Conservation biology of marine fishes: perceptions and caveats regarding assignment of extinction risk

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Abstract: Quantitative criteria used to assign species to categories of extinction risk may seriously overestimate these risks for marine fishes. Contemporary perception is that marine fishes may be less vulnerable to extinction than other taxa, because of great natural variability in abundance, high fecundity, rapid population growth, and an intrinsically high capability of recovering from low population size. Contrary to perception, however, there appears to be generally little theoretical or empirical support for the hypotheses that marine fish are more likely to experience large reductions in population size, to produce unusually high levels of recruitment, to have higher reproductive rates, or to recover more rapidly from prolonged population declines than nonmarine fishes. Although existing population-decline criteria may not accurately reflect probabilities of biological extinction, they do appear to reflect the converse—population recovery. Insufficient support for contemporary perceptions of their susceptibility to extinction, coupled with caveats associated with the assignment of extinction risk, suggest that significant increases in the population-decline thresholds used to assign marine fishes to at-risk categories would be inconsistent with a precautionary approach to fisheries management and the conservation of marine biodiversity.

Résumé : Il est possible que les critères quantitatifs qui servent à placer les espèces de poissons marins dans les diverses catégories de risque d'extinction surestiment grandement ces risques. On croit couramment que les poissons marins courent moins de risques d'extinction que les autres taxons, à cause de la grande variation dans leurs densités, de leur forte fécondité, de leur croissance démographique rapide et de leur habileté intrinsèque marquée à récupérer après un déclin de densité. Cependant, contrairement à ce que l'on pense, il a peu de fondements théoriques ou empiriques aux hypothèses selon lesquelles les poissons marins sont plus sujets à de fortes réductions de densité que les poissons non-marins, que leur recrutement peut atteindre des valeurs exceptionnellement élevées, que leurs taux de reproduction sont plus élevés et que leur récupération après un déclin est plus rapide. Bien que les critères actuels de déclin des populations ne reflètent pas correctement la probabilité d'extinction biologique, ils semblent mettre en lumière l'inverse, soit la récupération des populations. Puisque les perceptions courantes de la susceptibilité des poissons marins à l'extinction ne sont pas assez solidement démontrées et compte tenu des mises en garde inhérentes à l'établissement du risque d'extinction, un relèvement substantiel des seuils de déclin de population établis pour les diverses catégories de risque serait incompatible avec une attitude prudente dans l'aménagement des pêches et la conservation de la biodiversité marine.

[Traduit par la Rédaction]

Introduction

Worldwide overexploitation of commercially harvested fishes raises the question of whether the often spectacular declines in abundance associated with fishery collapses have significantly increased the extinction probability of targeted (e.g., Atlantic cod, *Gadus morhua*; IUCN 1996) and incidentally harvested (e.g., barndoor skate, *Raja laevis*; Casey and Myers 1998) marine species (Reynolds and Mace 1999; Roberts and Hawkins 1999; Musick et al. 2000). This is reflected in part by the work of national and international agencies responsible for assigning risk or threat categories to potentially endangered taxa. In 1996, the International Un-

ion for the Conservation of Nature (IUCN) assigned Atlantic cod to their "vulnerable" threat category (IUCN 1996). The same status was applied 2 years later in Canada by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Shank 1999). By the end of the 20th century, marine fishes designated as vulnerable by IUCN included haddock, *Melanogrammus aeglefinus*; Atlantic halibut, *Hippoglossus hippoglossus*; and yellowtail flounder, *Pleuronectes ferrugineus*. In addition to Atlantic cod, COSEWIC identifies Bering wolffish, *Anarhichas orientalis*, and Pacific sardine, *Sardinops sagax*, as marine fishes of "special concern" (as of May 2000, this term replaces the vulnerable category; COSEWIC 2000) (Shank 1999).

However, some criteria applied by national and international agencies responsible for assigning risk categories (Table 1) may significantly overestimate extinction threats to marine fishes and should, perhaps, be modified significantly to account for perceived differences between marine fishes and the other taxa to which these criteria are regularly applied, for example, plants, mosses, lichens, terrestrial ani-

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Table 1. Summary of the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and the International Union for the Conservation of Nature (IUCN) risk categories and criteria. For interpretation guidelines, refer to IUCN (1999).

Criteria A through F	Critically endangered (IUCN)	Endangered (IUCN/COSEWIC)	Threatened (COSEWIC) / Vulnerable (IUCN)
A. Declining population:			
a population decline rate, in 10 years or 3 generations, of at least	80%	50%	20%
B. Small distribution and decline or fluctuation:			
either extent of occurrence (km^2) of	<100	<5000	<20 000
or area of occupancy (km^2) of	<10	<500	<2000
and two of the following three:			
1. *either* severely fragmented into isolated populations with a low probability of recolonisation, if once extinct; *or* known to exist at locations numbering	1	≤5	≤10
2. continuing decline at any rate *in any of the following*:			
a. extent of occurrence			
b. area of occupancy			
c. area, extent, and (or) habitat quality			
d. number of locations or populations			
e. number of mature individuals			
3. a greater than 10-fold fluctuation *in any of the following*:			
a. extent of occurrence			
b. area of occupancy			
c. number of locations or populations			
d. number of mature individuals			
C. Small population size and decline:			
number of mature individuals	<250	<2500	<10 000
and one of the following two:			
1. decline rate of at least	25% in 3 years or 1 generation	20% in 5 years or 2 generations	10% in 10 years or 3 generations
2. continuing decline at any rate and			
either (*a*) fragmented with numbers of mature individuals in all populations of	≤50	≤250	≤1000
or (*b*) all mature individuals existing in a single population			
D. Population very small or restricted:			
either (1) the number of mature individuals is	<50	<250	<1000
or (2) the population is susceptible[†]	na	na	
E. Quantitative analysis:			
indicating the probability of extinction in the wild to be at least	50% in 10 years or 3 generations	20% in 20 years or 5 generations	10% in 100 years
F. Rescue-effect adjustment[‡]:			
if there is significant and on-going immigration from cross-border populations, downlist one category			

*Species and populations of Special Concern are those deemed particularly sensitive to human activities or natural events but are not Endangered or Threatened (COSEWIC 2000).

[†]For the threatened (COSEWIC) and vulnerable (IUCN) categories, the criterion is area of occupancy <100 km^2 or number of locations <5.

[‡]Used only by COSEWIC.

mals, and nonmarine fishes. It has been suggested that, because of their perceived great natural variability in abundance, high fecundity, rapid population growth, and remarkable ability to recover from population collapse, marine fishes may be less vulnerable to extinction than other taxa (e.g., Hudson and Mace 1996; Matsuda et al. 1997; Musick 1999; but see Carlton et al. 1999). Indeed, there appears to be nothing intrinsic to exploited marine fishes to prevent them from increasing at low population sizes (Myers et al. 1995*a*), although the generality of the conclusion that per-capita reproductive success increases at low population lev-

els may not be as widespread as previously thought (Leirmann and Hilborn 1997; Shelton and Healey 1999; Frank and Brickman 2000).

My purpose here is to explore the theoretical and empirical bases underlying contemporary perceptions of the resilience of marine fishes to population collapse, relative to nonmarine taxa. The paper was motivated by several factors, including: (*a*) proposed national endangered-species legislation in Canada, (*b*) increased concern that extinction threats to marine species merit attention (Carlton et al. 1999; Roberts and Hawkins 1999; Musick et al. 2000), (*c*) unresolved

110

Can. J. Fish. Aquat. Sci. Vol. 58, 2001

arguments that marine fishes warrant at-risk criteria that differ from nonmarine fishes (Musick 1999; Powles et al. 2000; see Reynolds and Mace 1999), and (*d*) the failure of many marine-fish populations to recover from collapse, for example, Northwest Atlantic cod (Hutchings 1999; Shelton and Healey 1999) and Iceland spring-spawning herring, *Clupea harengus* (Myers et al. 1995*a*).

Perception: marine fishes experience greater natural fluctuations in abundance than nonmarine fishes

If a reliable metric of abundance indicates that a population or stock (species in the case of IUCN) has exceeded a specific percentage decline over the longer of 10 years or three generations, the taxon can be assigned to one of several risk or threat categories (e.g., vulnerable – special concern, threatened, endangered, critically endangered). To date, this is the criterion by which IUCN and COSEWIC have assigned at-risk categories to marine fishes (see criterion A in Table 1). The population-decline criterion may, however, seriously overestimate extinction risks for marine fishes, because (*a*) large reductions in population size can represent a primary goal of fisheries management and (*b*) marine fishes are perceived to be naturally more variable and more likely to experience large reductions in abundance than other taxa.

The first component of this assertion is based on the prediction that a substantive reduction in the size of an unfished population must be effected before the maximum sustainable yield (MSY) for that stock can be harvested. The argument can be made, then, that a rapid decline in a commercially exploited marine-fish stock might simply represent the end point of a management goal, and need not be indicative of a population under threat of extinction (Hudson and Mace 1996; Musick 1999; see Reynolds and Mace 1999). Such an argument might have merit, if temporal trends in abundance estimates of marine fishes generally included virgin-stock sizes. However, given the low probability of knowing the virgin-stock size for most marine fish species, the MSY-based argument, in the context of overestimating extinction risks for marine fishes based on criterion A (Table 1), would seem to be moot for all but new fisheries.

New fisheries, for which virgin biomass might conceivably be estimated, may indeed be subject to a management-directed reduction in biomass to increase productivity, although one would be hard-pressed to identify many current examples. Under these circumstances, according to existing criteria, if a population decline was sufficiently large and sufficiently rapid, the stock may be subject to an at-risk designation. This need not, however, be interpreted as inappropriate from a management perspective, particularly if the time frame during which the at-risk designation would be invoked was interpreted as a "probationary" period. If managers were successful in preventing further decline, the stock would eventually be delisted. The history of fisheries overexploitation (Smith 1994) suggests that such a probationary period would not be undesirable.

The second component of this perception appears, at first glance, compelling. There is a general impression that population sizes of marine fishes are more variable than those of freshwater and anadromous fishes (e.g., Musick 1999;

Powles et al. 2000), leading to the possibility that 10-year or three-generation declines of more than 50 or 80% (see criterion A in Table 1) might simply represent "natural" fluctuations in abundance rather than increased risks of extinction. Importantly, however, it is not at all clear how one can reliably distinguish natural from fishing-induced fluctuations in abundance for commercially exploited species.

The observation that recruitment is highly variable in marine fishes was raised by the IUCN in its evaluation of the degree to which its criteria should be applied to marine fishes (Hudson and Mace 1996), although there is no evidence that recruitment variability in marine fishes exceeds that of anadromous fishes (Mertz and Myers 1996). In any event, it is the *reproductive* component of the population to which the IUCN and COSEWIC criteria apply. With reference to criterion A (Table 1), one can ask, then, whether marine fishes are more likely to experience large reductions in spawner population size than nonmarine fishes.

To address this question, I consulted the summary of worldwide spawner and recruitment data originally compiled by Myers et al. (1995*b*) and maintained by R.A. Myers (Department of Biology, Dalhousie University, Halifax, NS B3H 4J1, Canada) at http://fish.dal.ca/welcome.html. I used these data to quantify, and to compare among three groups of fishes (iteroparous marine fishes, iteroparous freshwater fishes, and semelparous salmonids), the frequency with which stocks experienced maximum three-generation declines (approximated as both 15 and 20 years for marine and iteroparous fishes) in spawner abundance or biomass of <50% (small decline), 50–79% (medium decline), and 80% or more (large decline).

Data were available for a minimum of 15 consecutive years or three generations for 163 stocks among 65 species of marine fishes, 106 stocks among five semelparous salmonids (*Oncorhynchus* spp.), and 14 stocks among seven iteroparous freshwater species. There were no significant differences in the incidence of small, medium, and large declines between marine and nonmarine fishes (Table 2; *G* tests, $p > 0.05$ for all possible comparisons), although the power of some comparisons was reduced by the relatively small sample of freshwater-fish populations. Nonetheless, comparing marine fishes with semelparous salmonids, for which sample sizes were large, the incidence of large (≥80%) reductions in population size was actually higher for salmonids, being 30 and 38%, respectively. Thus, based on data available for 283 stocks, there is no empirical support for the perception that the spawning component of marine fishes normally experiences declines with greater frequency than that of nonmarine fishes.

Perception: marine fishes are more productive and are more likely to produce unusually high numbers of offspring than other taxa

The perception that marine fishes are more productive and more resilient than other taxa can be traced to what might be termed the "ghost of inexhaustibility past" (sensu Connell 1980), which evidently continues to haunt some into concluding that the production of hundreds of thousands, often millions, of eggs by many marine fishes is associated with

Table 2. Incidence of three categories of maximal proportional decline experienced by populations of fishes during periods of 15 and 20 years (iteroparous marine and freshwater fishes) and three generations (semelparous salmonids).

		Proportional decline in mature fish biomass–abundance					
		0–49%		50–79%		≥80%	
	Period of decline	n	%	n	%	n	%
Marine fishes	15 years	59	36.2	55	33.7	49	30.1
	20 years	33	36.3	31	34.1	27	29.7
Semelparous salmonids	3 generations	28	26.5	38	35.8	40	37.7
Freshwater fishes	15 years	7	50.0	4	28.6	3	21.4
	20 years	3	37.5	2	25.0	3	37.5

increased productivity and with increased probability of producing unusually high levels of recruitment.

The ghost, who appeared before Lamarck in the early 19th century (Roberts and Hawkins 1999), was manifested by Thomas Huxley's famous utterance at the Great International Fisheries Exhibition in London in 1883 (see Smith 1994 for historical context), when Charles Darwin's confidant argued,

> That the cod fishery, the herring fishery, the pilchard fishery, the mackerel fishery, and probably all the great sea-fisheries, are inexhaustible; that is to say that nothing we do seriously affects the number of fish.

Huxley was overwhelmed by the vast numbers of eggs that marine fish produce, suggesting to his audience that this great reproductive potential would prevent fishing from having any significant impact on marine-fish stocks. Echoes of this refrain can be heard today, albeit in somewhat modified forms: the great fecundity of marine fishes renders them more resistant to overexploitation and better able to recover after being reduced to small population sizes than fish with more modest egg productivity (e.g., Cushing and Harris 1973; Mace and Sissenwine 1993; Malakoff 1997).

But this refrain is fundamentally flawed, in part because it obfuscates the fact that fecundity is but one of many characters that influence fitness. For example, as discussed by Hutchings (2000a), the porbeagle's (*Lamna nasus*) strategy of producing from one to five offspring every year for perhaps 10 or 15 years is equivalent, evolutionarily, to the Atlantic cod's strategy of producing several hundred thousand to a few million eggs every year for perhaps 5–10 years. The result of both strategies is replacement at equilibrium. Intuitively, then, the high fecundity of marine fishes need not imply greater productivity or reduced susceptibility to extinction (Carlton et al. 1999). Indeed, based on their examination of 266 stocks (including 80 species), R.A. Myers and J.A. Hutchings (unpublished data) could find no evidence that fecundity was positively associated with maximum reproductive rate, a reasonable proxy for resistance to extinction and a metric of productivity at low population size.

The theoretical constructs of this argument appear to be borne out by other empirical analyses. Mertz and Myers (1996) could find no association between fecundity and variance in reproductive rate among 36 species of marine fishes (including elasmobranchs, clupeids, gadids, scombrids, and pleuronectids), and a comparison of phylogenetically unrelated marine-fish taxa by Rickman et al. (2000) also suggests that, in general, species with high fecundity are no more likely to produce unusually high levels of recruitment than those with relatively low fecundity.

Furthermore, variance in maximum reproductive rate, r, does not appear to differ between marine and anadromous fishes. Mertz and Myers (1996) estimated variance in reproductive rate as the standard deviation of the natural log of recruitment residuals from a Ricker stock–recruitment model, that is, $\sigma_{\ln R}$. Among 36 marine fishes, $\sigma_{\ln R}$ ranged from ~0.2 for Peruvian hake (*Merluccius gayi*) and Greenland halibut (*Reinhardtius hippoglossoides*) to ~1.35 for chub mackerel (*Scomber japonicus*), a range similar to that observed among five anadromous species, for which $\sigma_{\ln R}$ ranged from 0.3 for Atlantic salmon (*Salmo salar*) to ~1.0 for pink salmon (*Oncorhynchus gorbuscha*). Thus, at low population sizes, marine fishes appear no more likely to produce unusually high numbers of offspring than nonmarine fishes.

Perception: marine fishes are more resilient and have intrinsically faster recovery rates than other taxa

Using the aforementioned fisheries database (Myers et al. 1995b), I recorded the largest 15-year percentage decline in mature-fish biomass experienced by each iteroparous marine and freshwater stock, the greatest three-generation population reduction by each semelparous salmonid population, and subsequent population sizes 5, 10, and 15 years (one, two, and three generations for the salmonids) thereafter. The 15-year interval was considered short enough to obtain a reasonably large sample of populations and long enough to be biologically meaningful, approximating the arbitrary three generation time period used to assess risk criterion A (Table 1) by IUCN and COSEWIC (Campbell 1996; IUCN 1999). Marine stocks were represented primarily by six families: Clupeidae (e.g., herring; sprat, *Sprattus sprattus*), Gadidae (e.g., cod, haddock), Scombridae (e.g., mackerel, *Scomber* spp.; tuna, *Thunnus* spp.), Sparidae (e.g., snapper, *Pagrus* spp.), Scorpaenidae (e.g., redfish, *Sebastes* spp.), and Pleuronectidae (e.g., plaice, *Pleuronectes* spp.; Greenland halibut). Semelparous salmonids were represented primarily by pink and sockeye (*O. nerka*) salmon, although some data were also available for chum (*O. keta*), coho (*O. kisutch*), and chinook (*O. tshawytscha*) salmon. The few freshwater species for which data were available for a minimum of 20 consecutive years (15 years for decline plus 5 years for recovery) included yellow perch, *Perca flavescens*; northern pike, *Esox lucius*; walleye, *Stizostedion vitreum*; and blue pike, *Stizostedion vitreum glaucum*.

As described by Hutchings (2000b), any increase following a decline in population size, N, could be interpreted as some sort of recovery. For example, recovery t years after a 15-year decline can be determined from a plot of N_{t+15}/N_0 on the ordinate against magnitude of population decline on the abscissa, that is, $1 - N_{t+15}/N_0$. On such a plot, populations exhibiting no recovery would fall on a straight line with a slope of –1 extending from (0,1) to (1,0). Populations continuing to decline would fall below this line, whereas those

112

Can. J. Fish. Aquat. Sci. Vol. 58, 2001

exhibiting some recovery would lie between this line and the full-recovery line (at which $N_{t+15} = N_0$) with a slope of 0 extending from (0,1) to (1,1) (Fig. 1).

Future population size is negatively correlated with magnitude of population decline for both marine and nonmarine fishes. Among 90 marine-fish stocks (38 species, 11 families), 15-year declines ranging from 13 to 99% were followed by 5-year changes to population sizes of 0.3–178% of the sizes from which the declines began, that is, N_0 (Hutchings 2000b; Fig. 1a). The negative association between 5 year recovery population size and population decline was stronger when clupeids were excluded from the analysis (Table 3). Data 10 and 15 years subsequent to the 15-year population declines were available for 45 and 25 marine stocks, respectively, being composed primarily of clupeids and gadids. Among all stocks, the magnitude of decline negatively influenced population size 10 years, but not 15 years (Fig. 1b), after the declines. However, when clupeid data were excluded, population decline was strongly and significantly associated with both 10 and 15 year recovery population sizes (Table 3).

Within families, population recoveries after 5 years were significantly correlated with population declines in gadids, sparids, scorpaenids, and pleuronectids (Table 3; Hutchings 2000b). The association was not significant within clupeids or scombrids, although the correlation was highly significant within the latter family when the outlier stock (eastern Pacific yellowfin tuna, *Thunnus albacares*) was removed from the analysis. At the family level, 15 year recovery population sizes were negatively associated with population decline within gadids but not within clupeids (Fig. 1b; Hutchings 2000b).

For the 86 stocks of semelparous salmonids and seven populations of iteroparous freshwater fishes, the largest three-generation or 15-year decline experienced by each was negatively associated with population size one generation and 5 years thereafter (Table 3; Fig. 2). Within species, the same was true for pink and sockeye salmon (Fig. 3). However, unlike marine fishes, the population sizes of semelparous salmonids were independent of the magnitude of population declines two and three generations after the declines had occurred (Fig. 4). Within species, excluding the outlier (Sunday Creek, Cook Inlet, Alaska; Fig. 3b), population sizes of pink salmon three generations after their maximum three-generation declines were negatively associated with the latter ($r = -0.58$, $p = 0.002$).

At the very least, population resilience appears similar for marine and nonmarine fishes, if not actually lower among marine fishes, based on linear regressions between population recovery and population decline (Table 3). For example, 5 years or one generation after experiencing 15-year or 3-generation declines of 80%, populations are predicted to recover to 34% (all marine fishes; 29% if clupeids are excluded), 56% (semelparous salmonids), and 17% (freshwater fishes) of the sizes from which the population declines began. Three generations after a three-generation decline of 80%, pink salmon (excluding the single outlier) are expected to recover to 75% of their population maxima during their declines, compared with only 20%—effectively no change at all—for gadids 15 years after 15-year declines of 80%.

A second comparison of marine and anadromous popula-

tions also suggests that the latter may be more likely to recover from collapse than the former. As described above, the broken and solid lines in Figs. 1–4 can be used to identify populations that recover fully (lie above the dashed line) and those that decline further (fall below the solid line) after experiencing their greatest 15-year or 3-generation percentage decline in spawner abundance or biomass. The incidence of full recovery among anadromous populations for the range of recovery periods considered here was more than twice that of marine fishes (Table 4). Similarly, further decline was twice as probable among marine fishes than among anadromous fishes.

Among marine fishes, population-recovery and -decline data suggest that, following prolonged decline, clupeids are more likely to recover to previously experienced population sizes and are more resilient than other marine fishes (Fig. 1; Table 3). As argued elsewhere (Hutchings 2000b), such an increased rate of recovery may be attributable to the comparatively younger age at which clupeids mature (Froese and Pauly 1999) and the higher intrinsic rate of increase that earlier maturity generally effects (Roff 1992). Higher reproductive rates are also expected to mitigate the negative influence of environmental stochasticity on the persistence of populations at small sizes (Lande 1993). Earlier age at maturity may also account for the observation that anadromous fishes appear more likely to recover from collapse than marine fishes.

However, the apparent increased resilience evident among clupeids may also be a consequence of differential species selectivities of fishing gear. Clupeids are typically fished by deploying purse seines or midwater trawls. Low species diversity within clupeid schools results in bycatch levels of from one to two orders of magnitude lower than the bottom-deployed seines and trawls used to catch groundfish (Alverson et al. 1994). Thus, when a clupeid stock collapses, it may be comparatively easy to eliminate fishing mortality on the affected population, because of the high species selectivity of clupeid fishing technology. By comparison, the collapse of a groundfish stock rarely results in cessation of bottom trawling in the affected region, meaning that fishing mortality on the collapsed stock can be reduced but rarely eliminated, because of the comparatively low species selectivity of the fishing gear used to capture a broad diversity of demersal marine fishes. In addition to the proposed influence of age at maturity, reproductive rate, and fishing-gear selectivity on recovery rates, it is highly probable that ecosystem-level consequences of exploitation—for example, alterations in food webs effected by changes to species community structure—also play a significant role (Pauly et al. 1997; Jennings and Kaiser 1998).

Thus, with the possible exception of some (but clearly not all) clupeids, there is little empirical support for the perception that marine fishes are more likely than nonmarine fishes to recover from prolonged reductions in abundance. Ideally, of course, it would be preferable to restrict such an analysis of population recovery to those stocks for which fishing mortality post collapse was zero. Unfortunately, such a determination is problematic, because of the difficulty in assessing the degree to which management targets, such as that of attaining a fishing mortality of zero, are met in reality.

From a broader perspective, to what extent might fishes be

Fig. 1. Bivariate associations between population recovery and population decline for marine fishes. Recovery refers to the size of a population 5 years after the proportionately largest 15-year decline experienced by that population, relative to the size of that population at the beginning of its 15-year decline. Populations that experienced some recovery are represented by points above the solid line. Fully recovered populations are represented by points on or above the dashed line. Each point represents a different marine-fish stock. Data are shown for all stocks (*a*) 5 years and (*b*) 15 years after their greatest 15-year population decline. Families and species represented here include: △, Clupeidae (Atlantic menhaden, *Brevoortia tyrannus*; herring, *Clupea harengus*; Spanish sardine, *Sardinops sagax*; sprat, *Sprattus sprattus*); ×, Engraulidae (anchovy, *Engraulis encrasicolus*; northern anchovy, *Engraulis mordax*); ▽, Osmeridae (caplin, *Mallotus villosus*); ▲, Gadidae (Atlantic cod, *Gadus morhua*; haddock, *Melanogrammus aeglefinus*; whiting, *Merlangius merlangius*; silver hake, *Merluccius bilinearis*; pollock, *Pollachias virens*; Norway pout, *Trisopterus esmarkii*); ◇, Nototheniidae (icefish, *Notothenia rossii*); ■, Scombridae (chub mackerel, *Scomber japonicus*; king mackerel, *Scomberomorus cavalla*; albacore tuna, *Thunnus alalunga*; yellowfin tuna, *Thunnus albacares*; southern bluefin tuna, *Thunnus maccoyii*; bigeye tuna, *Thunnus obesus*; Atlantic bluefin tuna, *Thunnus thynnus*); ◆, Sparidae (New Zealand snapper, *Pagrus auratus*; yellow sea bream, *Taius tumifrons*); ●, Pleuronectidae (petrale sole, *Eopseta jordani*; American plaice, *Hippoglossoides platessoides*; Pacific halibut, *Hippoglossus stenolepis*; common dab, *Limanda limanda*; longhead dab, *Limanda proposidea*; flounder, *Platichthys flesus*; yellowtail flounder, *Pleuronectes ferrugineus*; plaice, *Pleuronectes platessa*; Greenland halibut, *Reinhardtius hippoglossoides*); ○, Soleidae (sole, *Solea vulgaris*); +, Anoplopomatidae (sablefish, *Anoplopoma fimbria*); *, Scorpaenidae (Pacific ocean perch, *Sebastes alutus*; shortspine thornyhead, *Sebastes alaskanus*; redfish, *Sebastes* spp.). (After Hutchings 2000*b*.)
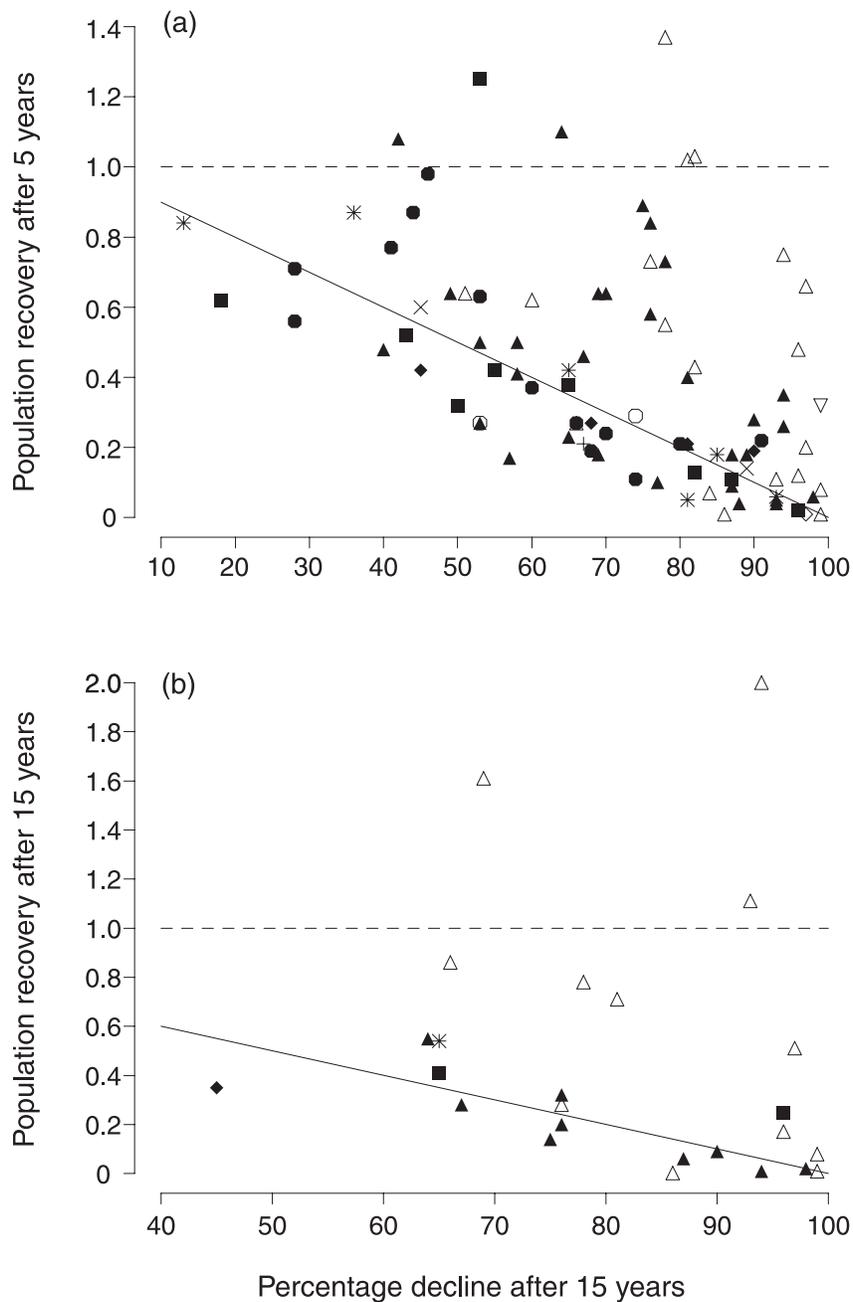
Table 3. Regression equations describing mature population size (y) after various recovery periods following a 15-year population decline for marine and freshwater fishes, relative to the population size at the beginning of the decline, as a function of population decline (x, percentage decline in mature fish population size over a period of 15 years or three generations).

Recovery period	Taxonomic group	Regression equation	n	p	r
Marine fishes					
5 years	Clupeidae	$y = 1.78 - 1.48x$	20	0.062	–0.42
	Gadidae	$y = 1.14 - 1.00x$	31	0.003	–0.52
	Scombridae	$y = 0.80 - 0.79x$	8	<0.001	–0.96
	Sparidae	$y = 0.65 - 0.53x$	4	0.013	–0.99
	Scorpaenidae	$y = 1.11 - 1.13x$	6	0.004	–0.95
	Pleuronectidae	$y = 1.16 - 1.19x$	13	0.0013	–0.79
	All	$y = 1.00 - 0.82x$	90	<0.0001	–0.46
	All except Clupeidae	$y = 1.04 - 0.94x$	70	<0.0001	–0.64
10 years	Clupeidae	$y = 2.74 - 2.46x$	15	0.083	–0.46
	Gadidae	$y = 1.86 - 1.87x$	16	0.007	–0.65
	All	$y = 1.41 - 1.19x$	45	0.012	–0.37
	All except Clupeidae	$y = 1.46 - 1.42x$	30	0.001	–0.56
15 years	Clupeidae	$y = 3.01 - 2.47x$	12	0.33	–0.32
	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
Semelparous salmonids					
1 generation	Pink salmon	$y = 1.78 - 1.51x$	48	0.0003	–0.50
	Sockeye salmon	$y = 1.74 - 1.42x$	25	0.009	–0.51
	All	$y = 1.59 - 1.29x$	86	<0.0001	–0.49
2 generations	All	$y = 1.38 - 0.72x$	37	0.42	–0.14
3 generations	All	$y = 2.11 - 1.42x$	26	0.21	–0.26
Freshwater fishes					
5 years	All	$y = 1.07 - 1.12x$	7	0.0007	–0.96

Note: The regression equation for the Scombridae excludes the outlying eastern Pacific yellowfin tuna stock for which the 5 year recovery population size was 1.25 times the maximum during the 15-year decline. Inclusion of this datum yields the following regression for the scombrids: $y = 0.99 - 0.93x$, $p = 0.078$, $r = -0.62$. Sample size (n) is number of stocks or populations.

expected to have greater resilience than other taxa? One means of assessing this is to compare maximum reproductive rates estimated for fish with those estimated for terrestrial mammals, the organisms upon which many of the extinction criteria used by COSEWIC and IUCN were originally based. R.A. Myers and J.A. Hutchings (unpublished data) documented a range in r among 80 fish species (the majority of which are marine) of between 0.02 and 1.50, with most estimates lying between 0.2 and 0.8. Interestingly, these maximum reproductive rates for fish are not dissimilar to those that have been estimated for large terrestrial mammals such as grizzly bear, *Ursus arctos* ($r = 0.33$; McCullough 1992); bighorn sheep, *Ovis canadensis* ($r = 0.38$; McCullough 1992); white-tailed deer, *Odocoileus virginianus* ($r = 1.00$; McCullough 1979); and saiga antelope, *Saiga tatarica* ($r > 1$; McCullough 1992).

Caveat: increased risk of biological extinction is associated with reduced probability of returning to former levels of abundance

Despite their heuristic value, species-status assessments that attempt to reflect extinction risks alone may not be very useful from an ecological, management, or ecosystem perspective. By intellectually and quantitatively focussing such assessments solely on the vulnerability of a species to

biological extinction, there is (not surprisingly) an overwhelming tendancy to critically examine the degree to which criteria such as those used by IUCN and COSEWIC (Table 1) reliably assess the likelihood, for any species, that abundance will decline to zero.

This has led to arguments concerning the quantitative basis for such assessments and the biological legitimacy of time-frame estimates within which specific extinction probabilities will purportedly be realised (see criterion E in Table 1). For example, Musick (1999) has suggested that a 70% decline over the longer of 10 years or three generations be the minimum required before a marine-fish species is assigned to any at-risk category. Basing his population-decline thresholds on maximum reproductive rate, Musick (1999) suggests that, for values of r in the ranges of <0.05 (very low productivity), 0.05–0.15 (low), 0.16–0.50 (medium), and >0.50 (high), a marine-fish species would have to decline, over the longer of 10 years or three generations, 70, 85, 95, and 99%, respectively, to be initially flagged as being vulnerable.

The primary difficulty with focussing one's interpretation of risk or threat categories solely on biological extinction is that, no matter how much modelling might be applied to a specific species, we truly do not understand how the multitude of factors that influence the extinction probability for a given population or species interact with one another

Fig. 2. Bivariate associations between population recovery and population decline for (*a*) semelparous salmonids and (*b*) iteroparous freshwater fishes. Recovery refers to the size of a population one generation (semelparous salmonids) or 5 years (freshwater fishes) after the proportionately largest 3-generation (semelparous salmonids) or 15-year (freshwater fishes) decline experienced by that population, relative to the size of that population at the beginning of its decline. The broken and solid lines represent the "full-recovery" and "no-recovery" lines, respectively. Each point represents a different population. Semelparous salmonids include: △, pink salmon, *Oncorhynchus gorbuscha*; ▲, sockeye salmon, *Oncorhynchus nerka*; ■, coho salmon, *Oncorhynchus kisutch*; ○, chum salmon, *Oncorhynchus keta*; and ●, chinook salmon, *Oncorhynchus tshawytscha*. Iteroparous freshwater species include: ■, yellow perch, *Perca flavescens*; ▲, walleye, *Stizostedion vitreum*; △, blue pike, *Stizostedion vitreum glaucum*; and ●, northern pike, *Esox lucius*.
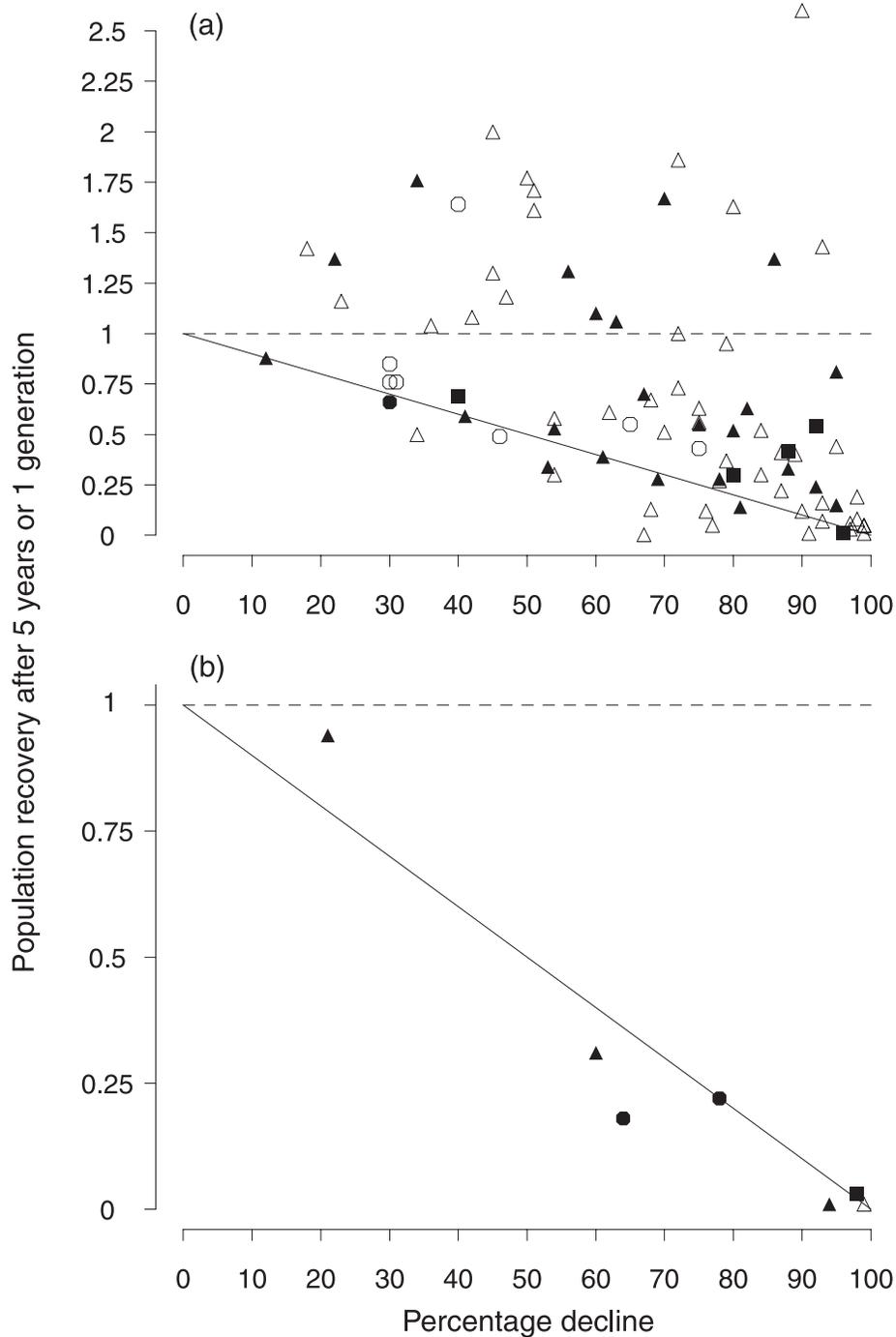
under specific physical and biological environments. This lack of knowledge, coupled with the absence of an empirical basis upon which to reliably assess quantitative listing criteria, provides a fertile breeding ground for arguments and counterarguments, many of which are based on the perceptions discussed above, concerning the notion that marine fishes should be treated differently from nonmarine fishes, and other taxa, when assigning at-risk status. For example,

Fig. 3. Population recovery of semelparous salmonids one generation (open symbols) and three generations (solid symbols) after the greatest proportional 3-generation decline experienced by each stock. Data are shown for (*a* and *b*) sockeye salmon, (*c* and *d*) pink salmon, (*e* and *f*; triangles) chum salmon, and (*e*; circles) coho salmon. The broken and solid lines represent the "full-recovery" and "no-recovery" lines, respectively.
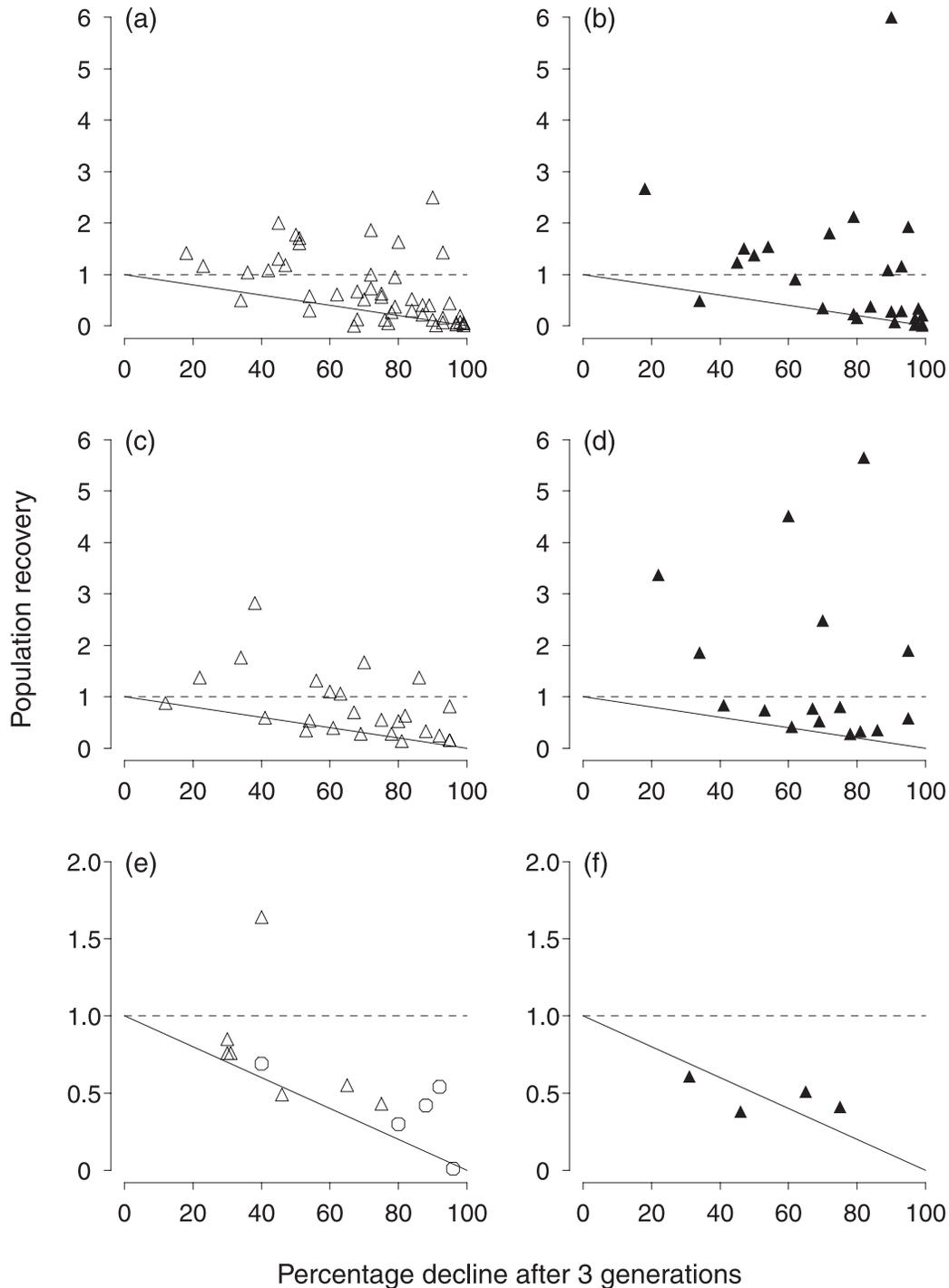
one could argue that, even after population declines of more than 95%, most commercially harvested marine fishes would still number in the hundreds of thousands, if not millions, of individuals, and should not be considered at any increased risk of extinction as a consequence. But, again, is it not simply a perception, or an intuition, that such numerical levels should be able to buffer the factors that may conspire to reduce population sizes further, even in the absence of exploitation? For, notwithstanding severe hunting pressures, species abundances numbering in the millions failed to prevent the extinction or extirpation of the passenger pigeon (*Passer domesticus*) or the Eskimo curlew (*Numenius borealis*) in

Fig. 4. Population recovery of semelparous salmonids (*a*) two generations and (*b*) three generations after the greatest proportional three-generation decline experienced by each stock. The broken and solid lines represent the "full-recovery" and "no-recovery" lines, respectively. Semelparous salmonids include: △, pink salmon, *Oncorhynchus gorbuscha*; ▲, sockeye salmon, *Oncorhynchus nerka*; ■, coho salmon, *Oncorhynchus kisutch*; ○, chum salmon, *Oncorhynchus keta*; and ●, chinook salmon, *Oncorhynchus tshawytscha*.
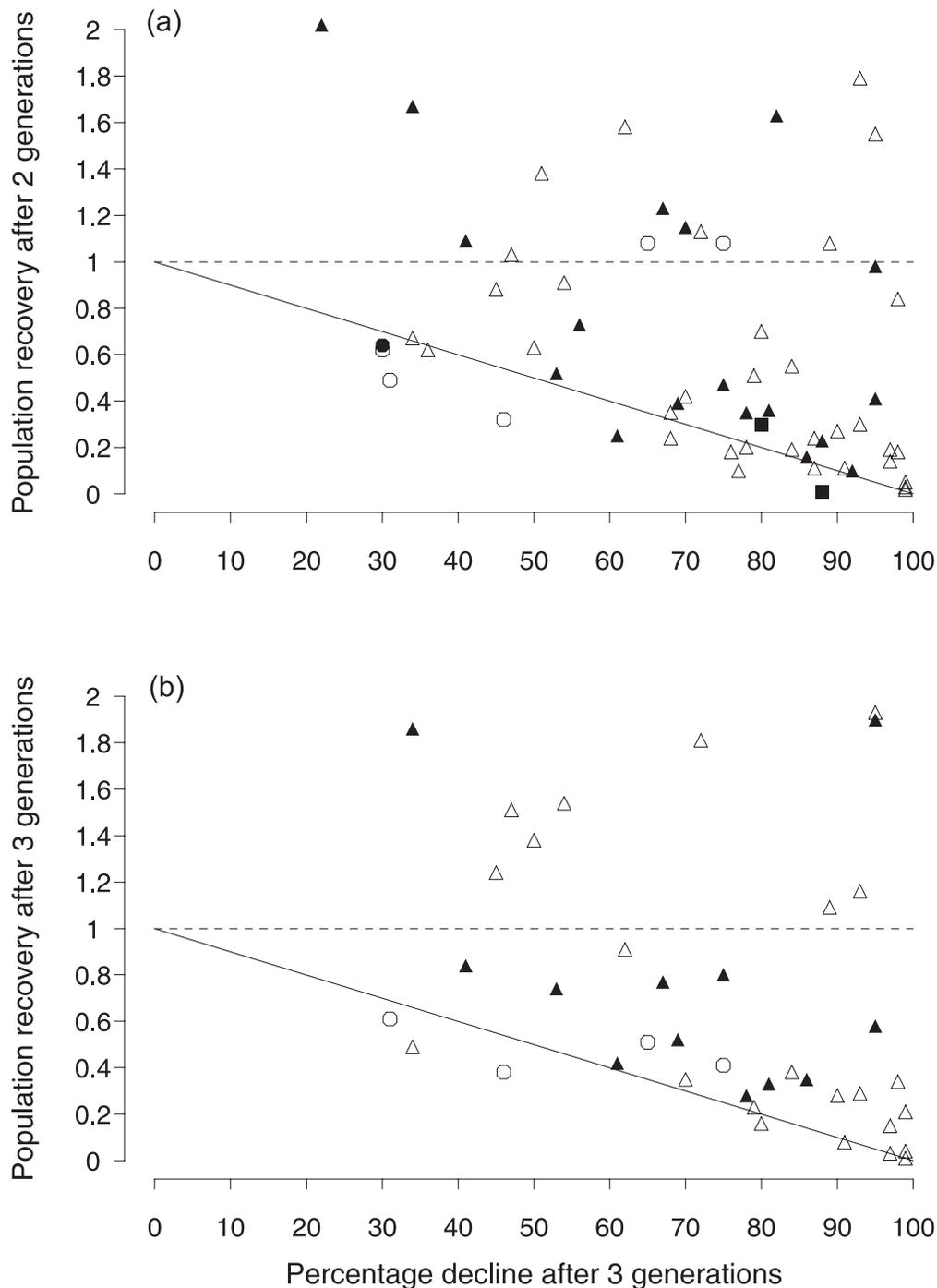
North America or, indeed, of marine gastropods in the North Atlantic and North Pacific in the 19th century (Carlton et al. 1999). Certainly, numerical abundance alone was not sufficient to prevent population collapses of Northwest Atlantic cod. And, even in the absence of fishing, numerical abundance alone appears insufficient to ensure recovery to former levels of abundance.

These observations underscore the point that the threat of extinction is a double-edged sword. It reflects not only the probability with which a species' abundance will decline to zero but, just as importantly, the probability with which a numerically depressed species will grow to previous levels of abundance. Northwest Atlantic cod again provide a useful case in point. Deterministic estimates of *r* for the six Canadian

118

Can. J. Fish. Aquat. Sci. Vol. 58, 2001

Table 4. Incidence (%) of full recovery and further decline among marine and semelparous anadromous fishes 5 years or one generation and 15 years or three generations after the greatest 15-year or 3-generation percentage decline in reproductive biomass or abundance experienced by each population.

	Full recovery		Further decline	
	5 years – 1 generation	15 years – 3 generations	5 years – 1 generations	15 years – 3 generations
Marine fish	7.8 (7)	12.0 (3)	41.1 (37)	40.0 (10)
Semelparous anadromous fish	25.6 (22)	25.6 (10)	22.1 (19)	17.9 (7)

Note: Values in parentheses are sample size (*n*).

cod stocks to which fishing moratoria were applied in the early 1990s fall within Musick's (1999) medium-productivity category (Myers et al. 1997), although one may be in the low-productivity category (Hutchings 1999). According to Musick's (1999) suggested criteria, these stocks would not have been considered vulnerable until their abundance had declined by at least 95% over the longer of 10 years or three generations. Although only one of these stocks (northern cod; Lilly et al. 1998) declined by this amount, all, with the exception of the stock that had declined least among the six (St. Pierre Bank cod), have failed to return to levels of abundance experienced in the 1980s. So, while there may be no foreseeable risk of biological extinction for these stocks (notwithstanding the potential losses of populations or substocks), there would appear to be a reasonably high probability that these stocks will not return to former levels of abundance.

Assurance that a stock is unlikely to decline to zero surely provides little solace, if that stock has a very low probability of returning, even to a modest extent, to former higher levels of abundance.

Caveat: risk assessments based on abundance trends for single species or stocks may underestimate extinction threats to constituent populations or substocks

Marine fishes typically occupy very broad geographical ranges. As such, many are almost certainly composed of more than one substock or population. This raises the question of whether at-risk designations based upon assessments conducted at the species or stock level are likely to provide risk-averse assessments for substocks within stocks and for populations within species.

Returning to the listing of Atlantic cod by COSEWIC, there was resistance to assigning stocks separately to at-risk categories (Comeau 1998), resulting in a single designation being assigned to the species as a whole in Canadian waters. For, if Atlantic cod are the migratory and evolutionary vagrants that some appear to consider them to be, local groups or substocks can be permitted to go extinct, because cod from other areas will simply fill in the recently vacated waters.

The logical fallacy of this argument lies, of course, in the premise that species, in general, are adapted to colonise new areas. Rather, natural selection tends to select against genotypes that abandon the environments and habitats in which they evolved and to which they have adapted their life histories, spawning times, and migratory behaviour, particularly in the absence of any density-dependent pressure to do so. Not surprisingly, from an ecological perspective, there is increasing evidence of local adaptation within Atlantic cod populations at spatial scales less than those used by management to delineate stocks. Evidence of genetically based population variation includes differences in growth rates (Svasand et al. 1996; Puvanendran and Brown 1998), antifreeze protein levels (Goddard et al. 1999), behavioural responses to photoperiod (Puvanendran and Brown 1998), and spawning time (J.A. Hutchings, unpublished data).

Caveat: reproductive rates differ among populations within species

The use of *r* as the primary metric for assessing extinction risk is not unreasonable; it is quantitative and has a sound theoretical basis in population and conservation biology. But, in practice, there are at least two reasons why reliance on this metric will be problematic. The first is that *r* differs among populations within species. Reproductive rate is primarily a product of age at maturity (α) and age- and size-specific rates of survival and fecundity, all of which differ, to greater or lesser degrees, among populations. Within Atlantic cod, one of the best-studied marine fishes from a life-history perspective, age at maturity prior to the commercial fishery collapses of the 1990s ranged between 2 years on Georges Bank and 7–8 years off Norway (Myers et al. 1997). As a consequence of these differences in α, deterministic estimates of maximum reproductive rate vary significantly among cod stocks, ranging at least from 0.17 to 1.15 (Myers et al. 1997; Hutchings 1999).

Returning to Musick's (1999) suggested classification scheme, which deterministic estimate of *r* would one choose for Atlantic cod? The intrinsic rates of increase for half of the 20 cod stocks examined by Myers et al. (1997) fall within Musick's (1999) high-productivity category ($r > 0.50$), while half fall in the medium-productivity category ($0.15 < r < 0.51$). There is also good reason to believe that *r* for at least one cod stock falls within the low-productivity ($0.05 < r < 0.16$) category (Hutchings 1999; Shelton and Healey 1999).

In the absence of estimates of the intrinsic rate of increase, Musick (1999) suggested that realised *r*, estimated at population densities at which density-dependent effects on population growth are likely minimal, might prove a useful substitute. One potential difficulty with this is that realised *r* will poorly reflect intrinsic *r*, if the population has experienced changes to age at maturity, individual growth rate, and longevity as a consequence of genetic or phenotypic changes to age at maturity effected by high fishing mortality, reduced

density, changes to interspecific relationships between predators, prey, and competitors, or some combination thereof.

Thus, species or population assessments are subject to the caveat that intraspecific variation in reproductive rate, or in any fitness-related characteristic, introduces the risk of assigning an inappropriate metric of reproductive rate to a given species or to a specific population within that species. One possible solution to this dilemma when assessing organisms at the species level, as IUCN does, would be to weight r by some metric of virgin-stock size and then to sum across stocks. This may not be an unreasonable approach, providing the number of stocks is small, but the confidence one would have in such a metric would diminish rapidly with increased numbers of stocks, because of the compounding of estimation errors inherent in such a calculation.

Caveat: deterministic estimates of reproductive rate overestimate true reproductive rates

When populations are reduced to very low sizes, their persistence is increasingly threatened by genetic, demographic, and environmental stochasticity (Lande 1993). Among these, environmental stochasticity, defined as unpredictable proportional changes in survival or fecundity that affect all individuals within a population equally, is probably the most important (Caughley 1994).

An attempt to incorporate the effects of environmental stochasticity on estimates of r was made by Hutchings (1999) for northeastern Newfoundland Atlantic cod. He concluded that reductions in age-specific survival as small as 10–20% reduced stochastic estimates of r for this stock from between 0.13 and 0.16 (straddling Musick's medium- and low-productivity categories) to between 0.07 and 0.10. Perhaps more importantly, irrespective of age at maturity or age-specific survival and fecundity, stochastic estimates of r were always less than deterministic estimates (Hutchings 1999).

This almost certainly holds true for all taxa (e.g., red deer; Benton et al. 1995). In general, the stochastic analogue of r in the deterministic model, s, is given by $s = r - \frac{1}{2}(\sigma_s^2)$, where r is the deterministic estimate of the intrinsic growth rate and σ_s^2 is the environmental variance of the intrinsic growth rate (Lande 1993; Lande et al. 1997). Thus, given that environmental influences on age-specific rates of survival and fecundity will never be nil, the true value of r, estimated by its stochastic analogue, will always be less than deterministic estimates of r. The magnitude of the difference between stochastic and deterministic estimates of maximum reproductive rate can be expected to differ among populations and may differ within populations through time. Thus, assessments of extinction risk based on deterministic estimates of r will be, to greater or lesser degrees, risk prone.

Concluding remarks

Contemporary perceptions of the ability of marine fishes to recover from population decline do not have particularly strong theoretical or empirical support. Marine fishes appear to be no more likely to experience reductions in population size than nonmarine fishes. The question of whether natural temporal variability in the reproductive component of marine-fish populations exceeds that of other taxa, including terrestrial mammals and birds, remains a relevant, and to date unexamined, research question. High fecundity is unlikely to provide any insurance against extinction, and available data provide no support for the hypothesis that marine fishes are able to recover rapidly from population collapse (Hutchings 2000b).

Based on these observations, I have suggested that to exempt marine fishes from the population-decline criterion used to assign extinction risk would be inconsistent with a precautionary approach to fisheries management and to the conservation of marine biodiversity (Hutchings 2000b). This is based, in part, on the argument that increased probability of extinction is logically associated with reduced probability of recovery, and that persistence at relatively low abundance and absence of recovery are scientifically defendable metrics of extinction probability. One could argue that such a conclusion is overly cautious and that "common sense" and "intuition" inform us that marine fishes warrant population-decline thresholds considerably higher than those considered applicable to all other taxa. If so, common sense also dictates that changes to at-risk criteria for marine fishes be based on analyses of empirical data rather than on intuitive perceptions.

Recently proposed decline thresholds for marine fishes, ranging from 70 to 99% over the longer of 10 years or three generations (Musick 1999), may be akin to threading the extinction needle just a little too finely. In any event, the degree to which any criterion adequately reflects extinction probability cannot be known until substantial numbers of species have gone extinct, an obviously undesirable necessity and one that may require considerable amounts of time. So, rather than changing the risk criteria, one could change the names of the risk categories so that they better reflected the goals of conservation and preservation of biodiversity. For example, even if an 80% decline in a cod population does not significantly increase its probability of extinction, it certainly appears to affect its probability of recovery to former levels of abundance. So, irrespective of whether quantitative criteria adequately reflect extinction risk, they do appear to adequately reflect recovery potentials, something of clear importance to resource managers, harvesters, ecologists, and conservation biologists. Rather than having risk categories named vulnerable, threatened, endangered, and critically endangered, one could replace them with conservation categories named priorities I, II, III, and IV.

By disentangling biological extinction probabilities from the process of identifying species and populations of conservation concern, one might eliminate, or at least reduce immensely, the largely unproductive attempts to produce new versions of ultimately imprecise extinction threat criteria. Such a change would also acknowledge that factors such as recovery potential are integral to, and not disassociated from, the process of evaluating extinction probabilities. The most compelling argument against such a name change, and the reason why IUCN and other organisations use extinction risk rather that another measure, such as recovery probability, is that the word "extinction" is more emotive and more readily grabs the attention of the public and decision-makers than does "recovery."

120

Can. J. Fish. Aquat. Sci. Vol. 58, 2001

It needs to be reiterated that, rather than quantifying extinction probabilities, the IUCN and COSEWIC criteria are only guidelines for assigning species to various at-risk categories, each of which *heuristically* reflects extinction probabilities, based on comparatively recent negative changes to a species' distribution and abundance. The primary value of assigning a given species, or population, to one of these categories lies in its conveyance to scientists, to resource managers, to politicians, and to society that a species' extinction probability has increased and (or) that its probability of recovering to some historically high benchmark of abundance is low. It behooves us as scientists not only to recognise the extraordinary value inherent in communicating such a message, but to objectively assign species to at-risk categories independently of managerial, governmental, or political considerations (Hutchings et al. 1997; Leiss 2000).

Acknowledgements

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