



Influence of population decline, fishing, and spawner variability on the recovery of marine fishes

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Based on an analysis of 90 marine fish populations, collapses (the greatest proportional reduction in spawner biomass over 15 years) are predicated typically by dramatic increases in fishing mortality and recoveries are more likely to occur when exploitation is reduced. However, among populations for which fishing mortality declined after collapse, recovery was independent of exploitation rate, even when fishing mortality (F) post-collapse was expressed as a function of each population's maximum growth rate (r). After a period of 15 years, many populations that experienced 15 year declines >60% exhibited little or no recovery, despite considerable reductions in fishing mortality. This suggests that factors other than fishing may be considerably more important to recovery, and fishing less important, than previously thought. Furthermore, among populations for which fishing mortality decreased post-collapse, rate of population decline was a reliable predictor of recovery. With the possible exception of clupeids, variation in marine fish breeding population size was found to differ little from that of other vertebrates, and such variability appears to have no effect on rate of recovery. In addition to providing an empirical framework for the study of population collapse and recovery, the analyses presented here provide a means of assessing the precautionary nature of various population-decline thresholds used to assign extinction risks to marine fish.

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Key words: conservation; collapse; risk criteria; population growth rate; spawning stock biomass.

INTRODUCTION

The conservation status of taxa worldwide is increasingly based on assessments of the degree to which species or populations fulfil various quantitative biological criteria. These criteria specify, among other factors, rates of population decline and reductions in geographical range that, if attained or exceeded, could be sufficient to assign a species or a population to a category intended to reflect an increased risk of extinction. Some agencies, such as the Geneva-based IUCN (World Conservation Union), tend to apply their criteria very strictly, while others, such as Canada's COSEWIC (Committee on the Status of Endangered Wildlife in Canada) and CITES (Convention on International Trade in Endangered Species), tend to use the quantitative criteria as heuristic guidelines rather than strict thresholds.

Irrespective of how these criteria are applied, they share the constraint that they are subjective evaluations of extinction probability that have little, if any, empirical basis for most of the taxa to which they are applied. It is this uncertainty, coupled with a suite of intuitive hypotheses, that has lead many fisheries scientists, resource managers and government bureaucrats to question whether the criteria used by organizations such as IUCN and COSEWIC should be applied to marine fishes.

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Prior to the 1990s, conservation organizations focussed on increased extinction threats faced by large terrestrial mammals, birds, and to a lesser extent freshwater fishes. Increased attention to the conservation status of marine fishes was precipitated by the collapse of Atlantic cod *Gadus morhua* L. and several other groundfish throughout the North Atlantic in the early 1990s (Hutchings & Myers, 1994; ICES, 1994; Myers *et al.*, 1996). In 1996, the IUCN assigned Atlantic cod to its Vulnerable category, the same category to which more than 100 marine fishes have been assigned, including haddock *Melanogrammus aeglefinus* (L.), Atlantic halibut *Hippoglossus hippoglossus* (L.) and whale shark *Rhinocodon typus* Smith (Hilton-Taylor, 2000). Marine fishes in the IUCN's Critically Endangered category include the elasmobranchs Brazilian guitarfish *Rhinobatus horkeli* Müller & Henle and common sawfish *Pristis pristis* L. (Hilton-Taylor, 2000). By comparison, Canada has 'listed' only six wholly marine fishes: spotted wolffish *Anarhichas minor* Olafsen and northern wolffish *Anarhichas denticulatus* (Krøyer) have been designated as Threatened, while Atlantic cod, Bering wolffish *Anarhichas orientalis* Pallas, Atlantic wolffish *Anarhichas lupus* L., and Pacific sardine *Sardinops sagax* (Jenyns) are considered to be of Special Concern (COSEWIC, 2001). Based on criteria considerably different from those used by IUCN and COSEWIC (Musick, 1999), the American Fisheries Society (AFS) recently assigned 167 marine and anadromous fishes to various categories of extinction risk (Musick *et al.*, 2000).

Despite general agreement of the need to identify and protect potentially endangered marine fishes (Reynolds & Mace, 1999), there has been little consensus as to how this should be done. This disagreement would appear to stem from two premises. The first is that extinction probabilities of marine fishes are significantly lower than those of all other taxa. Despite lacking substantive empirical and often theoretical support (Hutchings, 2001), this perception persists based on arguments that low extinction probabilities in marine fishes can be attributed to (1) high fecundity, (2) great variability in population size, and (3) high resilience to population collapse (Musick, 1999; Powles *et al.*, 2000). The second premise is that at-risk criteria should be based solely on extinction risk. Although this constraint is implicit to the definitions of Red List categories used by IUCN (2001), one can question the general utility of focussing attention solely on extinction, rather than recovery to, and persistence at, ecologically meaningful levels of abundance (Hutchings, 2001).

The arguably undue emphasis on extinction has predictably led to critical examinations of the degree to which the criteria used to assign species to at-risk categories adequately reflect the likelihood that a particular population or species will decline to zero. This has been particularly true of marine fishes. One consequence of this is a recent change to the population-decline thresholds applied by the IUCN, notably for commercially harvested taxa. Specifically, these changes will apply to taxa for which 'the causes of the reduction [in population size] are: clearly reversible AND understood AND ceased (upper case letters in original)' (IUCN, 2001). Independently, the AFS has adopted its own population-decline criteria for marine fishes (Musick *et al.*, 2000). The primary difference between the two sets of criteria is the decline threshold required for species to be assigned to the Vulnerable category, being 50% over the greater of

TABLE I. A comparison of population decline criteria adopted by IUCN (World Conservation Union) and the AFS (American Fisheries Society) to assign taxa to at-risk categories. The IUCN criteria are those to be applied to taxa for which 'the causes of the reduction are clearly reversible AND understood AND ceased' (IUCN, 2001). If sufficient data are available, the AFS designations are based on r , the intrinsic rate of natural increase (Musick *et al.*, 2000)

Organization	Risk or threat category	r	Population decline over the greater of 10 years or three generations (%)
IUCN	Critically endangered	—	90
	Endangered	—	70
	Vulnerable	—	50
AFS	Vulnerable	<0.05	70
		0.05–0.15	85
		0.16–0.50	95
		>0.50	99

10 years or three generations for commercially exploited taxa by the IUCN and ranging from 70 and 99% for the AFS (Table I).

The objectives here are three-fold. First, the present study evaluates whether rate of population decline is, to a first approximation, a reliable metric of population recovery. Given the obvious lack of data on actual extinctions, recovery is used as a metric of extinction probability. This is not unreasonable given that increased probability of extinction is logically associated with reduced likelihood of recovery (Hutchings, 2001), and small populations are more vulnerable to extinction than large populations (Lande, 1993). This analysis also requires a consideration of what constitutes an appropriate biological benchmark against which recovery can be assessed. Based on the results of this analysis, the question of whether the population-decline thresholds used by the IUCN and the AFS are likely to provide risk-prone or risk-averse assessments of recovery and extinction probability in marine fishes is addressed. The second objective is to examine the effects of fishing on population recovery. Despite the widely-held, and not unreasonable, perception that a reduction in fishing mortality will bring about stock recovery, this hypothesis has not been empirically examined across a wide range of species. The third objective is to explore the validity of the oft-proposed assertion that (a) marine fishes are more temporally variable than other taxa, and that (b) increased variability is associated with increased potential for recovery after population decline.

MATERIALS AND METHODS

The most comprehensive numerical fisheries database available, maintained by R.A. Myers, Department of Biology, Dalhousie University, Halifax, Canada, at <<http://www.mscs.dal.ca/~myers/welcome.html>>, was used to address the objectives identified above. The data analysed included estimates of spawner biomass and, when available, fishing mortality for each marine fish stock for which a sufficiently long time series (see

below) was available. These data were used to quantify metrics of population decline and recovery for each stock. Specifically, the greatest 15 year percentage decline in spawner biomass experienced by each population was recorded, as were subsequent population sizes 5, 10, and 15 years thereafter. The 15 year interval is short enough to obtain a reasonably large sample of populations, and long enough to be biologically meaningful, approximating for many of the species considered here the three-generation time period specified by the population-decline criterion used by IUCN, COSEWIC, and AFS. For simplicity, the term 'collapse' is used to identify these maximal reductions in spawner biomass experienced by each stock.

After collapse, any increase in population size, N , could be interpreted as some sort of recovery. Graphically, recovery t years after a 15 year decline can be discerned from a plot of $N_{15+t} N_0^{-1}$ on the ordinate against magnitude of population decline on the abscissa, i.e. $(N_0 - N_{15}) N_0^{-1}$ (Fig. 1). On such a plot, populations exhibiting no recovery, i.e. $N_{15+t} = N_{15}$, would fall on a straight line with slope of -1 extending from (0,1) to (1,0) (the solid lines in Fig. 1). Those continuing to decline would fall below this line, while those exhibiting some recovery would fall above this line. Similarly, populations falling on the line with slope of 0 extending from (0,1) to (1,1) (the dashed lines in Fig. 1) would be said to have fully recovered, i.e. $N_{15+t} = N_0$, while those above this second line would have increased relative to the size from which their population declines had begun. These metrics of decline and recovery in spawner biomass have been previously analysed elsewhere (Hutchings, 2000a, 2001).

In addition to trends in spawner biomass, estimates of exploitation rate were examined to quantify fishing mortality prior to and following population collapse. For this analysis, pre-collapse fishing mortality was calculated as the average exploitation rate experienced by a given stock during the 5 years immediately preceding the year of collapse (E_{pre}), while post-collapse fishing mortality was similarly defined as the average exploitation rate experienced by each stock during the t years following the collapse (E_{post}). Thus, stocks for which exploitation rates increased or declined following collapse would be represented by ratios of $E_{post} : E_{pre} >$ or < 1 , respectively.

To compare post-collapse fishing mortality with that which could be considered sustainable for each population, recovery t years following collapse was regressed against the average fishing mortality experienced during those t years relative to that population's estimated maximum rate of growth, i.e. $F r^{-1}$. To estimate r for each population, the exponential population growth model was applied for the 10 year period encompassing the 5 years immediately preceding each collapse and the 5 years immediately following each collapse, that is, the years during which the populations would have been at or near their lowest sizes. Specifically, r was estimated for each year i from the following equation: $N_{i+1} N_i^{-1} = (r_i - F_i) N_i$ where N_i is spawner population size in year i , as approximated by spawning stock biomass. The estimate of r for each population was equal to the average of r_i over the 10 year period.

RESULTS

CAN RECOVERY BE PREDICTED BY RATE OF POPULATION DECLINE?

The question of whether rate of population decline is a reliable metric of stock recovery was initially addressed by Hutchings (2000a). This analysis was based on 90 marine fish stocks (representing 38 species among 11 families) for which data were available at the aforementioned web site for at least a 20 year period (15 years for the collapse, and a 5 year recovery period). Five years after collapse (i.e. maximal 15 year decline in spawner biomass), 37 (41%) of the 90 stocks continued to decline, 46 (51%) exhibited some recovery, while seven (8%) had fully recovered to the spawner biomass from which they had originally declined [i.e. N_0 ; Fig. 1(a)]. Data 10 and 15 years subsequent to each stock's collapse were

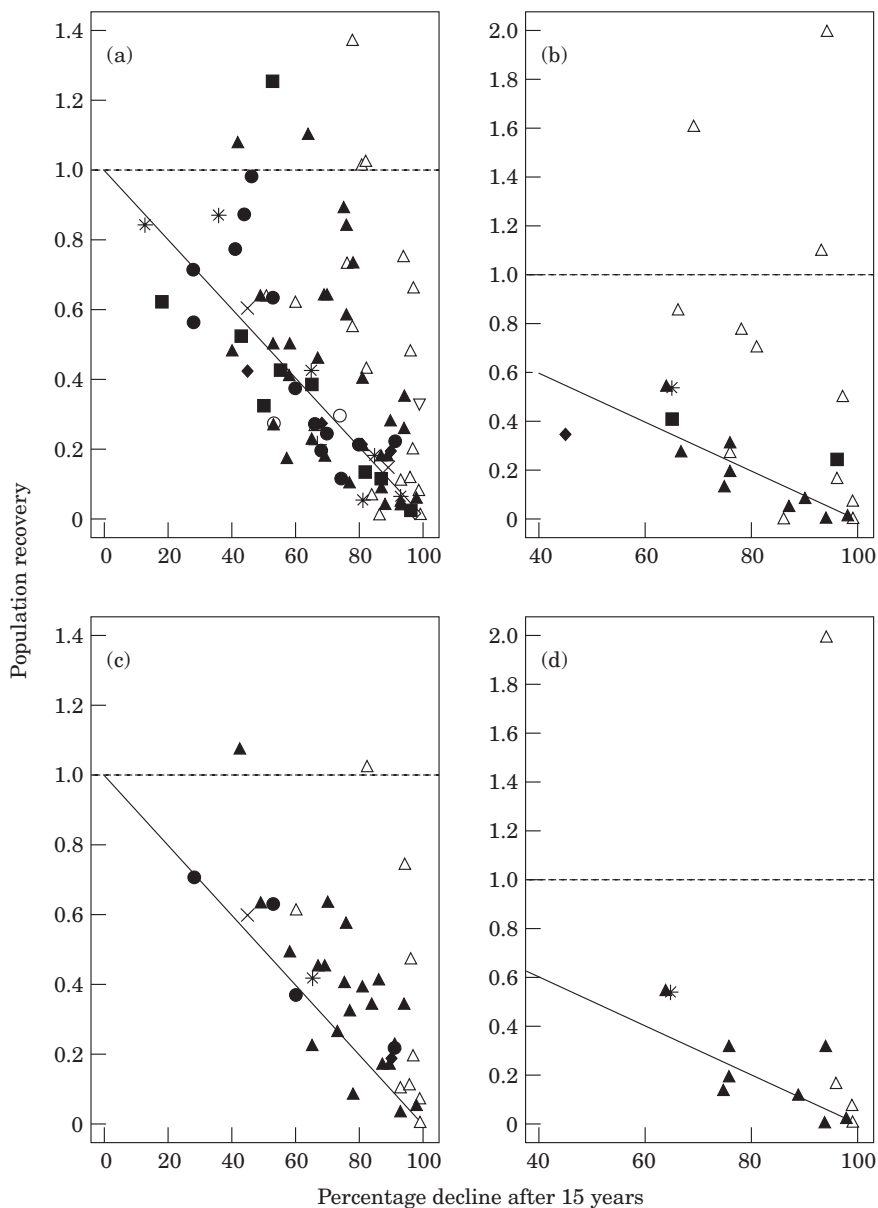


FIG. 1. Bivariate associations between population decline and subsequent population size for marine fish stocks. The ordinate refers to the size of a population 5 years (a),(c) and 15 years (b),(d) after the proportionately largest 15 year decline experienced by that population, relative to its size at the beginning of its 15 year decline. (a), (b) Include data (Hutchings, 2000a) irrespective of changes to fishing mortality post-collapse; (c), (d) include only those populations for which fishing mortality data are available and for which fishing mortality declined post-collapse. Populations that experienced some recovery are represented by points to the right of the solid lines. Fully recovered stocks are represented by points on and above the dashed lines. One datum in (a), a 69% population decline of one clupeid followed by a 1.78 recovery, has been omitted for clarity. \times , Engraulidae; \triangle , Clupeidae; ∇ , Osmeridae; \blacktriangle , Gadidae; $*$, Scorpaenidae; $+$, Anoplopomatidae; \blacklozenge , Sparidae; \diamond , Nototheniidae; \blacksquare , Scombridae; \bullet , Pleuronectidae; \circ , Soleidae.

TABLE II. Regression equations describing mature population size 5 and 15 years following a 15 year population decline relative to the population size (N_0) at the beginning of the decline, (y), as a function of population decline [x , proportional decline in mature fish biomass over a period of 15 years, i.e. $(N_0 - N_{15})N_0^{-1}$]

Recovery period	Family	Regression equation	Number of stocks	P	r
All stocks (Hutchings, 2000a)					
5 year	Clupeidae	$y = 1.78 - 1.48x$	20	0.062	-0.42
	Gadidae	$y = 1.14 - 1.00x$	31	0.003	-0.52
	All	$y = 1.00 - 0.82x$	90	<0.0001	-0.46
15 year	All except Clupeidae	$y = 1.04 - 0.94x$	70	<0.0001	-0.64
	Gadidae	$y = 1.22 - 1.28x$	9	0.002	-0.88
	All	$y = 1.06 - 0.60x$	25	0.58	-0.12
	All except Clupeidae	$y = 0.91 - 0.87x$	13	0.004	-0.74
Stocks for which fishing mortality declined after collapse (present study)					
5 year	Clupeidae	$y = 1.80 - 1.57x$	9	0.122	-0.55
	Gadidae	$y = 1.34 - 1.27x$	21	<0.0001	-0.78
	All	$y = 1.09 - 0.90x$	37	<0.0001	-0.63
	All except Clupeidae	$y = 1.13 - 1.01x$	28	<0.0001	-0.79
15 year	Gadidae	$y = 1.10 - 1.07x$	8	0.045	-0.73
	All	$y = 0.70 - 0.41x$	13	0.74	-0.01
	All except Clupeidae	$y = 1.25 - 1.24x$	9	0.012	-0.79

available for 45 and 25 stocks, respectively; these were comprised primarily of clupeids and gadids (69 and 84%, respectively). Among all stocks, notably when clupeids were excluded from the analysis, the magnitude of decline was negatively associated with population size 10 and 15 years after the declines. Indeed, 15 years after their declines, 12% of marine stocks (all clupeids) had exhibited full recovery while 40% (primarily gadids, but some clupeids) had essentially experienced no recovery at all [Fig. 1(b)].

Based on these results, Hutchings (2000a) concluded that maximal population decline was a reliable metric of population recovery in marine fishes, and that it was not unusual for many fishes to exhibit little or no recovery 10 or 15 years after collapse.

The primary criticism that can be directed at these conclusions is the caveat that the preceding analysis was not restricted to those stocks for which fishing had ceased. However, if one were to apply this criterion, there would be little or no data to analyse. Even after stock declines >90%, various combinations of reduced quotas, discarding, by-catch, high-grading and illegal fishing ensure that exploitation rates of zero are rarely achieved in practice.

Of the 90 stocks originally examined, fishing mortality data were available for only 56. Among these, exploitation rate declined after collapse for 36 stocks. The collapse and recovery of those stocks for which fishing declined post-collapse are shown in Fig. 1(c),(d). Although the number of stocks in the analysis is reduced, relative to that considered by Hutchings (2000a), the conclusions drawn from the previous analysis are, if anything, strengthened, as reflected by higher correlation coefficients for the regressions between recovery and collapse (Table II).

DOES FISHING MORTALITY INFLUENCE POPULATION COLLAPSE OR RECOVERY?

To quantify changes in fishing pressure during the 15 year period of collapse for each stock, the average exploitation rate during the last 5 years of each collapse was compared with the average exploitation rate during the first 5 years of each collapse. Of the 49 stocks for which data were available, 37 (76%) population collapses were associated with an average 99% increase in exploitation rate during the period of decline. Among 14 populations of Atlantic cod, the best-represented species, the collapses of 12 (86%) were associated with an average 48% increase in exploitation rate during the period of decline. It would seem reasonable to conclude that, in general, stock collapses are predicated by substantive increases in fishing mortality.

The question more germane to the present study is whether stock recoveries are influenced by changes to fishing mortality. The strong correlation between population decline and recovery (Table II), and the failure of many stocks to recover rapidly after collapse (Fig. 1), may be attributable to the fact that those stocks that recover slowly are those for which fishing mortality has remained high, relative to that experienced prior to collapse. This can be evaluated by testing the hypothesis that stock recovery is negatively associated with post-collapse fishing mortality, relative to pre-collapse fishing mortality, i.e. $E_{\text{post}} : E_{\text{pre}}$.

There are three general points that can be drawn from this analysis. First, there is no association between fishing mortality and stock recovery 5 years post-collapse, whether one includes all the data ($r = -0.24$, $P = 0.083$) or only those for which fishing mortality declined following collapse ($r = 0.10$, $P = 0.70$) [Fig. 2(a)]. The same lack of association between post-collapse fishing mortality and recovery is evident 10 ($r = -0.12$, $P = 0.561$, $n = 27$) and 15 years ($r = -0.02$, $P = 0.958$, $n = 14$) post-collapse. Second, the average 5-year recovery among stocks for which fishing mortality was reduced following collapse (0.39 ± 0.04 s.e.) was greater, although not significantly so ($P = 0.167$), than it was among those for which fishing mortality remained constant or increased (0.29 ± 0.05 s.e.).

Third, irrespective of fishing mortality, populations that declined $<50\%$ over 15 years had a significantly greater average recovery 5 years post-collapse (0.67 ± 0.08 s.e.) than those that had declined 50–79% (0.38 ± 0.03 s.e.; $F_{1,29} = 14.68$, $P = 0.001$) and those that had declined more than 80% (0.24 ± 0.05 s.e.; $F_{1,30} = 18.37$, $P < 0.0001$) [Fig. 2(b)]. The stocks in the latter two categories also differed significantly from one another ($F_{1,47} = 5.22$, $P = 0.027$). Again, comparing stocks for which fishing had declined after collapse with those for which fishing remained unchanged or increased after collapse, recovery was greater among the former for stocks that had declined $<50\%$ (recovery: 0.76 ± 0.11 v. 0.56 ± 0.11), 50 to 79% (0.42 ± 0.05 v. 0.32 ± 0.05), and 80% or more (0.28 ± 0.06 v. 0.11 ± 0.04), although none of these differences was statistically significant.

Fishing then appears to be the primary factor responsible for population declines. Although stock recovery almost certainly depends on a reduction in fishing mortality, recovery appears to be independent of the magnitude of this reduction.

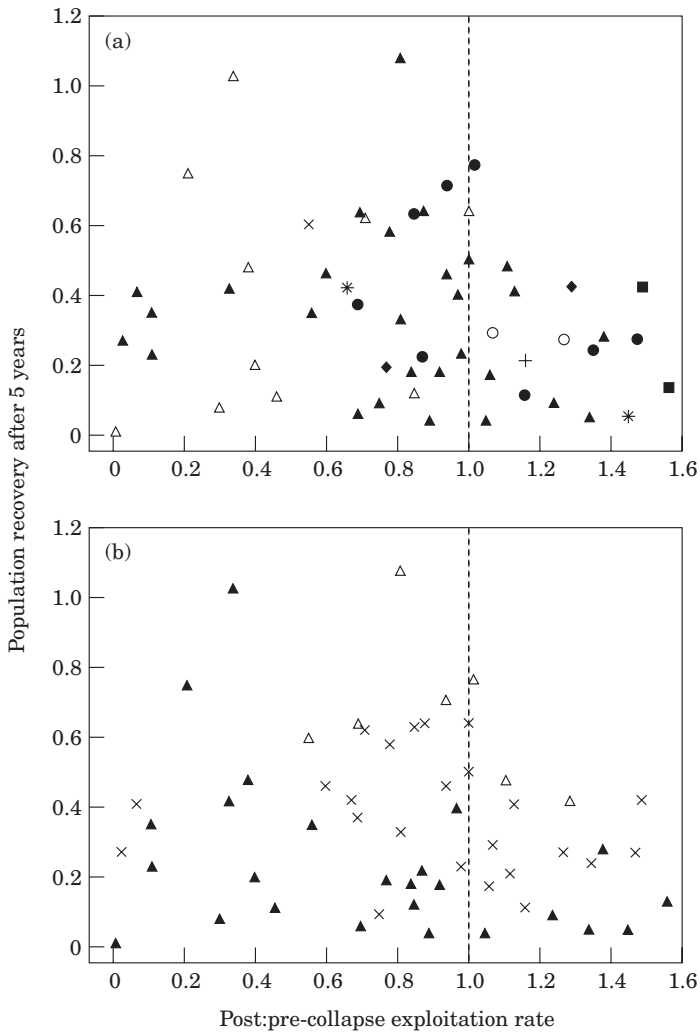
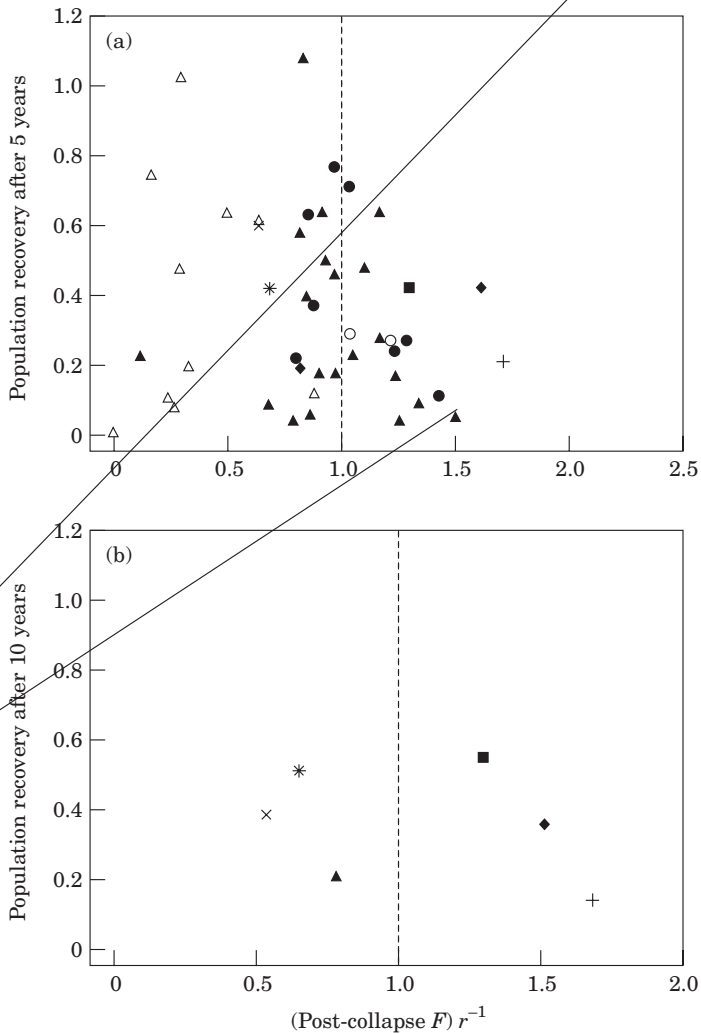


FIG. 2. Population recovery 5 years after the proportionately largest 15 year decline by that population as a function of exploitation rate following collapse relative to that prior to collapse. Fishing mortality post-collapse declined and increased for populations to the left and right of the dashed lines, respectively. (a) Symbols are those defined in Fig. 1; (b) Δ , collapse <50%; \times , collapse between 49 and 80%; \blacktriangle , collapse >79%.

One potential shortcoming of the previous analysis is that although exploitation rate might have declined for a particular stock, the level of fishing mortality may still be in excess of what that stock can sustain, i.e. F may be $> r$. However, even when one plots recovery against F , as a function of r (Fig. 3), the conclusion that recovery is independent of fishing mortality post-collapse remains. None of the correlation coefficients for the regressions between recovery and (Fr^{-1}) is significant (5 year recovery period: $r = -0.22$, $P = 0.13$, $n = 48$; 10 year recovery period: $r = -0.13$, $P = 0.15$, $n = 25$; 15 year recovery period: $r = -0.23$, $P = 0.47$, $n = 12$).



IS THE METRIC OF RECOVERY BASED ON SPAWNER BIOMASS UNDULY STRINGENT?

Population recovery has been defined here relative to the highest spawner biomass observed during a stock's maximal 15 year percentage decline. It could be argued that such a benchmark is unduly stringent, and that it is not at all surprising that few stocks approach or attain full recovery after collapse. The premises underlying this argument are that (1) spawner biomass is naturally extraordinarily variable, (2) the highest spawner biomass during a stock's maximum 15 year decline is likely to be the greatest ever experienced by that stock, and, combining these two assertions, (3) the greatest spawner biomass ever experienced by a given stock is likely to be significantly higher than any other

experienced by that stock. If these assertions were true, one could indeed argue that the spawner biomass benchmarks used here to identify full recovery are too high.

To examine this proposition, each of the three premises identified above was addressed separately. The first will be examined in the following section. The second can almost certainly be dismissed for most, if not all, of the stocks considered here because of the long period of time during which these stocks have been fished relative to the period of time during which data on spawner biomass have been estimated. None of the stocks for which data are available were virgin, unfished stocks at the time when spawner biomass data first became available. Thus, it seems likely that the highest documented spawner biomass for a given stock is almost certainly less than the highest spawner biomass ever experienced by that stock.

The third premise can be examined empirically by comparing the highest spawner biomass observed during each stock's maximum, 15 year decline (hereafter, the spawner biomass benchmark, or N_0) with the highest spawner biomass ever estimated for that stock, N_{\max} . For the 90 stocks examined here, the spawner biomass benchmark was, on average, $81.4 \pm 0.1\%$ that of the maximum observed spawner biomass. Within the two families for which most data were available, the clupeid spawner benchmarks were $70.1 \pm 0.1\%$ ($n=20$) of their observed maxima, while those of the gadids were $75.3 \pm 0.1\%$ ($n=31$) of their observed maxima. Within species, spawner benchmarks for herring and cod were $67.9 \pm 0.1\%$ ($n=16$) and $63.5 \pm 0.1\%$ ($n=17$) of their respective maxima.

Irrespective of the magnitude of the spawner biomass benchmark, one can ask whether there is any association between this benchmark and population recovery. The argument is that populations having a benchmark close to one may be less likely to exhibit recovery than those for which the benchmark is considerably <1 . For the 90 stocks of marine fish analysed here, 5 year recovery is negatively associated with spawner biomass benchmark ($P=0.002$), although the explained variation is very low ($r^2=0.10$; Fig. 4). However, within all families but the Scombridae, there is no correlation between recovery and spawner biomass benchmark (Clupeidae: $r^2=0.05$, $P=0.181$, $n=20$; Gadidae: $r^2=0.01$, $P=0.391$, $n=31$; Scombridae: $r^2=0.68$, $P=0.004$, $n=9$; Scorpaenidae: $r^2=0.21$, $P=0.20$, $n=6$; Pleuronectidae: $r^2=0.24$, $P=0.06$, $n=12$). And within the Scombridae, one population [eastern Pacific yellowfin tuna *Thunnus albacares* (Bonnaterre)] is responsible for the statistical significance of the association. When that population is excluded from analysis, the association between spawner biomass benchmark and recovery within the Scombridae is not significant ($r^2=0.02$, $P=0.50$, $n=8$).

There would seem, then, little basis for the argument that the spawner biomass benchmarks used here and elsewhere (Hutchings, 2000a, 2001) to identify full recovery are unduly stringent benchmarks that ought not to be applied in practice.

IS POPULATION VARIABILITY A RELIABLE METRIC OF RECOVERY?

One of the fundamental perceptions concerning marine fishes, and perhaps the one most dominant in discussions of extinction risk, is that they are far more variable than other taxa and that this increased variability confers rapid ability

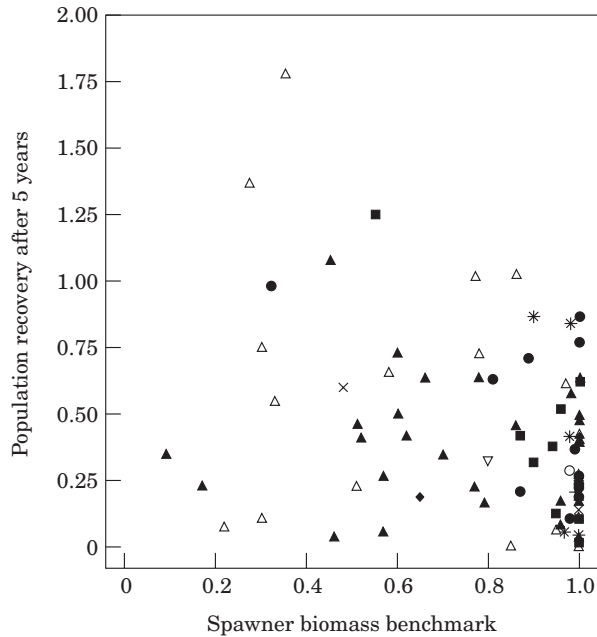


FIG. 4. Population recovery 5 years after collapse as a function of the spawner biomass benchmark, i.e. the spawner biomass at the beginning of a stock's maximum 15-year proportional decline divided by the highest spawner biomass ever documented for that stock. The families corresponding to each symbol are given in Fig. 1.

to recover from collapse and conversely reduced probability of extinction (Musick, 1999; Powles *et al.*, 2000). Recruitment can indeed be highly variable in marine fishes (Cushing, 1996). But, as noted by Hutchings (2001), it is not recruitment variability that is important when assessing risks of extinction but variability in the size of the breeding part of the population. The premise identified above then leads to two questions: (1) does natural variability in breeding population size of marine fishes exceed that of other taxa and (2) is increased variability in spawner biomass associated with increased ability to recover from population collapse?

Perhaps the simplest metric of variation in the size of the mature part of any population, and the one for which data are most likely to be available, is the ratio of maximum to minimum size, i.e. ($N_{\max} : N_{\min}$). For the 90 fish stocks analysed here, the back-transformed mean of the \log_{10} -transformed ratios is 13.0 ± 1.2 s.e. That is, on average, the maximum spawner biomass for a population of marine fish is 13 times greater than the minimum.

However, as revealed by a comparison among families, this average is greatly influenced by the Clupeidae ($n=38$ stocks), for which maximum spawner biomass is 14.2 ± 1.4 s.e. times that of the minimum. The clupeids are almost twice as variable as the gadids and the scombrids, for which the $N_{\max} : N_{\min}$ ratio averaged 8.2 ± 1.2 s.e. ($n=36$) and 7.6 ± 1.6 s.e. ($n=12$), respectively. Within the two remaining families for which sufficient data are available, maximum spawner biomass is four to five times greater than the minimum: Scorpaenidae (4.9 ± 1.4 , $n=9$), Pleuronectidae (4.6 ± 1.2 , $n=24$).

A preliminary comparison of $N_{\max} : N_{\min}$ ratios suggests that, with the exception of clupeids, temporal variability in marine fish breeding population size may not differ appreciably from that experienced by other taxa. For example, there are many species of birds and terrestrial mammals for which $N_{\max} : N_{\min}$ is considerably greater than the range of 4–8 reported for marine fish families (excluding the clupeids). Among birds, the most extreme differences in breeding population size may be those of the medium ground finch *Geospiza fortis* Darwin and cactus finch *Geospiza scandens* Gould on the Galapagos Islands, for which the maxima are 102 and 58 times higher than their respective minima (Grant & Grant, 1992). Included among the many bird species for which there is a greater than 10-fold range in breeding population size are the song sparrow *Melospiza melodia* Wilson (Smith *et al.*, 1991), tits *Parus* spp. (Lack, 1954; McCleery & Perrins, 1985), garden warbler *Sylvia borin* Boddaert and redpoll *Carduelis flammea* L. (Enemar *et al.*, 1984), and the prairie chicken *Tympanuchus cupido* L. (Westemeier *et al.*, 1998). Among mammals for which maximum population breeding size exceeds the minimum by more than one order of magnitude are moose *Alces alces* L. (Mlot, 1993; Krohne, 2001), lynx *Lynx canadensis* Kerr and snowshoe hare *Lepus americanus* Erxleben (MacLuilch, 1937), house mice *Mus musculus* L. (Pearson, 1963), and collared lemmings *Dicrostonyx groenlandicus* Traill (Shelford, 1945).

One important caveat to be drawn from this comparison is the fact that the data for marine fishes over-estimate the natural variability in breeding population size in these species. By contrast, only the snowshoe hare and lynx data among the birds and mammals mentioned here are known with certainty to have been influenced by harvesting.

The second question posed above can be addressed by testing the hypothesis that variability in spawner biomass is positively associated with population recovery. If variability in spawner biomass *per se* confers resilience, one would expect a positive association between $N_{\max} : N_{\min}$ and population recovery. Instead, one finds a significantly negative correlation between the ratio of maximum to minimum spawner biomass and recovery 5 years post-collapse ($r^2=0.13$, $P<0.0001$, $n=90$).

DISCUSSION

There are three general conclusions that can be drawn from the foregoing analyses. The first is that rate of population decline is a defensible and empirically reliable metric of rate of population recovery. Second, recovery appears to be independent of the degree to which fishing mortality is reduced following collapse, although an increase in exploitation rate almost certainly reduces the probability of recovery, and thirdly, there is no empirical support for the assertion that increased variability in spawner biomass is associated with increased resilience; in fact the opposite may well be true.

Rate of population decline has been one of the primary criteria used to identify marine fishes whose persistence may be imminently threatened (Table I). Based on analyses similar to those conducted here (Hutchings, 2000a), it was concluded that 15 year declines of 50 and 80% were reliable predictors of recovery within a 5 or 15 year period. Given the logical association between recovery and

extinction probability, [Hutchings \(2000a\)](#) suggested that arbitrary changes to population-decline criteria for marine fishes, particularly in the absence of empirical analysis, would not be precautionary. One of the objectives of the present paper was to address criticisms that this previous analysis has received: (a) the effects of fishing on recovery were not accounted for; (b) the spawner biomass benchmark used to indicate full recovery was too stringent; (c) there was no attempt to account for the extraordinary variability of marine fishes, and the presumed positive influence of such variability on resilience. Given the lack of empirical support for these criticisms reported here and elsewhere ([Hutchings, 2001](#)), [Hutchings' \(2000a\)](#) conclusion regarding the utility of the 50 and 80% population-decline thresholds does not appear unreasonable.

Recovery may not depend on the magnitude of reduction in fishing mortality. Given the myriad direct and indirect effects of fishing on marine ecosystems ([Pauly *et al.*, 1997](#); [Jennings & Kaiser, 1998](#)), the potential for Allee effects at small population size ([Liermann & Hilborn, 1997](#); [Frank & Brinkman, 2000](#)), and the difficulty in predicting the responses of fish populations even to potentially large changes in mortality ([Yodzis, 2001](#)), perhaps such a result is not surprising. Indeed, such a finding is consistent with the observation that many fish stocks have failed to recover after extended periods during which directed fishing for the stock in question ceased ([Sadovy, 2001](#)). Most Canadian stocks of Atlantic cod, for example, have not shown substantive signs of recovery almost a decade after cessation of targeted commercial fishing activity. The independence of fishing mortality and recovery suggested here implies that while a reduction in exploitation rate following collapse should halt population decline, such a management response may often be insufficient to ensure population recovery.

The finding that variability in spawner biomass, reflected by the ratio of maximum to minimum breeding population size, is not positively associated with population recovery runs counter to intuitive arguments presented elsewhere ([Musick, 1999](#); [Powles *et al.*, 2000](#)). This may be because the metric of spawner variability used here was inappropriate, or that such a relationship simply does not exist. It also appears that the widely-held perception that marine fishes are more variable than terrestrial vertebrates merits detailed empirical analysis and perhaps re-evaluation.

The data presented here have the potential to provide a quantitative element, lacking in the past, to the implicit predictive capability associated with risk assessments undertaken by agencies such as IUCN, COSEWIC and AFS. For example, when taxa are assigned to at-risk categories based on the population-decline criterion, it would be useful if such categories could then be associated with estimates of the future status of such taxa. Using the regressions presented in [Table II](#), one can estimate the magnitudes of population recovery 5 and 15 years post-collapse for the population-decline thresholds proposed or applied by IUCN and AFS. (Given the apparent difference in the resilience of clupeids, an observation that merits study in its own right, the regressions used here excluded this family.)

Perhaps the most parsimonious interpretation of the results of this exercise is that, after a 15 year decline, the breeding population size of the taxon under study can be expected, on average, to remain unchanged or to experience a

TABLE III. Predicted population sizes of marine fish stocks 5 and 15 years after 15 year declines, ranging from 50 to 99%, that correspond to the IUCN's proposed and the AFS's current population-decline criteria for marine fishes. The regressions used to predict future population size following collapse are those in Table II for all stocks (irrespective of changes to fishing mortality) and for those stocks for which fishing mortality declined after collapse

Organization	Collapse Maximum 15 year population decline (%)	No change	Recovery			
			5 years post-collapse		15 years post-collapse	
			All	Fishing declined	All	Fishing declined
AFS	99	0.01	0.11	0.13	0.05	0.02
AFS	95	0.05	0.15	0.17	0.08	0.07
IUCN	90	0.10	0.19	0.22	0.13	0.13
AFS	85	0.15	0.24	0.27	0.17	0.20
AFS, IUCN	70	0.30	0.38	0.42	0.30	0.38
IUCN	50	0.50	0.57	0.62	0.48	0.63

modest increase 5–15 years thereafter (Table III). For example, if a stock experienced a 70% decline over three generations (the IUCN's Endangered criterion likely to be applied to exploited fishes), and if it was known with certainty that the fishing mortality (targeted or incidental) experienced by that stock had declined, the spawner biomass of that stock 5–15 years later would be expected to have increased to *c.* 40% of the spawner biomass from which the 15 year decline began.

Given the associations between collapse and recovery documented here, the population-decline criteria proposed by IUCN would seem reasonable and precautionary, particularly if one finds substance in the argument that there is more to conservation than the assessment of extinction (Hutchings, 2001). By contrast, assuming the regressions presented have some predictive value, it would be difficult to interpret the higher decline thresholds adopted by the AFS as being risk-averse. Rather, by establishing higher population-decline thresholds, the AFS may be unintentionally accepting lower population sizes, at which marine fishes would persist for longer periods of time, before such species were deemed to be at risk. This may be unwise from a multi-species, ecosystem-based perspective of conservation. A second difficulty with the AFS categories lies in their association with estimates of r (Table I). Theoretically, this association makes eminent sense, r being inversely associated with extinction probability. Practically, however, one runs the risk of presuming levels of accuracy and precision in estimates of r that simply do not exist. For example, the standard errors associated with many recent estimates of maximum population growth rate for marine fishes (Myers *et al.*, 1999) overlap the differences in r within and among the AFS's four categories of productivity (Table I), reducing significantly the accuracy with which species (let alone populations within species) could be assigned to productivity categories, and population-decline thresholds, based on r .

The present study is one of a series (Hutchings, 2000a, b, 2001; Sadovy, 2001; R. A. Myers & J. A. Hutchings, unpubl. data) that examines the empirical basis for the perception that extinction probabilities of marine fish differ from those of other vertebrates, if not all other taxa. To date, this body of work has provided evidence that: (1) marine fishes may be no more likely to experience large, natural reductions in population size than non-marine fishes (Hutchings, 2001); (2) variation in breeding population size of marine fish may not differ appreciably from that of other vertebrates (present study, unpubl. data); (3) high variability in spawner biomass may not be associated with faster recovery rates (present study); (4) marine fish (with the possible exception of clupeids) do not typically recover rapidly after collapse (Hutchings, 2000a; Sadovy, 2001), even following a reduction in fishing mortality (present study); (5) high fecundity is not associated with rapid population recovery (Hutchings, 2000b, 2001; Sadovy, 2001); (6) marine fishes may have slower recovery rates than non-marine, anadromous salmonids (Hutchings, 2001).

The value of this research lies not in the degree to which it accurately depicts reality, but in the degree to which it encourages others to assess its veracity. The motivation for such research is predicated upon the extraordinary ignorance of the factors that affect recovery rates in marine fishes. Complicating this scenario considerably is the distinct possibility, suggested here, that the one factor presumed to have been understood, fishing, may be of considerably less importance to recovery than previously thought. Until empirical analyses suggest otherwise, it would be prudent and precautionary to assume that marine fishes do not differ from other taxa with respect to their vulnerability to extinction.

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