

Marine Fish Population Collapses: Consequences for Recovery and Extinction Risk

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*Rapid declines threaten the persistence of many marine fish. Data from more than 230 populations reveal a median reduction of 83% in breeding population size from known historic levels. Few populations recover rapidly; most exhibit little or no change in abundance up to 15 years after a collapse. Reductions in fishing pressure, although clearly necessary for population recovery, are often insufficient. Persistence and recovery are also influenced by life history, habitat alteration, changes to species assemblages, genetic responses to exploitation, and reductions in population growth attributable to the Allee effect, also known as depensation. Heightened extinction risks were highlighted recently when a Canadian population of Atlantic cod (*Gadus morhua*) was listed as endangered, on the basis of declines as high as 99.9% over 30 years. Unprecedented reductions in abundance and surprisingly low rates of recovery draw attention to scientists' limited understanding of how fish behavior, habitat, ecology, and evolution affect population growth at low abundance. Failure to prevent population collapses, and to take the conservation biology of marine fishes seriously, will ensure that many severely depleted species remain ecological and numerical shadows in the ecosystems that they once dominated.*

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The world's ocean ecosystems are experiencing biological change at an unprecedented rate. Potentially permanent influences on species interactions, food web structure, and trophic dynamics are most dramatically reflected by staggering declines in the abundance of marine fishes. Large pelagic sharks, including threshers (*Alopias* spp.), great whites (*Carcharodon carcharias*), and hammerheads (*Sphyrna* spp.), have declined more than 75% in the Northwest Atlantic since 1986 (Baum et al. 2003). Similar reductions over the past 50 years have been reported for other predatory marine fishes (Christensen et al. 2003, Myers and Worm 2003; see also Walters 2003). One of these, the Atlantic cod (*Gadus morhua*), a species that supported one of the largest and economically most important fisheries throughout the North Atlantic for almost 500 years, has declined by as much as 99.9% in some areas since the early 1960s (COSEWIC 2003). Ultimately, failure to arrest these declines will result in the loss of species from parts of their current geographical ranges, a fate already experienced by more than 55 marine fish species and one that has resulted in the probable global extinction of at least 3 of these species over the last two centuries (Dulvy et al. 2003).

Against this profoundly unsettling backdrop, our objective is to describe and then evaluate the consequences of severe population decline for the recovery and vulnerability to extinction of marine fishes. We begin by summarizing the

magnitude of marine fish population declines over various periods of time. We evaluate the consequences of decline for recovery from a broad taxonomic perspective, first using data on more than 35 species composed of 90 different populations, and then from the perspective of a single species, Atlantic cod. Embedded within these analyses is a discussion of the primary correlates of recovery in marine fishes. We conclude with an exploration of the degree to which rates of decline provide information on risks of extinction.

The scale of the problem

At the outset, we consider the maximum reductions in breeding population size that have been observed across a broad range of species. The primary constraint on such an exercise is that these supposed historic rates of decline will always

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underestimate actual declines, because true historic population maxima will have occurred well before fishery management agencies began collecting data on fish abundance. For most fish populations, reliable quantitative data on abundance have only been available for the past 2 to 3 decades. One extremely useful database in this regard has been maintained by Ransom Myers at Dalhousie University (<http://fish.dal.ca/~myers/data.html>, hereafter the Myers database). In this database, spawning stock size, recruitment, catches by the fishery, and fishing mortality, all estimated by the national or international agency responsible for the management of each population, are available for numerous fishes.

It is clear that marine fishes have experienced extraordinary declines relative to known historic levels (figure 1). These data are based on populations for which time series extend at least 10 years, with a mean of 25 years and a maximum of 73 years. Taken as a whole, the median maximum population decline among the 232 populations for which data are available is 83%; well over half of the populations (58%) exhibited maximum declines of 80% or more. The strong negative skew in the data, and the high median decline in abundance, are also evident at lower taxonomic levels. Among 56 populations of clupeids (including Atlantic herring, *Clupea harengus*), 73% experienced historic declines of 80% or more.

Within the Gadidae (including haddock [*Melanogrammus aeglefinus*] and cod [*G. morhua* and other species]), of the 70 populations for which there are data, more than half declined 80% or more. And among 30 pleuronectid populations (flatfishes, including flounders, soles, and halibuts), 43% exhibited declines of 80% or more.

These results are sobering for two reasons. First, many of them have occurred in spite of an enormous effort to prevent them from happening. Second, as noted above, they are based on “historic” maxima that are not really historic at all, most fisheries having been well under way decades or centuries before the time series of data began. In the absence of longer-term data, researchers’ perceptions tend to scale to time periods that they, or perhaps their parents, can remember. This results in the “shifting baseline syndrome” (Pauly 1995), whereby scientists accept data from more and more recent periods as baselines, forgetting that this allows drastically reduced populations to substitute for the much higher baselines that occurred before humans began having major impacts on populations.

Associations between decline and recovery

Three studies by Hutchings (2000, 2001a, 2001b) examined directly the empirical evidence for the ability of marine fish populations to recover after a population decline. For many populations, it was possible to find the greatest 15-year decline in adult biomass and then ask what became of the population sizes 5, 10, and 15 years thereafter. The 15-year time frame for a population decline (termed “collapse” hereafter) was chosen for two reasons. First, it was short enough to obtain a reasonably large sample of populations. Second, it was long enough to approach, for many species, the three-generation time interval to which bodies such as IUCN (World Conservation

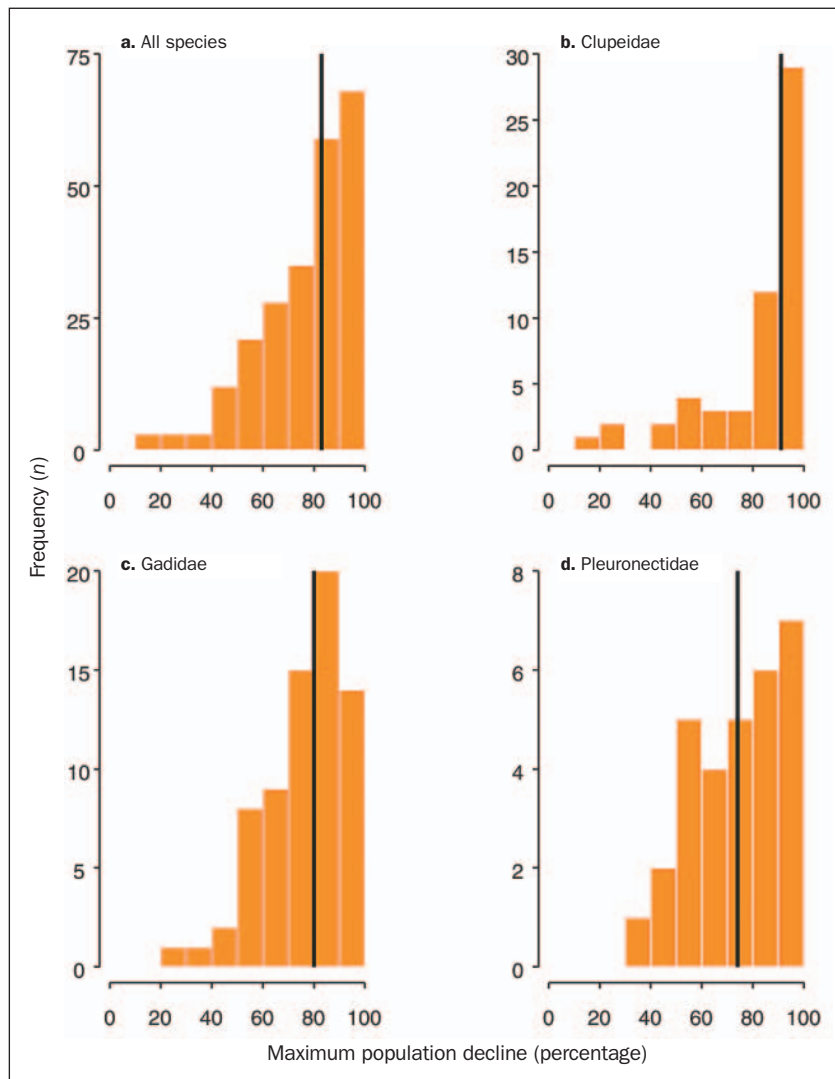


Figure 1. Frequency distributions of maximum known declines among marine fish populations over periods of at least 10 years, shown (a) for all 232 populations (the median decline of 83% is identified by a vertical line) and for three families: (b) Clupeidae (n = 56, median decline = 91%; includes Atlantic herring, *Clupea harengus*); (c) Gadidae (n = 70, median decline = 80%; includes Atlantic cod, *Gadus morhua*, and haddock, *Melanogrammus aeglefinus*); and (d) Pleuronectidae (n = 30, median decline = 74%; includes flatfishes such as flounder, sole, and halibut).

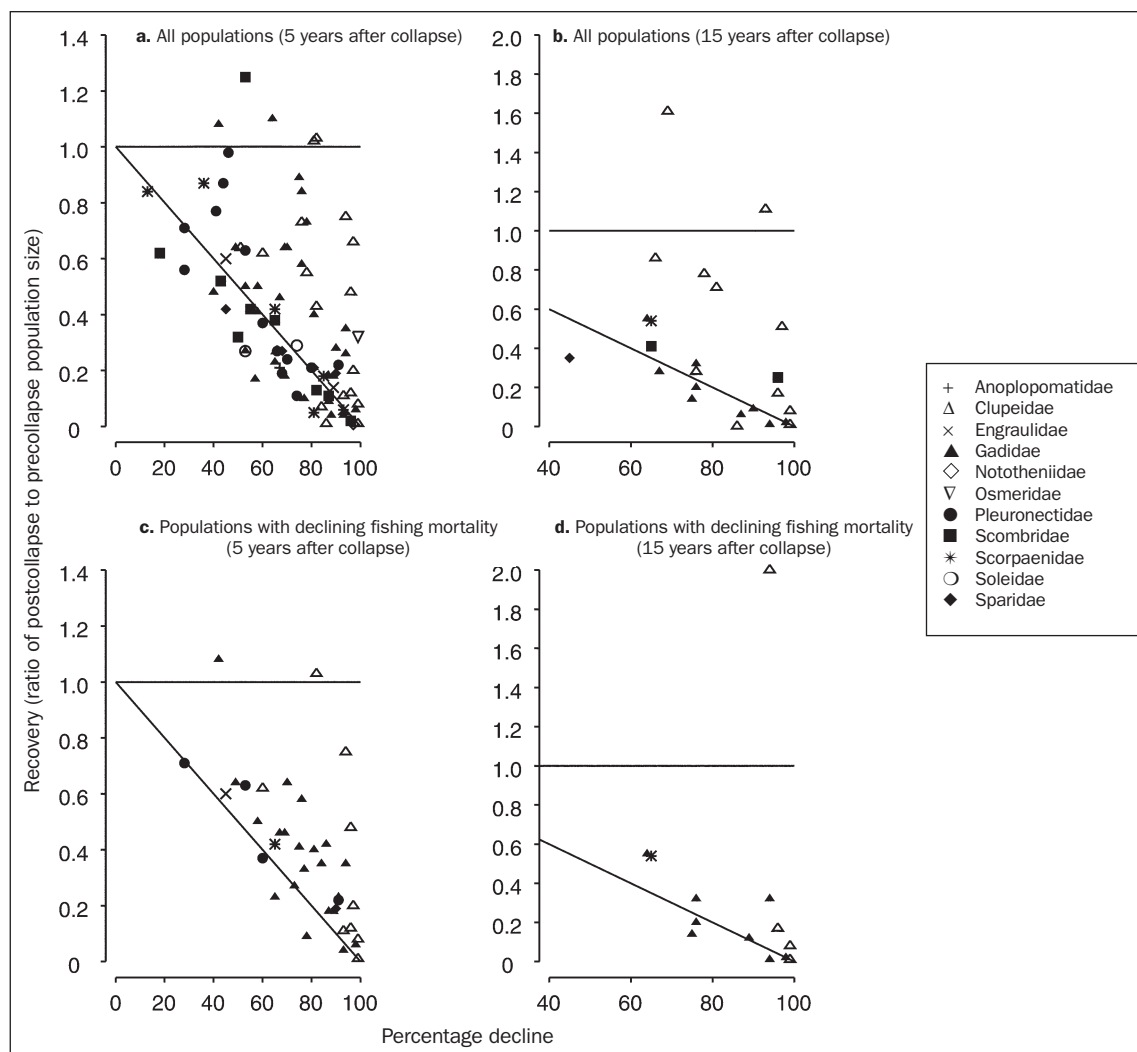


Figure 2. Bivariate associations between population decline and subsequent population size for marine fish populations. The y-axis refers to the size of a population 5 years (a, c) and 15 years (b, d) after the proportionately largest 15-year decline experienced by that population, relative to its size at the beginning of its 15-year decline. Panels a and b include data irrespective of changes to fishing mortality after a collapse; panels c and d include only those populations for which fishing mortality data are available and for which fishing mortality declined after a collapse. Populations that experienced some recovery are represented by points to the right of the slanted lines. Fully recovered stocks are represented by points on and above the horizontal lines. One datum in panel a (69% population decline of one clupeid followed by a 1.78 recovery) has been omitted for clarity.

Union) and COSEWIC (Committee on the Status of Endangered Wildlife in Canada) apply their decline-rate criteria to assess extinction risk.

Recovery was negatively associated with collapse among the 90 marine fish populations, representing 38 species among 11 families, for which data were available (for all populations, $r = -0.46$, $p < 0.0001$; excluding clupeids, $r = -0.64$, $p < 0.0001$). Five years after collapse, 41% of the 90 populations continued to decline, 51% exhibited some recovery, and 8% had fully recovered to the adult biomass from which they had originally declined (figure 2a). The magnitude of population collapse was also negatively associated with recovery 10 and

15 years after the declines. Indeed, 15 years after collapse, only 12% of marine stocks (all of them clupeids) had exhibited full recovery, while 40% (primarily gadids, but some clupeids) had essentially experienced no recovery at all (figure 2b).

Fishing mortality data were available for 56 of the populations. Among these populations, the exploitation rate declined after collapse for 36 stocks. When we examined only those populations for which fishing declined after collapse, over periods of 5 or 15 years, population recovery was still highly negatively associated with magnitude of population decline (for all populations, $r = -0.63$, $p < 0.0001$; excluding clupeids, $r = -0.79$, $p < 0.0001$) (figure 2c, 2d; Hutchings 2001b).

It could be argued that the metric of collapse used here sets an unduly stringent benchmark for recovery, if the initial adult biomass against which the collapse is calculated corresponds to the highest spawner biomass ever experienced by that population. But it does not, because none of the stocks were unfished at the start of the time series, and the adult biomass benchmark for the 90 populations examined here was, on average, only 81% of the maximum observed (Hutchings 2001b). Within the two families for which the most data were available, the spawner benchmarks for herring and their relatives were 70% of their observed maxima, while those of the cod family were 75% of their observed maxima. Within species, adult benchmarks for herring and cod were 68% and 63% of their respective maxima.

Three main conclusions can be drawn. First, the rate of population decline is an empirically defensible predictor of population recovery. Second, it is not unusual for populations that have declined more than 60% over 15 years to exhibit little or no recovery as much as 15 years later, even when fishing mortality has been reduced following collapse. Third, the association between collapse and recovery differs among marine fish taxa. Clupeids, which include herrings and sardines, appear to be more likely to recover from collapse than other species. This apparent increased resilience may be attributable to an earlier age at maturity, to reduced vulnerability to incidental exploitation or bycatch, and possibly, given the clupeid's pelagic life cycle, to reduced probability of habitat destruction by fishing gear (Hutchings 2000, 2001b). However, notwithstanding their greater ability to recover as a group, clupeids have been eliminated from parts of their range in the past century (Dulvy et al. 2003).

Correlates of recovery in marine fishes

The preceding analyses suggest that the recovery of marine fishes may be related to taxonomic affiliation (herring versus cod), habitat (pelagic versus demersal), fishing (targeted catch versus bycatch), and life history (early versus delayed maturity). Here we consider these and other potential correlates of marine fish recovery (see Dulvy and colleagues [2003] for additional discussion).

Fishing. The premise behind most management strategies and recovery plans is that the primary factor inhibiting recovery is fishing. While this seems logical, especially because fishing is always strongly implicated in a population's initial decline, the support for this idea is surprisingly equivocal.

To examine whether recovery is strongly linked to reductions in fishing, Hutchings (2001b) collated estimates of exploitation rate (the amount of fish taken by a fishery in relation to what is available to be taken, including incidental or bycatch mortality when such data are available) from the Myers database. Using these estimates, Hutchings calculated the ratios of exploitation rates for each population 5 years after collapse (E_{post}) to exploitation rates in the 5 years before collapse (E_{pre}). Thus, a decrease in a population's exploitation rate after collapse would yield a ratio ($E_{post}:E_{pre}$) less than 1 (figure 3).

As expected, populations recovered more quickly when fishing mortality declined after collapse. Populations returned to an average of 39% of their precollapse size when fishing mortality declined, compared with an average of only 29% recovery when fishing mortality remained constant or increased. Therefore, it appears that a reduction in fishing mortality is indeed necessary for recovery. Surprisingly, however,

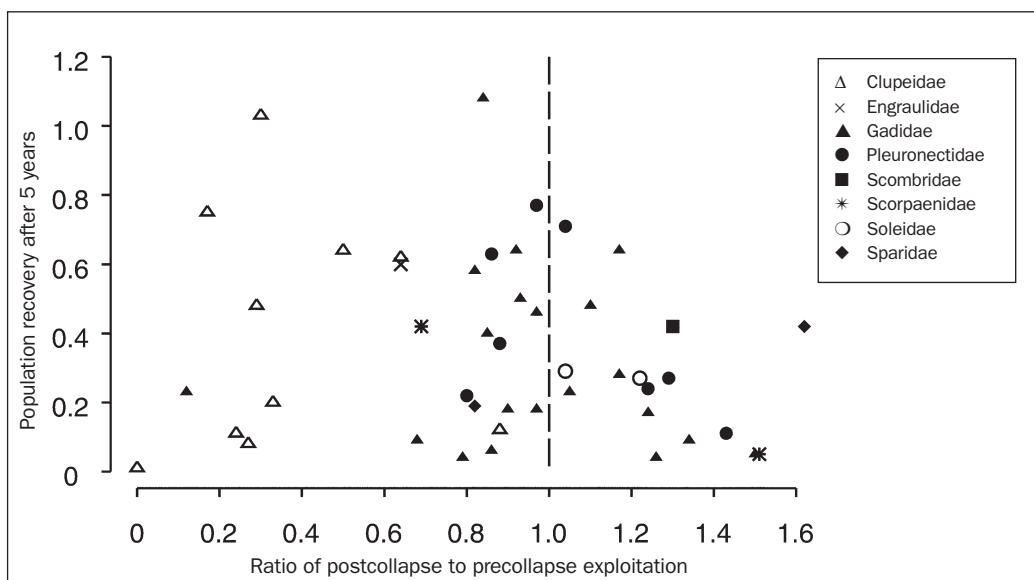


Figure 3. Recovery of marine fish populations 5 years after the proportionately largest 15-year decline by each population (as a ratio of postcollapse to precollapse exploitation rate). Populations that experienced reductions in fishing mortality after the collapse are shown to the left of the dashed line; those in which exploitation increased are to the right.

the extent to which fishing mortality was reduced after a collapse had no detectable effect on recovery 5, 10, or 15 years later. This proved to be the case whether or not one accounted for population differences in the maximum potential population growth rate, r_{max} (Hutchings 2001b).

The lack of association between reductions in fishing mortality and rates of recovery 5 years or more after a collapse should not be interpreted as evidence that reduced fishing has no beneficial influence on recovery. Clearly, some populations have responded very favorably to reductions in

Table 1. Variables that are hypothesized to influence the recovery of marine fishes.

Variable	Correlate of recovery	Influence on recovery
Societal response	Rapidity of response	The sooner remedial action is taken following collapse, the greater the recovery of abundance and age structure.
	Probability of reducing fishing mortality to zero	Low for bottom-dwelling or demersal fishes for which bycatch is high; higher for midwater or pelagic fishes (Alverson et al. 1994).
	Scientific folklore	Empirically unsupported perceptions can negatively affect the timing and the nature of the managerial response.
Life history	Age at maturity	Age at maturity is negatively associated with maximum population growth, or r_{max} (Roff 2002), and thus with potential recovery rate (Denney et al. 2002).
	Fecundity	Although very low fecundity (< 100 eggs) is characteristic of species (e.g., elasmobranchs) that have low r_{max} (Musick 1999b), fecundity is otherwise independent of recovery.
	Size at maturity	Large-maturing species have slower recovery rates than do small-maturing species (Denney et al. 2002, Dulvy and Reynolds 2002, Dulvy et al. 2003), given the general link between large size and delayed maturity in fishes (Hutchings 2002).
	Growth rate	Faster potential recovery is associated with rapid individual growth rather than slow individual growth (Denney et al. 2002).
Allee effect (depensation)	Reduced per capita growth rate	Hypothesized but untested causes include increased predation, reduced mating success, and reduced fertilization success at low population sizes, all of which may delay or prevent recovery.
Habitat modification	Pelagic, open-water habitat versus demersal, bottom habitat	If bottom-deployed fishing gear negatively affects essential habitat, pelagic species can be expected to have faster recovery rates than do demersal, bottom habitat species (Hutchings 2000).
Interactions among species	Changes to species assemblages	Reduced abundance of adults can increase interspecific competition and predation experienced by juveniles (e.g., Swain and Sinclair 2000, Walters and Kitchell 2001), thereby delaying or negating recovery.
	Loss of top predators; narrowing of trophic breadth	Reduced abundance of top predators (Hutchings 2000, Baum et al. 2003, Christensen et al. 2003, Myers and Worm 2003) has unpredictable consequences for ecosystems but almost certainly negative consequences for recovery of top predators.
Genetic and evolutionary responses to exploitation	Loss of genetic variation	Reductions in population size are associated with reduced genetic variation, a consequence considered detrimental to recovery (Lande 1993).
	Selection response	Fishing-induced changes to fitness-related traits, such as age and size at maturity, can negatively affect r_{max} (e.g., Hutchings 1999) and negatively influence recovery.

fishing mortality, while others have not (figure 3). Reductions in fishing appear to be necessary, but not always sufficient, for recovery. Several other potential correlates of recovery in marine fishes (table 1) can be identified from the literature and from known or suspected links between various factors and r_{max} .

Societal and managerial responses. Recovery depends on how societies and governments respond to population collapse. This is often a political matter, settled in the usual political ways, with decisionmakers balancing bleak scientific assessments against short-term economic pressures to avoid harsh reductions in fishing. The speed with which managerial action is taken to halt population decline will influence the age and size structure of the population at the time of collapse, both of which can significantly affect recovery. Societal responses to collapse can also be influenced by what might be termed scientific and professional folklore: institutional or

collective beliefs that are based on intuition rather than on peer-reviewed data analysis.

Effective management requires good cooperation with fishers and strong enforcement of rules to force fishers to comply. Fishers often have large debts to pay because of capital investments in fishing boats and gear. As fish stocks decline, the fishers' financial gains per day decline as well. This has the understandable, but environmentally perverse, effect of causing fishers to react strongly against controls on their activities. Arguments about short-term pain for long-term gain tend to fall on deaf ears when times are bad. Furthermore, there is the question of who, exactly, will gain from stringent management measures. Most fisheries involve competition among fishers. The "tragedy of the commons" ensures that longer-term benefits from rebuilding programs may well go to someone else. If that someone else is from another country, fishers can enlist wider public support for their lobbying against controls. Fish population recovery, therefore,

requires institutional structures that either entice fishers to leave the business, through expensive buyout schemes of fishing boats and licenses, or else force them to reduce fishing activities.

Life history. Life-history traits influence recovery because of their intimate association with r_{max} . According to life-history theory (Hutchings 2002, Roff 2002), a high recovery rate should be correlated with low age at maturity, small body size, short life span, and rapid individual growth (Reynolds et al. 2001, Reynolds 2003). These expectations have been borne out by empirical work on marine fishes (Denney et al. 2002, Dulvy and Reynolds 2002, Dulvy et al. 2003). Although rapid recovery has been hypothesized to be associated with high fecundity (Musick 1999a, Powles et al. 2000), this postulate enjoys neither theoretical (Hutchings 2001a, 2001b, Sadovy 2001, Dulvy et al. 2003) nor empirical support (Reynolds et al. 2002). The latter point is underscored by the lack of recovery of some highly fecund fishes, such as Atlantic cod (COSEWIC 2003), and the near extinction of others, such as the Chinese bahaba (*Bahaba taipingensis*; Sadovy and Cheung 2003). Indeed, because there is a positive correlation between body size and fecundity, high fecundity may actually be associated with low recovery potential (Denney et al. 2002).

An important point to bear in mind when considering the links between life history and recovery is that fishing always truncates size and age distributions. Given that fecundity increases exponentially with female weight (McIntyre and Hutchings 2003), populations composed of small individuals will have reduced reproductive potential (Scott et al. 1999) and potentially increased variance in offspring survival (Hutchings and Myers 1993). Furthermore, studies of Atlantic cod have shown that egg size and early survival of larvae are reduced in younger females (Trippel 1998). Together, these effects may conspire to reduce the potential for recovery to a much greater extent than one would predict if changes in size and age structure of populations were ignored.

Genetic and evolutionary responses to exploitation. Most fisheries target some age or size classes within a population over others. Typically, larger, older, faster-growing individuals are more likely to be caught than smaller, younger, slower-growing individuals. Classical population genetics stipulates that only two conditions need be fulfilled for this selectivity to bring about evolutionary change: The mortality experienced by some phenotypes must be sufficiently high and different from that experienced by other phenotypes, and the characteristics that render some individuals more vulnerable than others must be heritable. These conditions are probably fulfilled in many fisheries (Haugen and Vøllestad 2001, Law 2001, Conover and Munch 2002). For example, mortality caused by fishing is usually considerably higher than natural mortality, and it is often biased intentionally toward larger individuals, both because of their increased value and because of management tactics, such as minimum mesh and fish

landing sizes, that increase the chance that smaller fish will be able to breed before being caught. Numerous studies have shown that key traits such as growth rates and body size have significant heritabilities (Roff 2002).

The combination of heritability and strong selectivity appears to have caused evolutionary change in some exploited populations. North Sea plaice (*Pleuronectes platessa*) and Atlantic cod have both shown considerable reductions in age at maturity in the past century (Rijnsdorp 1993, COSEWIC 2003). Cod in some areas have also become smaller at a given age (Sinclair et al. 2002) and are reproducing at smaller sizes than those observed historically (COSEWIC 2003). Although it is difficult to know with certainty that these declines represent genetic change rather than phenotypic plasticity, the argument for evolutionary responses appears to be particularly strong in some cases, including the fishery for Newfoundland cod (Hutchings 1999). For example, in a study of pink salmon (*Oncorhynchus gorbuscha*) in northwestern North America, Ricker (1981) found that 57 of 97 populations underwent a reduction in body size between 1951 and 1975. These fish were caught in size-selective fisheries that caught an average of 80% of the adult population each year. Ricker concluded that the observed reduction in body size could represent an evolutionary response to selection against large individuals if the heritability for size was 0.3, an empirically defensible estimate (Roff 2002). In addition, there were no obvious changes in salinity or temperature, which might affect body size through phenotypic plasticity, during the time of the study. Indeed, the reductions in fish density caused by fishing would, if anything, be expected to produce larger body sizes by reducing competition for food and space.

Reductions in age and size at maturity may affect recovery negatively (Hutchings 2002, Roff 2002). Earlier maturity can be associated with reduced longevity, increased post-reproductive mortality, and smaller sizes at reproductive age. Evolutionary reductions in body size may also lead to the problems mentioned earlier—reduced fecundity, smaller egg size, and increased variance in offspring survival—all of which would be expected to have a negative effect on population growth.

The Allee effect. Slow rates of recovery may be a product of what is known in the fisheries literature as “depensation” and better known throughout the ecological literature as the “Allee effect.” This refers to situations in which rates of population growth per capita decline when population sizes fall below some threshold level of abundance. The existence of an Allee effect has been suggested as one explanation for the relatively slow recovery of Atlantic cod and other marine fishes (Shelton and Healey 1999, Frank and Brickman 2000, Hutchings 2001a, 2001b). For several populations of cod in the Northwest Atlantic, per capita mortality has increased in recent years, possibly because of changes in predator–prey interactions (Smedbol et al. 2002, COSEWIC 2003). Per capita birth rates may also have been affected negatively by

reduced mate availability, lower fertilization success, changes to operational sex ratios, and reduced intensity of social interactions during spawning (Rowe and Hutchings 2003). However, despite increased attention to the Allee effect as a factor responsible for slow recovery rates in marine fishes, a dearth of empirical work stands as a significant barrier to understanding in this area.

Habitat modification. Relative to overexploitation, habitat modification is of secondary (albeit significant) importance as a cause of population decline in marine fishes (Reynolds et al. 2002, Dulvy et al. 2003). Nonetheless, for species not restricted to nearshore or coral reef habitats, bottom trawling may pose a threat to recovery. Repeated dragging of a net in a given area tends to smooth and flatten the bottom, reducing physical heterogeneity (Collie et al. 1997, Kaiser and de Groot 2000). If physical structure is critical to the survival of demersal (bottom-dwelling) marine fishes, notably in the form of plants, physical relief, and corals, then demersal species such as cod may be subjected to greater habitat loss and slower rates of recovery than pelagic species such as herring.

There is no reason to think that fish species should be any more immune than terrestrial species to the impact of accelerating habitat loss. The differences, if there are any, may be that habitat alteration is less visible in the marine environment and, in some cases, that it may be less advanced than the loss of many terrestrial habitats. This is certainly not the case for Caribbean reefs, where there has been an 80% reduction in the area of live coral over the past 25 years (Gardner et al. 2003). We are not aware of any area of forest this size having undergone such a drastic change in such a short time period. Surprisingly little is known about the basic habitat requirements of the vast majority of fish species; this is an area of research that requires considerably more attention than it has received in the past.

Changes to species assemblages and food webs. The past few decades have been witness to extraordinary declines in the abundance of large predatory fishes, a process that has resulted in a “fishing down” of the food chain (Pauly et al. 1998). Studying populations for which at least 20 years of abundance data were available in the Myers database, Hutchings (2000) reported that 42% of the gadid populations, 37% of the scombrid populations (including tunas and mackerels), and 50% of the scorpaenid populations (including redfish, rockfish, and ocean perch) had declined by 80% or more. Baum and colleagues (2003) reported that 15 species of large coastal and oceanic sharks had declined more than 50% in the Northwest Atlantic in the previous 15 years, with some declining 75% or more. Similarly extensive declines over the past 50 years have been reported across a broad range of predatory marine fishes (Christensen et al. 2003, Myers and Worm 2003). Although the overall consequences for recovery of such narrowing of trophic breadth are not known, changes to community structure, in the form of altered predator–prey interactions and changes to interspecific competition, appear to be impeding the recovery of Atlantic cod in Canadian waters.

The collapse of Atlantic cod in Canada

Before assessing the degree to which population collapses such as those documented here and elsewhere might affect extinction risks in marine fishes (see also Reynolds et al. 2002, Dulvy et al. 2003), we will initially limit the discussion to Atlantic cod, a species with unparalleled historical and socioeconomic importance throughout the North Atlantic. After examining genetic, life-history, and demographic data within the empirical and theoretical constructs of recognizing evolutionarily significant units (Waples 1991), COSEWIC assigned status to four cod populations in May 2003. One of these—the Newfoundland and Labrador population—was assigned endangered status (table 2; COSEWIC 2003), mark-

Table 2. Historical and three-generation rates of decline estimated by virtual population analysis for Canadian stocks of Atlantic cod, as reported by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC 2003).

COSEWIC population	COSEWIC status	Atlantic cod stock (current abundance as a percentage of the COSEWIC population)	Three-generation rate of decline (years)
Arctic	Special concern	Not applicable	Insufficient data
Newfoundland and Labrador	Endangered	Northern Labrador cod (2%) Northern cod (95%) Southern Grand Bank cod (3%)	Insufficient data 97% (1968–2001) 98% (1968–2001)
Laurentian North	Threatened	St. Pierre Bank cod (56%) Northern Gulf of St. Lawrence cod (44%)	46% (1968–2001) 93% (1975–2002)
Maritimes	Special concern	Southern Gulf of St. Lawrence cod (82%) Cabot Strait cod (2%) Eastern Scotian Shelf cod (6%) Western Scotian Shelf and Bay of Fundy cod (6%) Georges Bank cod (Canadian portion) (4%)	23% (1973–2002) 95% (1981–2000) 75% (1970–1997) 78% (1979–2002) 70% (1979–2002)

COSEWIC, Committee on the Status of Endangered Wildlife in Canada.

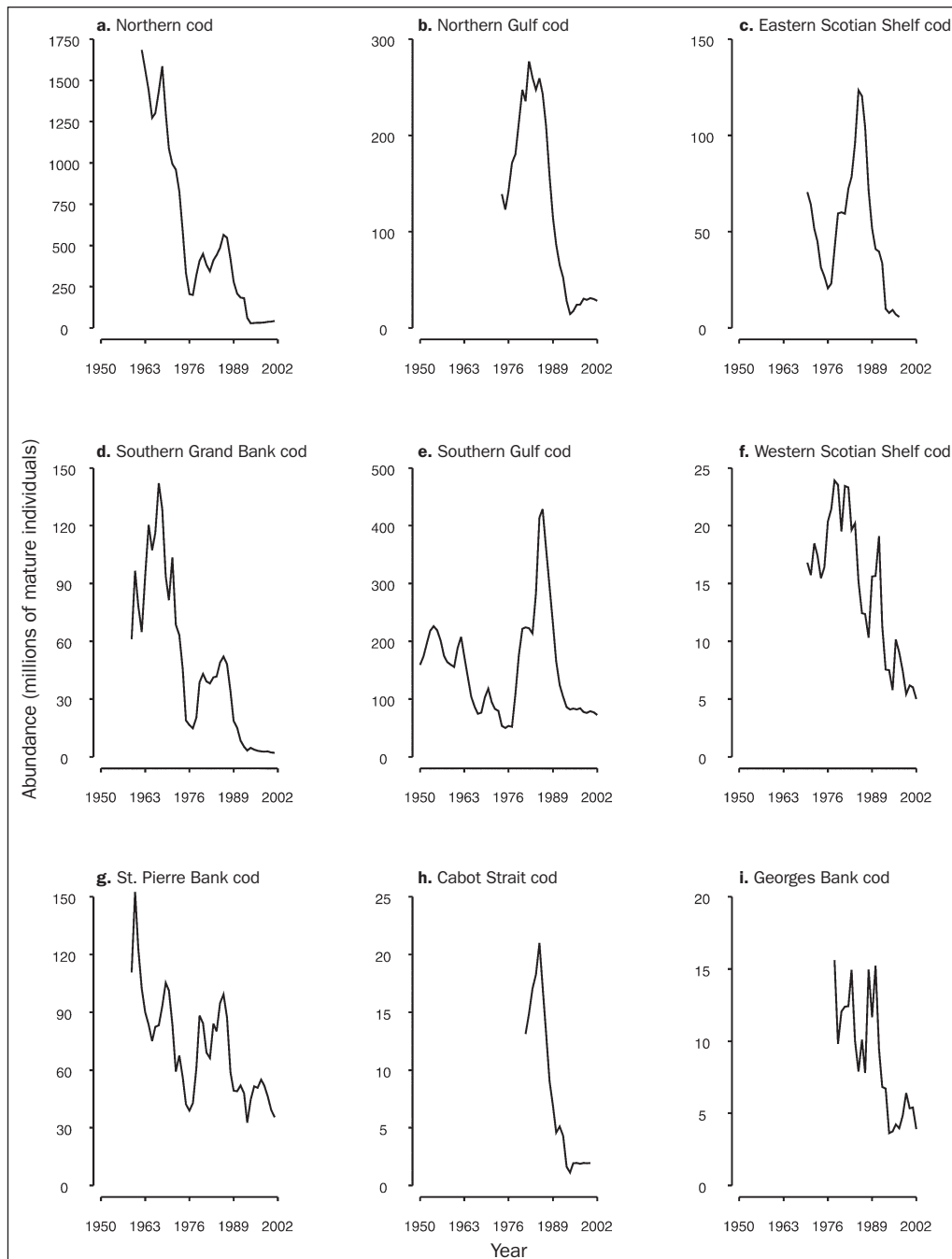


Figure 4. Time series of spawner abundance data for nine Canadian stocks of Atlantic cod (*Gadus morhua*). The stocks, and the alphanumeric NAFO (Northwest Atlantic Fisheries Organization) management units in which they belong, are (a) northern cod, 2J3KL; (b) northern Gulf of St. Lawrence cod, 3Pn4RS; (c) eastern Scotian Shelf cod, 4VsW; (d) southern Grand Bank cod, 3NO; (e) Southern Gulf of St. Lawrence cod, 4T; (f) western Scotian Shelf and Bay of Fundy cod, 4X; (g) St. Pierre Bank cod, 3Ps; (h) Cabot Strait cod, 4Vn; and (i) Georges Bank cod (Canadian portion), 5Ze.

ing the first time that any listing body had recognized Atlantic cod as an endangered species. Three of the four COSEWIC populations were composed of more than one cod management unit, or stock. With the exception of northern Labrador cod, stock-specific abundance data were available for periods

of time ranging from 20 to more than 50 years; these data were based on the outputs of virtual population analysis (VPA) models provided by the Canadian Department of Fisheries and Oceans. Virtual population analysis is a widely used technique for estimating past annual stock sizes and fishing mortality rates; it is based primarily on data from commercial landings, which are calibrated with survey data and combined with estimates of natural mortality.

The collapse of Atlantic cod in Canada has been extraordinary (table 2, figure 4). The greatest decline was experienced by what once was one of the world's most abundant cod stocks. In the early 1960s, the northern cod stock (extending from southeastern Labrador south to the northern half of the Grand Bank) numbered almost two billion breeding individuals and comprised 75% to 80% of Canada's cod (COSEWIC 2003). Over the past three generations, according to VPA estimates of the numbers of cod aged 5 years and older, northern cod have declined by 97% (table 2). According to another source of abundance data—catch rates from fisheries' independent surveys—northern cod have declined by 99.9% since 1983 (COSEWIC 2003).

The primary cause of the reduction in Atlantic cod throughout its Canadian range was overexploitation (Hutchings and Myers 1994, Hutchings 1996, Myers et al. 1997, Fu et al. 2001, Smedbol et al. 2002). In some areas, either reductions in individual growth (attributable to the environment or to size-selective fishing) or increased natural mortality may have exacerbated the rate of decline

(Smedbol et al. 2002, COSEWIC 2003). Identifiable threats to recovery include directed fishing (a consequence of setting quotas), nondirected fishing (a consequence of illegal fishing, catch misreporting, and discarding fish at sea), and bycatch from other fisheries. Additional threats include altered biological ecosystems and concomitant changes to the magnitude and types of species interactions (such as an increase in cod mortality attributable to seal predation; McLaren et al. 2001), all of which appear to have resulted in increased mortality among older cod. Fishery-induced changes to life history, such as trends toward smaller size and earlier age at maturity, may also have reduced population growth rate by reducing longevity and by increasing postreproductive mortality (Beverton et al. 1994, Roff 2002).

Consequences of population decline for risk of extinction

The fact that many marine fishes have experienced unprecedented reductions in abundance is incontestable. There is a lack of consensus, however, on the question of whether rate of decline reflects risk of extinction. The perception that collapsed marine fishes are not at imminent risk of extinction seems pervasive among fisheries managers, who do not seem to appreciate the dramatic influence that relatively small catches can have on the recovery of depleted populations. Further compounding this perception is the near absence of discussion of the effects that declining population size can have on genetic variability, a metric of considerable importance to population persistence.

Population-decline criteria used to assess extinction risk.

Since IUCN listed Atlantic cod as a vulnerable species in 1996, debate has ensued as to whether the criteria that are used to assess extinction risk for terrestrial animals, plants, and freshwater fishes should also be used to assess extinction risk in marine fishes. This debate has included both intuitive arguments in favor of treating marine fishes differently (Musick 1999a, Powles et al. 2000) and empirical analyses suggesting that the extinction probabilities of marine fishes are unlikely to differ from those of other taxa (Hutchings 2000, 2001a, 2001b, Sadovy 2001, Reynolds et al. 2002, Dulvy et al. 2003). From a quantitative perspective, the arguments against treating marine fishes as one would treat other taxa ultimately hinge on the question of how adequately the rates of decline used to assign species to at-risk categories reflect the likelihood that a particular population or species will decline to zero. This is a legitimate question, but it is one that should be asked of all taxa, not just marine fishes.

The criterion in question specifies thresholds for population decline that, if attained or exceeded over the longer of three generations or 10 years, may cause a taxon to be assigned to a particular category of extinction risk. The extinction risk faced by taxa for which "the causes of the reduction [in population size] are clearly reversible AND understood AND ceased" (IUCN 2001; capital letters in original) is assessed

using the following thresholds for rates of decline: 90% (critically endangered, IUCN); 70% (endangered, IUCN and COSEWIC); and 50% (vulnerable, IUCN; threatened, COSEWIC). It is against these three-generation thresholds for rates of decline that one can expect many marine fishes to be assessed. This seems reasonable, when the primary causes of decline and the primary threats to recovery include neither habitat destruction nor invasive species introductions.

Using the population decline and recovery data described previously (figure 2a, 2b), we empirically assessed the utility of these decline-rate thresholds as metrics of extinction by quantifying the probability of recovery to arbitrary, but defensible, levels of abundance. Specifically, for each 15-year rate of decline, we calculated the proportion of populations that, between 5 and 15 years afterward, either recovered to half of their population size at the start of the decline or recovered fully. For some populations, there were no data beyond 5 years after a collapse (figure 5). Among those for which data extended to 15 years after a collapse, it is distressing to note the frequency with which abundance increased 5 years after the collapse only to decline again thereafter.

The data in table 3 suggest that the decline-rate thresholds used by IUCN and COSEWIC to assign status are appropriate, insofar as the probability of recovery is a reliable metric of extinction risk. This is particularly true if clupeids, the family with comparatively high resilience among marine fishes (figure 5a, 5c), are excluded from the analysis. Following 15-year declines of 70% and 90%, only 11% of the nonclupeid fish populations recovered to 50% of their previous size, and none of them recovered to 100% (figure 5b, 5d). Given these low probabilities of attaining very modest levels of recovery, one could argue that there is no compelling reason to discount the population-decline criteria that are currently applied to taxa, including marine fishes, for which neither habitat loss nor species invasions can account for population reduction.

Fishing. Foremost among threats to recovery is fishing. It has proved exceedingly difficult for managers to reduce the fishing mortality of collapsed populations to zero. Even if targeted fishing is banned, with few exceptions (such as schooling pelagic fishes), depleted species continue to be caught as bycatch in other fisheries (Alverson et al. 1994). More troublesome is the reality that closed fisheries tend to be reopened at the first sign of population increase, rather than after the attainment of some target level for recovery.

Some people have termed fisheries for recovering species "limited fisheries" because of their low catch quotas relative to historic levels. However, such a term can be dangerously misleading, given that these fisheries often exact high mortality tolls on depleted populations. For example, although northern cod quotas between 1999 and 2002 were small relative to those set in the mid-1980s (5600 to 9000 metric tons [t] compared with quotas exceeding 200,000 t), the demographic impact was high because abundance was correspondingly low. In 2002, among cod older than 3 years, 20% were estimated to have died as a consequence of fishing;

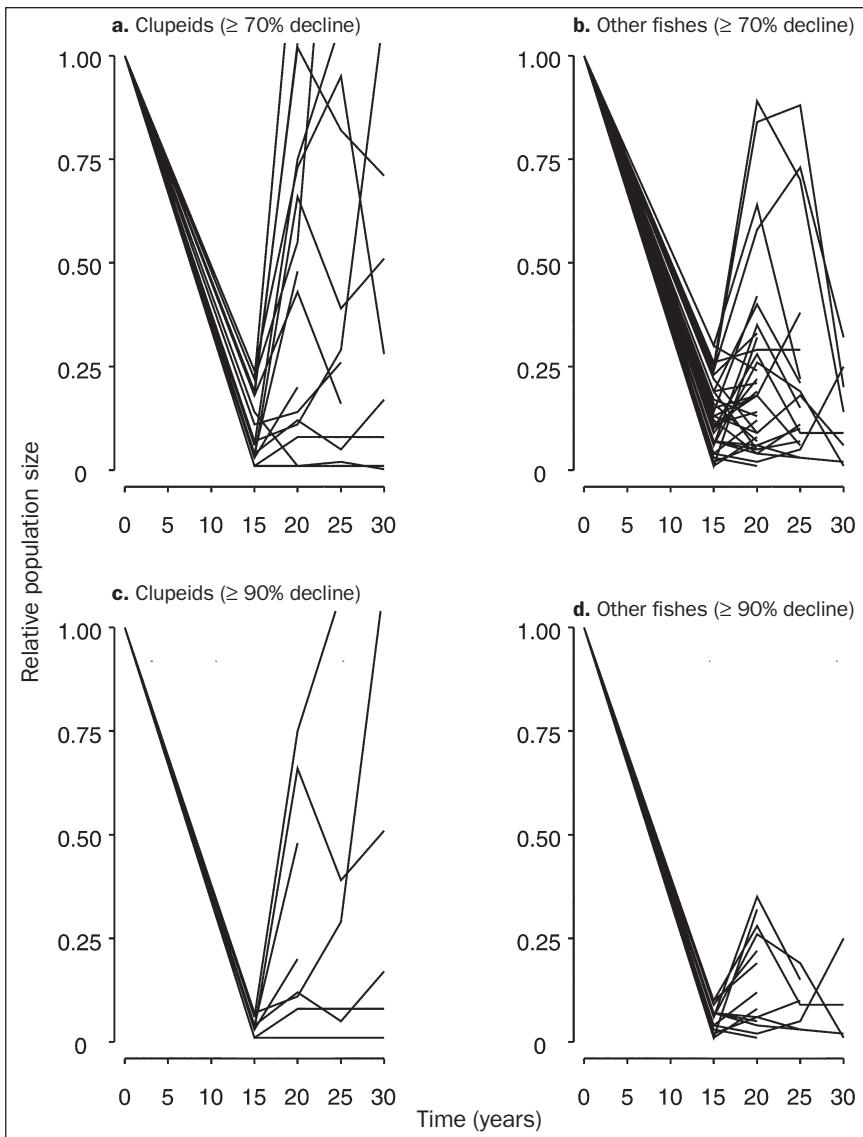


Figure 5. Proportional 15-year population declines ($\geq 70\%$ and $\geq 90\%$) and subsequent recovery of clupeids ([a] $\geq 70\%$ decline, $n = 16$ populations; [c] $\geq 90\%$ decline, $n = 9$) and all other species ([b] $\geq 70\%$ decline, $n = 38$; [d] $\geq 90\%$ decline, $n = 16$). Data are from Hutchings (2000).

among cod older than 5 years, more than 35% were extracted by the fishery (DFO 2003). These exploitation rates exceed the rate (18%) considered sustainable in the 1980s (Hutchings and Myers 1994) and the 10%–20% per annum range in r_{max} estimated for northern cod (Hutchings 1999).

Effective genetic and demographic population size. It might be tempting to downplay or even dismiss suggestions that marine fish populations can become extinct, because fish abundance can remain relatively high despite dramatic rates of decline (e.g., Matsuda et al. 1998). For example, despite having declined 99.9% since the early 1960s, breeding northern cod in the first few years of the 21st century number in the millions (COSEWIC 2003). However, from both a genetic and a demographic perspective, it would be premature to

assume that high levels of abundance in depleted populations will ensure long-term population survival. In fact, the complacency embodied in the “safety in numbers” argument may represent a notable threat to marine fish recovery.

Although abundance can appear high, it is important to acknowledge that census estimates of mature individuals (N_c) do not reflect the actual numbers of individuals that contribute genes during spawning, as reflected by the effective population size (N_e). For broadcast-spawning organisms such as Atlantic cod, it has been estimated that N_e is two to five orders of magnitude lower than N_c because of the increased variance in individual reproductive success associated with this type of mating system (Hedgecock 1994). Empirical support for a similar $N_e:N_c$ ratio has recently come from studies of marine fishes. Estimating N_e from declines in heterozygosity and temporal fluctuations in allele frequency over 46 to 48 years, Hauser and colleagues (2002) concluded that effective population size in the broadcast spawning New Zealand snapper (*Pagrus auratus*) was five orders of magnitude less than the census population size, which numbers in the millions. The effective number of female red drum (*Sciaenops ocellatus*) in the Gulf of Mexico, estimated from both mitochondrial (Turner et al. 1999) and microsatellite DNA (Turner et al. 2002), is 0.001 times that of the female census population size.

The dynamics of small populations are governed largely by the misfortunes of each individual. Thus, in addition to genetic considerations, the viability of a small population is a function of chance realizations of individual probabilities of death and reproduction. These chance events are products of demographic and environmental stochasticity, that is, of unpredictable environmental factors that affect the survival or fecundity of some (in demographic stochasticity) and sometimes all (in environmental stochasticity) individuals in a population (Lande 1993). Small populations may be far more likely to become extinct as a result of demographic or environmental stochasticity rather than as a result of the negative genetic consequences associated with small N_e (Lande 1993, Caughley 1994).

Risks to historically small populations are further exacerbated by the fact that as populations decline, their geographical range tends to decline as well, as individuals seek and remain in the most favorable habitats (Swain and Wade

Table 3. Probability of recovery (over a period of 5 to 15 years) to 50% and 100% of the abundance (N_0) from which marine fish populations experienced their greatest 15-year population decline.

Marine fish species	15-year rate of decline	Number of populations	Probability of recovery	
			to 0.5 N_0	to N_0
All	≥ 50%	77	29%	10%
	≥ 70%	54	22%	11%
	≥ 90%	23	13%	9%
All except Clupeidae	≥ 50%	58	17%	2%
	≥ 70%	38	11%	0%
	≥ 90%	16	0%	0%
Clupeidae (including herring)	≥ 50%	19	63%	37%
	≥ 70%	16	50%	37%
	≥ 90%	7	43%	29%
Gadidae (including Atlantic cod, haddock)	≥ 50%	25	20%	0%
	≥ 70%	19	21%	0%
	≥ 90%	6	0%	0%

Source: Data updated from Hutchings (2000); see also figures 2 and 5.

1993). Such range contractions can increase the risk of exposing collapsed populations to environmentally stochastic events that reduce survival. Again, northern cod provides an instructive example. In early 2003, probably more than 1500 t of mature cod, of which only about 1000 t were retrieved, died in a very small area of Trinity Bay along the northeast coast of Newfoundland (Hoag 2003). Although various causes for the deaths have been hypothesized, an unpredictable oceanographic event that trapped cod in supercooled water may provide the most parsimonious explanation. Irrespective of the cause, given that the entire inshore spawning population of northern cod in 2003 was estimated to be only 14,000 t (DFO 2003), this environmentally stochastic event probably resulted in the death of more than 10% of the inshore breeding population, thus having a disproportionately large influence on population recovery relative to the geographic area over which it took place.

Epilogue

In autumn 2003, the International Council for the Exploration of the Sea (ICES), the body responsible for providing scientific advice to European governments on the status of Northeast Atlantic fishes, concluded that cod in and adjacent to the North Sea were at or near their lowest recorded levels, their breeding populations having declined almost 90% since the 1970s (ICES 2003). Unremittent increases in fishing strongly implicated exploitation as the cause of the collapses (in 2001, two out of every three cod older than 1 year were being caught by the fishery). To restore depleted stocks as quickly as possible, ICES recommended that both targeted and bycatch fisheries for cod be closed. However, these drastic measures will almost certainly not be implemented.

All too often, society seems to lack the collective institutional and political will to prevent the depletion of marine fishes and to resist the temptation to exploit them before they have achieved ecologically meaningful levels of abundance. Canada's

reopening of a targeted fishery for northern cod in 1999 (closed again in 2003), applying pressure on a population that had declined 99.9% and shown no scientifically defensible signs of recovery, serves as one of the more unfortunate examples of a nation's repeated abuse of marine ecosystems.

Equivocal responses by severely depleted marine fishes to reductions in fishing are disquieting. They suggest that restrictions on the only thing that humans can control—fishing, managed by catch or effort limits—are not always sufficient to allow recovery by collapsed populations. The current low population sizes represent uncharted territory in which the scientific capacity to predict future biological dynamics is severely diminished.

The research conducted to date on the collapse, recovery, and extinction risks of marine fishes draws attention to the risks posed to fish and to fisheries by allowing populations to decline to the extraordinarily low levels evident today. Comprehensive recovery strategies require greater understanding of how fish behavior, habitat, ecology, and evolution affect population growth at low abundance. Such strategies also require the managerial fortitude to place long-term conservation benefits to fish and fisheries ahead of short-term political expediency.

The collapse of Newfoundland's northern cod can be considered the marine equivalent of the hunting of buffalo to pitiable levels of abundance. Failure to take the conservation biology of marine fishes seriously will ensure that other similarly depleted species remain ecological and numerical shadows in the ecosystems where they once dominated.

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