgotten (Jackson *et al.* 2001; Lotze & Milewski 2004). Importantly, these declines have occurred worldwide and even in the most remote and ‘pristine’ parts of the ocean, leaving no sanctuaries (Myers & Worm 2003; Pandolfi *et al.* 2003), with the possible exception of the abyssal deep sea. The supposed high fecundity of marine fishes has also been dismissed; using meta-analysis of maximum reproductive rates it has been shown that reproductive capacity in marine fish populations is surprisingly low and uniform, generally ranging

between one and seven replacements per year (Myers *et al.* 1999).

As most fisheries are catching multiple target and bycatch species, the problem of overfishing becomes a community problem. Sensitive bycatch species are of particular concern, because they may sustain much lower mortality than target species, and may therefore decline more rapidly. Because fishery management is typically geared to the target species, the disappearance even of large conspicuous bycatch species can go unchecked and unnoticed (Brander 1981; Casey & Myers 1998; Baum & Myers 2004). Depletion of top predators, changes in community structure and disappearance of sensitive species represent important consequences of current fishing practices, and are the focus of this paper. We will compile quantitative evidence for the depletion of large predatory fish communities, and attempt to predict the extinction, survival or recovery of large predatory fishes as they may occur under different management regimes.

2. FROM THE PAST TO PRESENT: THE FACTOR-OF-10 HYPOTHESIS

In accordance with the now-famous ‘shifting baseline’ hypothesis (Pauly 1995), recent studies have suggested that the magnitude of historic declines in marine predators, such as large fishes (Myers & Worm 2003), marine reptiles (Jackson 1997) and mammals (Roman & Palumbi 2003) may have been underestimated. For large predatory fishes, a meta-analysis of longline catch rates for tuna and billfish, as well as research surveys for large groundfish, revealed global patterns of rapid decline in community biomass to

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One contribution of 15 to a Theme Issue ‘Fisheries: a future?’.

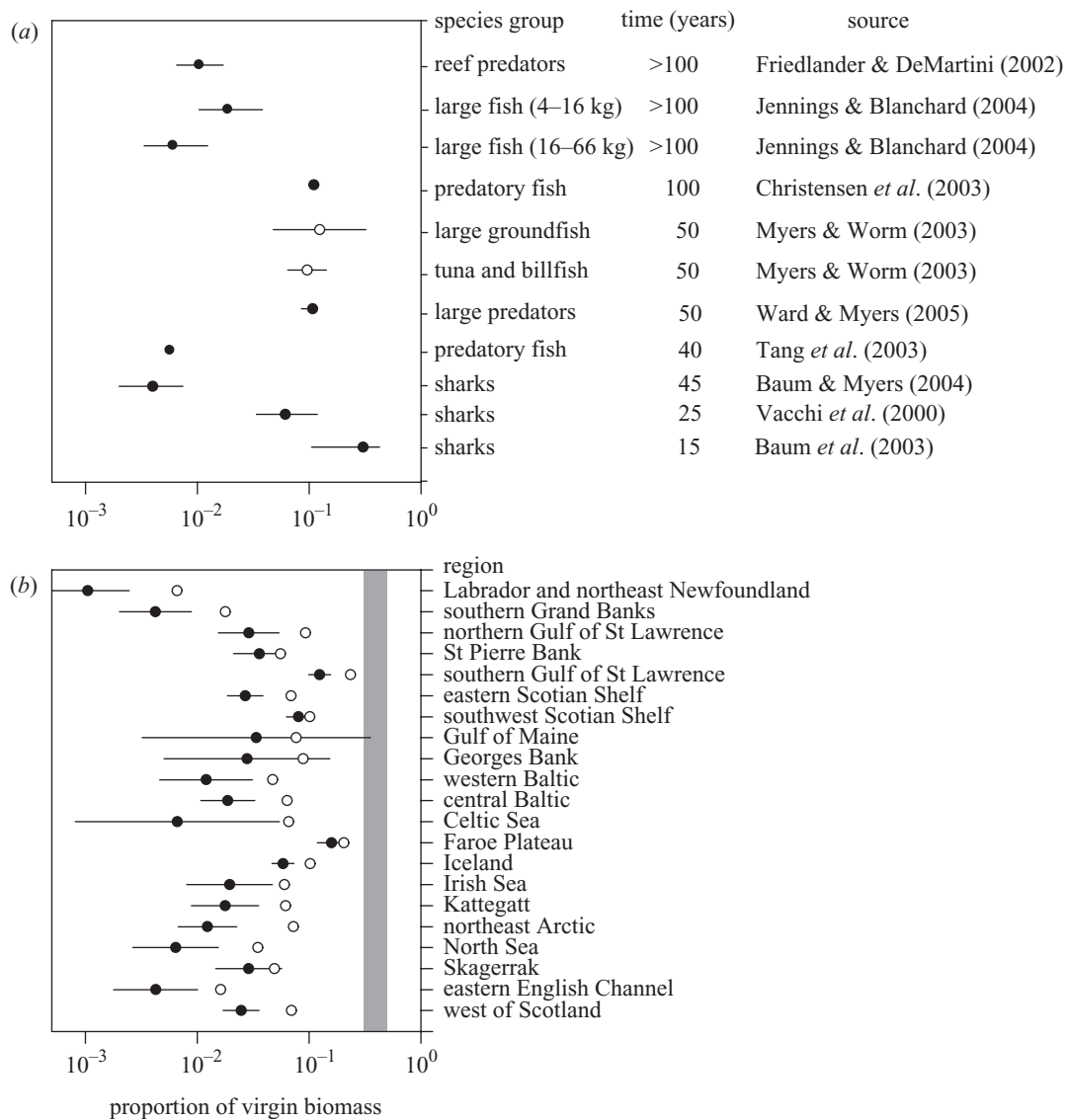


Figure 1. The present status of large predatory fishes. (a) Estimates of the residual biomass proportion for predatory fish communities on regional and global scales. (b) Estimates of residual spawning stock biomass proportion for Atlantic cod (*Gadus morhua*) populations. Error bars are 95% confidence intervals (where available), except for large fishes (4–16 and 16–66 kg), where bars refer to the range of possible outcomes under different assumptions about ecological transfer efficiencies. In (a) the time-scale of the study and species groups are indicated. Estimates were derived from the following sources: Friedlander & DeMartini (2002), Hawaiian reefs; Jennings & Blanchard (2004), North Sea; Christensen *et al.* (2003), North Atlantic; Myers & Worm (2003), global; Ward & Myers (2003), north Pacific; Tang *et al.* (2003), Bohai Sea; Baum & Myers (2004), Gulf of Mexico; Vacchi *et al.* (2000), Mediterranean Sea; Baum *et al.* (2003), northwest Atlantic. Estimates in (b) were derived from an analysis of cod carrying capacity (closed circles: Myers *et al.* 2001b) and cod recruitment (open circles: see text (§ 2) for details). The shaded bar refers to the proportional biomass commonly assumed to allow for maximum sustainable yield ($0.3 < B_{MSY} < 0.5$).

ca. 10% of pre-industrial abundance (figure 1a, open circles; Myers & Worm 2003). In contrast to earlier studies concerned with fish populations, this study showed that large declines extended across entire communities, and occurred on a global scale.

We compare these previous results with several independent studies to check the generality of the ‘factor-of-10 hypothesis’, which predicts 10-fold declines in large marine predators (figure 1a, filled circles). These studies represent a diversity of approaches, using very different methodologies, but all aimed at estimating virgin versus present biomass. Importantly, none of the datasets, methods or regions used by Myers & Worm (2003), was used in any of the other studies. However, they show remarkably similar

patterns (figure 1a). For example, detailed scientific surveys of fished and unfished reef islands in Hawaii revealed that the biomass of large predatory fishes, such as sharks and jacks, is only 1.5% on fished reefs, compared with unfished ones (Friedlander & DeMartini 2002). Large predators represented 54% of total fish biomass in the near-pristine reefs of the northwest Hawaiian islands, but less than 3% in the exploited reefs of the main Hawaiian islands (Friedlander & DeMartini 2002). Using size-based food-web models based upon macroecological theory, Jennings & Blanchard (2004) calculated that the current biomass of large fishes in the North Sea weighing 4–16 kg and 16–66 kg, respectively, is 2.6% and 0.8% of what it would have been in the absence of fisheries exploitation.

For the entire North Atlantic, a decline of large predatory fishes (trophic level greater than 3.75) to 11% of the biomass in 1900 was estimated using mass-balance models of marine ecosystems and historic catch data (Christensen *et al.* 2003). Similarly, comparison of standardized longline survey data from the 1950s and 1990s revealed a decline of large predatory fishes (sharks, tuna and billfishes greater than 20 kg mean weight) to 11% of the previous abundance in the north Pacific (Ward & Myers 2003). Fishery survey data from the Bohai Sea revealed a decline of total fish biomass to 5% and predatory fish biomass (total biomass minus shrimp and small pelagics) declined to 1% between 1959 and 1998 (Tang *et al.* 2003). Remarkably, these changes appeared to trigger a trophic cascade, with approximately threefold increases in zooplankton and threefold decreases in phytoplankton abundance throughout this region (Tang *et al.* 2003). As for shark communities, comparison of standardized longline survey data from the 1950s and 1990s revealed a decline of pelagic and coastal-pelagic sharks to only 1% in the Gulf of Mexico (Baum & Myers 2004). As a consequence, formerly abundant species such as the oceanic whitetip shark (*Carcharhinus longimanus*) are now considered rare exceptions in the Gulf of Mexico (Baum & Myers 2004). In the Mediterranean, elasmobranchs caught in Italian tuna traps declined to 7% of former abundance at the beginning of the twentieth century, between 1898 and 1922 (Vacchi *et al.* 2000). The only apparent exception to the 10% rule comes from a study of northwest Atlantic sharks, which showed a decline to 30% of former abundance, on average, over the past 15 years. The short time-frame of this study certainly leads to an underestimation of total depletion. Extrapolation of current rates of decline in shark populations (3.6–14.6% per year, mean 7.6%) over the past 50 years of exploitation leads to estimates of 2% of sharks left in the northwest Atlantic. This is remarkably close to the Gulf of Mexico estimate above (1% left), derived from independent data.

A comprehensive analysis of Atlantic cod (*Gadus morhua*) populations revealed similar results (figure 1*b*). Random-effects meta-analysis of spawner–recruit relationships was used to estimate the equilibrium virgin biomass, i.e. potential abundance or carrying capacity of cod in the Atlantic Ocean (Myers *et al.* 2001*b*). Cod was used as an example, because it had been a dominant predatory fish in many temperate marine ecosystems, and was assessed reliably over long time periods, using research surveys. We compared the empirical Bayes estimates of carrying capacity for each population (Myers *et al.* 2001*b*) with current estimates of spawning stock biomass (averaged over the past 5 years) taken from the most recent assessments (database available at <http://fish.dal.ca> and Myers *et al.* (1995)) to estimate the proportional biomass left. The carrying capacity, i.e. virgin biomass, for cod was simultaneously modelled for the 21 cod stocks in the north Atlantic assuming the maximum reproductive rate and the carrying capacity per unit area are random variables using a nonlinear mixed model. The spawner–recruitment model was parameterized as a Beverton–Holt model (see Myers *et al.* 2001*b* for further details).

The analysis indicates declines to 0.1–1% of previous abundance across all cod populations with the exception of the Faroe Plateau (figure 1*b*, filled circles). In an alternative

analysis, using minimal assumptions, we simply calculated the potential number of spawners that could be produced from estimated recruit densities of cod, averaged over time (typically 25 years of data, taken from <http://fish.dal.ca> and Myers *et al.* (1995)), assuming no fishing. Natural mortality, growth rates and age at maturity were assumed as in the original stock assessments. Then we compared these estimates of potential spawning stock biomass with the most recent assessments, as above. This analysis is very conservative, because it assumes that no subpopulations have been lost, and there is no decrease in recruitment with decreasing spawning biomass. Nevertheless, the results (figure 1*b*, open circles) mirror those of the analysis of carrying capacity (figure 1*b*, filled circles).

We conclude that the 10% figure is probably a general, and in many cases conservative, estimate of the depletion of large predatory fishes (reasons for this are discussed in Myers & Worm (2003)). This estimate is almost certainly too high for sensitive species such as sharks, which have been reduced to *ca.* 1% in some cases (figure 1*a*). Ten per cent may also be too high for communities that have been very accessible to exploitation (such as reef predators; figure 1*a*) or for some dominant species that have been exploited heavily over long time periods (e.g. cod; figure 1*b*). It may be exceeded only in particularly well-managed regions, such as the Faroe Islands (figure 1*b*), or the Gulf of Alaska (Witherell *et al.* 2000). We regard this as the current state of large predators worldwide. In the following sections, we shall turn to prediction of future scenarios.

3. THE FUTURE: PREDICTING EXTINCTIONS

From the land it is well known that large species with high ages at maturity are particularly vulnerable to extinction (Purvis *et al.* 2000). There is no reason to believe that this may be different in the ocean (Myers & Mertz 1998; Hutchings 2001; Dulvy & Reynolds 2002; Dulvy *et al.* 2003). With declines continuing, the extinction of sensitive populations and species is a real threat. Often these species are not target species, but caught as bycatch, so their disappearance is rarely noted. For example, 14 species of large elasmobranchs disappeared from the Gulf of Lions (northwest Mediterranean) from trawl surveys between 1957 and 1995 (Aldebert 1997), and nine species of elasmobranchs have disappeared from the Bay of Biscay since 1727 (Quero 1998). Similarly, the near extinctions of two formerly common skate species in the northwest Atlantic (Casey & Myers 1998) and Irish Sea (Brander 1981) were only recognized many years later.

Predicting future population collapses and extinctions is relatively straightforward, using published information on maximum reproductive rates (Myers *et al.* 1999). The lifetime maximum reproductive rate $\hat{\alpha}$ represents the number of reproductive females (spawners) produced by each spawner over its lifetime at very low spawner abundance, i.e. assuming no density dependence. Similarly, the annual maximum reproductive rate $\tilde{\alpha}$ is defined as the number of spawners produced per spawner each year, with a lag that equals the age at first maturity. Both parameters are closely related to the maximum rate of population increase r_{\max} , which is perhaps the most fundamental parameter in population biology (Myers *et al.* 1997*b*). As $\tilde{\alpha}$ controls the ability of the population to compensate losses to fishing, it is the

key parameter to set annual fishing mortalities. A recent meta-analysis revealed that $\tilde{\alpha}$ is surprisingly constant among fish populations, generally ranging between 1 and 7, and averaging 3 for populations with multiple datasets available (Myers *et al.* 1999). This means that fish populations have similar capacity for population growth as many mammals, for example, and are equally sensitive to excessive exploitation.

We plotted the maximum lifetime and annual reproductive rate $\hat{\alpha}$ and $\tilde{\alpha}$ from 114 populations against winter temperature to see whether sensitive species were more common in certain climatic habitats. These ranged from tropical to polar habitats in all oceans, encompassing coastal, shelf and oceanic species (Myers *et al.* 1999). The analysis shows that sensitive species, which are characterized by low maximum reproductive rates, are common across habitats (figure 2*a,b*). It further shows that given these low reproductive rates an annual fishing mortality of only 0.2 would cause the extinction of 14 species (12%), distributed across habitats (figure 2*c*). A more typical fishing mortality of 0.4 would cause the extinction of 42 species (37%); (note that this proportion also depends critically on the age-specific fishing mortality; see figure 3). This means that sensitive species with low extinction thresholds will need to be considered in almost all management situations.

If management is tuned to only the target species, fishing mortality may be easily too high for sensitive bycatch species, which may then eventually go extinct. The fishing mortality that is required to drive a population to extinction is defined here as the extinction fishing mortality F_{extinct} (Mace 1994), also called the biological limit of fishing mortality (Myers & Mertz 1998). It is implicitly given by

$$\tilde{\alpha} = e^{F_{\text{extinct}}(a_{\text{mat}} - a_{\text{sel}} + 1)} \left(1 - e^{-(M + F_{\text{extinct}})} \right), \quad (3.1)$$

where a_{mat} is the age at maturity, a_{sel} is the age at which fishes enter the fishery, and M is the natural mortality (Myers & Mertz 1998). In this model it is assumed that fishing mortality is knife-edge, i.e. zero up to a_{sel} and constant thereafter. Importantly, F_{extinct} estimates are conservative, because they are for the deterministic case, which assumes no stochastic variation, and no uncertainty about population status.

We predict the proportion of populations that will go extinct under different scenarios of fishing, using all published vital rates for sharks ($n = 26$ populations; Smith *et al.* 1998) and marine bony fishes ($n = 151$ populations; Myers *et al.* 1999), respectively. We summarize data as the cumulative proportion of populations that will decline to extinction, which is smoothed across individual species estimates (figure 3). To generalize from this to all marine fishes, we would have to assume that our sample of species is broadly representative. For bony fishes, age at recruitment and age at maturity were taken from the most recent stock assessments. For sharks, age at maturity was taken from Smith *et al.* (1998) and age at recruitment was set as 1. Results show that sharks show at least twice the extinction risk of bony fishes for a range of moderate fishing mortalities, and that extinction risk declines as fishing becomes more selective for older age classes. Extinction rates are very high if recruits enter the fishery (figure 3*a*), moderate when fishes enter the fishery at half the age at maturity (fig-

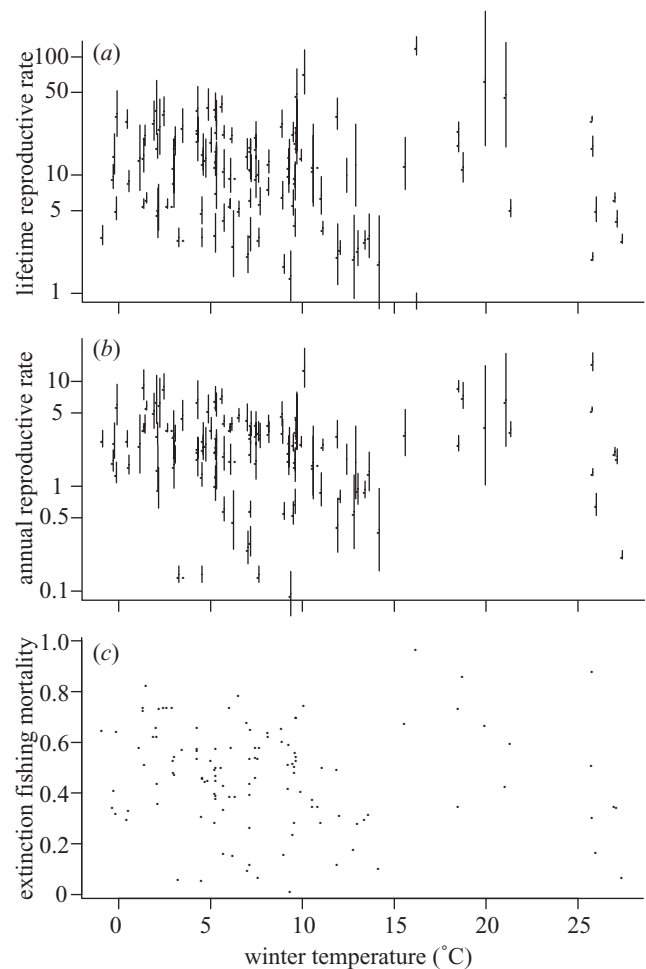


Figure 2. Predicting the occurrence of sensitive species. (a) The lifetime maximum reproductive rate $\hat{\alpha}$, (b) the annual maximum reproductive rate $\tilde{\alpha}$, and (c) the predicted extinction fishing mortality F_{extinct} are shown in relation to the mean temperature of the habitat. Fishing mortality was converted from an instantaneous rate to the proportion removed per year, and assumed zero to the midpoint between age at recruitment and age at maturity, and constant thereafter.

ure 3*b*), and lowest when fishes enter the fishery at the age of first maturity (figure 3*c*). The data predict that if recruits are fully vulnerable to the fishery, a removal rate of 0.4 (i.e. 40% removed per year) leads to the extinction of all sharks and about half of the bony fishes. If fishing occurs at age of first maturity, the same removal rate is predicted to lead to extinction of 40% of sharks and less than 20% of bony fishes. Reasons for the high sensitivity of sharks are their large size coupled with low fecundity, low reproductive rates and high ages at maturity of up to 20 years (Myers & Mertz 1998). Similar conclusions have been reached for skates and rays (Brander 1981; Casey & Myers 1998; Dulvy & Reynolds 2002).

4. PREDICTING SURVIVAL

A minimal management solution to avoid species extinction in multi-species fisheries is to reduce fishing mortality enough to allow sensitive species to survive. We will discuss this for several shark species, which have been reduced to low population levels. For this calculation, we need estimates of the rate of decline at low population size \hat{d} ,

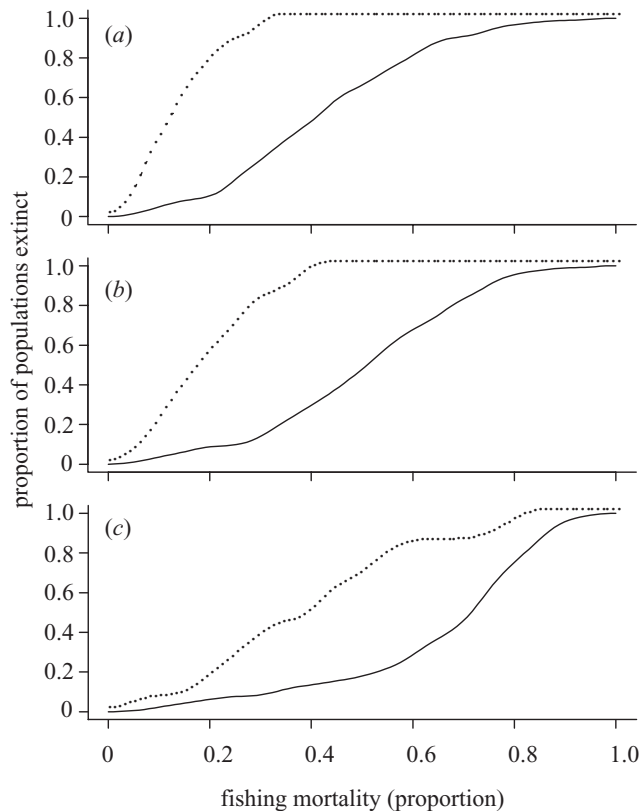


Figure 3. Predicting extinctions of sensitive species. Shown is the fishing mortality required to drive populations of sharks (dotted line) and bony fishes (solid line) to extinction under three scenarios. The scenarios are (a) fishing mortality is constant at the age of recruitment, (b) fishing mortality is constant at the midpoint between age at recruitment and age at maturity, and (c) fishing mortality is constant at the age of first maturity. Lines represent the cumulative probability of extinction obtained by smoothing across individual estimates for 26 species of sharks and 151 species of bony fishes, respectively. In each case fishing mortality is assumed zero to a given age, and constant thereafter. Fishing mortality was converted from an instantaneous rate to the proportion removed per year for clarity.

which is estimated as in Baum *et al.* (2003) and an estimate of the maximum population growth rate, r_{\max} .

The simplest assumption for this case is

$$\frac{dx}{dt} = r_{\max}x(1 - g(x)) - Fx, \quad (4.1)$$

where $g(x)$ is the density-dependent term (for logistic population growth $g(x) = x/K$) and F is the instantaneous fishing mortality (Clark 1990). If the population is reduced to low population size, which is a reasonable assumption for many exploited shark populations, then density dependence will be small, and we can assume that $g(x) \approx 0$. If we have independent estimates of the rate of decline \hat{d} , this gives $-\hat{d}x \approx r_{\max}x - Fx$. The fishing mortality required to drive a population to extinction is $F_{\text{extinct}} = r_{\max}$. Therefore, this represents the upper bound to sustainable fishing mortality. Here, the maximum rate of increase r_{\max} was calculated from the well-known Euler–Lotka equation

$$\sum_j l_j m_j e^{-r_{\max}j} = 1, \quad (4.2)$$

where l_j is the fraction surviving to age j and m_j is the number of offspring per animal produced at age j (Myers *et al.* 1997b). Estimates of adult mortality and fecundity were taken from Smith *et al.* (1998). Calculations were made based upon the assumption that at low population size juvenile mortality is the same as adult mortality, or alternatively twice the adult mortality. We can then calculate the minimum proportional reduction in fishing mortality that is needed to ensure survival, given by

$$\delta_{\text{survival}} = \frac{\hat{d}}{r_{\max} + \hat{d}}. \quad (4.3)$$

For most of the large coastal and pelagic sharks in the northwest Atlantic, a 40–80% reduction in fishing mortality is needed for survival (figure 4). This estimate provides a minimal baseline for the reduction in fishing mortality required for survival of sharks. This is because the simple model described above ignores the effect of stochastic variations in survival, which will decrease the estimate of fishing mortality, required to drive the population extinct (Lande *et al.* 2003). Similarly, we ignore possible Allee effects, which will again lower the threshold for the fishing mortality needed to cause extinction. Reduction in fishing mortality for sharks could be implemented by reducing overall fishing effort, by reducing fishing in areas with high shark bycatch or by gear modifications that reduce bycatch mortality. Although we have performed these calculations for sharks, similar calculations can be made for most fish species based upon published analyses of vital parameters (Myers *et al.* 1999, 2001a).

5. PREDICTING RECOVERY

One of the most general patterns in fishery science is the increase in community biomass that occurs when fishing pressure is reduced. For example, this is well documented for both World Wars, which reduced fishing effort to near zero in large parts of the North Sea in 1913–1919 and again in 1938–1946. Both times groundfish biomass increased between two- and fourfold within a few years (Pope & Macer 1996; Rijnsdorp & Millner 1996). Similar changes occurred in many regions with the introduction of the 200 mile limit to foreign fishing implemented in 1977 (Myers *et al.* 1997a), and on a much smaller scale within marine reserves, which are increasingly used as a management tool to initiate recovery of depleted communities (Jennings 2000). Recently, Halpern compiled available data from 85 fully protected marine reserves across the world (Halpern & Warner 2002; Halpern 2003). He showed that full protection from fishing resulted in rapid increases of fish density, biomass, average size and diversity. Biomass, for example, increased between 2- and 10-fold within the first 3 years of protection (figure 5a), and species diversity (figure 5b) increased up to twofold over the same time-frame. These effects were persistent over at least four decades of protection (figure 5), and also independent of reserve size (Halpern 2003). These results suggest that the effects of reductions in fishing on entire communities are general and surprisingly constant over time. An illustrative case study of large-scale recovery comes from Georges Bank, an important groundfish area off New England (Murawski *et al.* 2000). Beginning in 1994, three large areas, totalling 17 000 km² on the Amer-

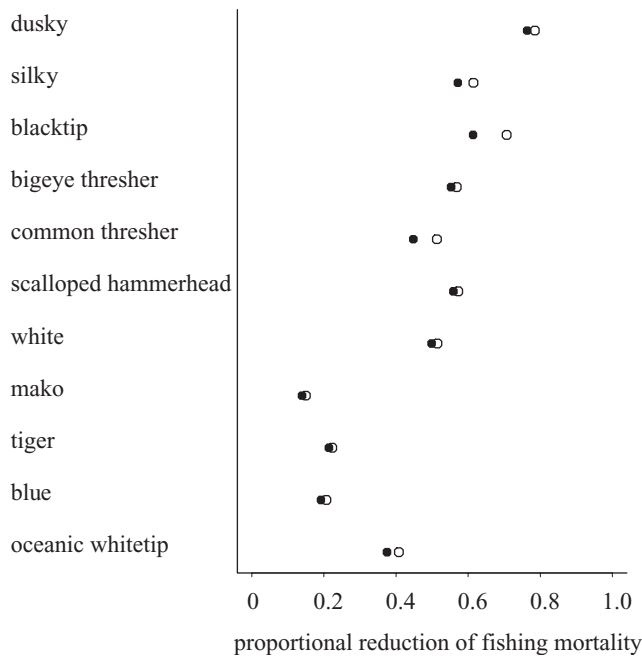


Figure 4. Predicting survival of sensitive species. The minimum proportional reduction of instantaneous rate of fishing mortality needed to allow the survival of shark species in the northwest Atlantic was calculated under two assumptions: that juvenile mortality is the same as adult mortality at low population sizes (filled circles) and that juvenile mortality for the first year is twice the adult mortality at low population sizes (open circles). See text (§ 4) for details.

ican side of Georges Bank were closed to all fishing except lobstering. Research surveys indicate that the closure was immediately successful in reducing fishing mortality and initiating rebuilding. After only 4 years, commercial groundfish stocks had increased steadily in abundance, some of them, like haddock, for the first time in decades (Murawski *et al.* 2000). Commercial invertebrate stocks also benefited from the closed area, with a 15-fold increase in commercial-sized sea scallops after 4 years (Murawski *et al.* 2000). Large-scale closures like this may also be used in the open ocean to halt declines of threatened large pelagics, such as sharks (Hyrenbach *et al.* 2000; Baum *et al.* 2003; Worm *et al.* 2003). The protection of areas of high diversity, or hotspots, in particular appears to maximize conservation benefits for many sensitive species at once (Worm *et al.* 2003). However, whereas closures can help to reduce fishing mortality locally, reserves are most likely to be effective only when overall fishing capacity is also cut. Otherwise, relocation of fishing effort simply leads to spatial displacement, and may even cause overall increases in fishing mortality (Baum *et al.* 2003; Worm *et al.* 2003).

Predicting recovery at the species level is often harder than predicting general increases of community biomass and diversity (Jennings 2000). Whereas some species recover quickly, recovery may occur slowly or not at all for others. On Georges Bank, for example, haddock and yellowtail flounder increased between three- and fivefold within the first 5 years of protection, whereas cod showed only slight increases. An analysis of the trajectories of exploited fish populations worldwide found that there was strong variation in recovery times among families (Hutchings 2000). For example, clupeids such as herring

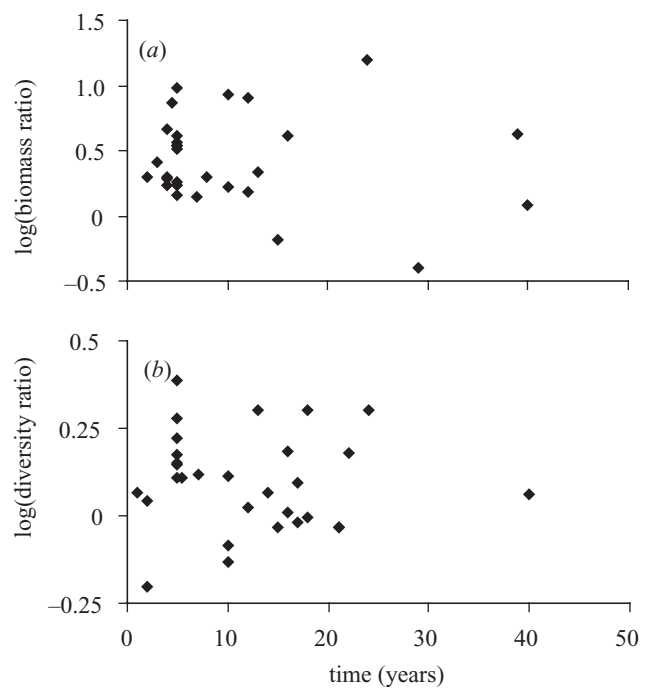


Figure 5. Predicting community recovery. Data compiled from 85 no-take marine reserves demonstrate rapid increases in (a) biomass and (b) diversity of fish communities, when fishing mortality is reduced to zero. Data from Halpern (2003). Positive values indicate increases, negative values decreases in biomass or diversity within a reserve. A log-ratio of 0.3 equals a 100% increase.

and sardines often (but not always) showed rapid recovery (5–10 years after depletion), whereas gadoids and the Antarctic nototheniids showed generally no, or slow, recovery 5–15 years after depletion (Hutchings 2000). Reasons for non-recovery may include the continuation of fishing (through directed fisheries or bycatch), changes in habitat, recruitment limitation, Allee effects or changes in species interactions. Here, we focus on the last of these. Recently, evidence has been mounting that fishing alters species interactions, with implications for stock recovery. For example, the depletion of a dominant predator (or the entire predator guild) can result in large biomass increases in its prey species. For example, where Atlantic cod is a dominant predator, the collapse of cod stocks leads to large increases in benthic crustaceans (Worm & Myers 2003) and pelagic fish (Fogarty & Murawski 1998), both a major food source of cod. This could inhibit the recovery of cod, because large increases in pelagic fishes may be correlated with low cod survival (Swain & Sinclair 2000), probably because of intense predation on cod eggs and larvae (Köster & Möllmann 2000). It has been suggested that these processes may lead to alternative stable states in which either groundfish or pelagic fishes dominate community biomass and recovery from overfishing is slowed by compensatory predation (the cultivation/depensation hypothesis of Walters & Kitchell (2001)). Such shifts in species interactions can have ramifications for ecosystem structure and function. This is best documented for kelp forests, where the removal of fish and invertebrate predators can release sea urchins from predation, which then increase and often overgraze kelp (Estes & Duggins 1995).

Thereby, fishing of urchin predators can transform very productive kelp forests into unproductive urchin barrens (Tegner 2000). However, this process is also reversible. Marine protected areas in New Zealand have shown rapid recovery of predatory fishes and lobsters, which then regain control of sea urchin populations and restore kelp dominance in these ecosystems (Babcock *et al.* 1999).

To summarize, it has been shown that the relaxation of fishing pressure invariably leads to rapid and potentially long-lasting increases in community biomass. The trajectories of individual species, however, are more difficult to predict, and are probably influenced to a large degree by the outcome of species interactions, and changes in natural mortality. As fishery science becomes more focused on conservation and restoration, this represents an important research priority for future years.

6. CONCLUSION

We conclude that industrial fisheries have changed marine ecosystems in fundamental ways. Large marine predators, representing the top of the food web, have been reduced by at least one order of magnitude. Current fishing mortalities projected into the future will deterministically lead to the extinction of sensitive species such as large elasmobranchs, and other large, late-maturing, slow-growing species. Because sensitive species are not unique to particular climates, habitats or fisheries, management needs to change fundamentally, to at least 'keep all the pieces' that make marine ecosystems function. We have shown how existing information on maximum reproductive rates can be used to set maximum fishing mortalities to ensure survival of sensitive species. Managing multi-species fisheries for the most sensitive (instead of the most robust) species will also help to avoid depletion of target stocks. We have also shown that community recovery is usually occurring when fishing mortality is reduced through reduction of fishing effort or spatial closures. Closures, however, need to be combined with overall reduction in fishing effort, to avoid problems caused by effort displacement and relocation. Based on this evidence, we recommend a combination of four management tools to halt and reverse declines of large predatory fish communities: (i) reduce fishing mortality enough to avoid extinction of the most sensitive species; (ii) reduce bycatch mortality wherever possible; (iii) use spatial closures to initiate recovery; and (iv) establish permanently closed marine reserves in key areas, such as spawning grounds and diversity hot spots. We conclude that today's management decisions will determine whether we will enjoy biologically diverse, economically profitable fish communities 20 or 50 years from now, or whether we will have to look back on a history of collapse and extinction that was not reversed in time.

The authors thank J. Baum, B. Halpern, S. Jennings, I. Jonsen, D. Kehler, H. Lotze and P. Ward for comments and data, and W. Blanchard for technical advice. They acknowledge funding by The Pew Charitable Trusts, NSERC, The Sloan Foundation (FMAP program) and the Deutsche Forschungsgemeinschaft.

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