

Review

Biology of extinction risk in marine fishes

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We review interactions between extrinsic threats to marine fishes and intrinsic aspects of their biology that determine how populations and species respond to those threats. Information is available on the status of less than 5% of the world's approximately 15 500 marine fish species, most of which are of commercial importance. By 2001, based on data from 98 North Atlantic and northeast Pacific populations, marine fishes had declined by a median 65% in breeding biomass from known historic levels; 28 populations had declined by more than 80%. Most of these declines would be sufficient to warrant a status of threatened with extinction under international threat criteria. However, this interpretation is highly controversial, in part because of a perception that marine fishes have a suite of life history characteristics, including high fecundity and large geographical ranges, which might confer greater resilience than that shown by terrestrial vertebrates. We review 15 comparative analyses that have tested for these and other life history correlates of vulnerability in marine fishes. The empirical evidence suggests that large body size and late maturity are the best predictors of vulnerability to fishing, regardless of whether differences among taxa in fishing mortality are controlled; there is no evidence that high fecundity confers increased resilience. The evidence reviewed here is of direct relevance to the diverse criteria used at global and national levels by various bodies to assess threat status of fishes. Simple life history traits can be incorporated directly into quantitative assessment criteria, or used to modify the conclusions of quantitative assessments, or used as preliminary screening criteria for assessment of the ~95% of marine fish species whose status has yet to be evaluated either by conservationists or fisheries scientists.

Keywords: fisheries; conservation; life histories; IUCN; CITES

1. INTRODUCTION

There are more species of fish than of all other vertebrate groups combined. When freshwater and marine species are included, fishes may also be one of the most threatened groups of vertebrates (Baillie *et al.* 2004). Taken together, these two observations might lead one to expect that fish species would deserve top priority from conservation biologists. But with the exception of the commercially exploited species that are assessed by fisheries agencies, they receive far less attention than birds and mammals (Clark & May 2002; Reynolds 2003). Notwithstanding the observation that commercially exploited fish populations ($n=232$) have experienced maximum population declines of 83% over the past 2–3 decades from known historical levels (Hutchings & Reynolds 2004), many fisheries biologists consider the risk of extinction for commercially exploited species to be quite low. This perception contributed to the substantial difficulties in having the first marine fishes listed in Appendix 2 of CITES (Convention on International Trade of Endangered Species) in November 2002.

The objective of this review is to summarize current knowledge of the threat status of marine fish species, including brief comparisons with other vertebrate groups. This consideration highlights how little is known either globally or regionally. We then consider biological correlates of vulnerability, with an emphasis on life history characteristics that are expected to bear directly on demographic responses to human impacts. This information is used to consider how a better understanding of the biology of vulnerability might resolve current controversies about criteria that can be used to assess extinction risk, thereby improving national and international priorities for conservation.

2. STATUS

Status assessments of marine fishes lag far behind those of most other vertebrate taxa. Whereas the global conservation status of all of the world's birds, mammals and amphibians have been assessed by the IUCN (World Conservation Union), only 6% of the world's fishes have been examined, including freshwater species (Baillie *et al.* 2004). In part, this can be attributed to the logistical difficulties associated with surveying things that live

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Table 1. Number of marine fish species (excluding anadromous species) for which formal assessments have been made of extinction-risk or resource status.

(The number of threatened species includes those assessed as critically endangered, endangered, threatened or vulnerable according to the specific criteria of the relevant bodies. For consistency these data are summarized at the species level; in the USA and Canada some species have been assessed below the species level. We have pooled this information to provide an overall assessment of the species' status across its range within each country. Data in the last column are for species subject to stock assessments, and do not include additional species recorded in surveys whose fisheries status is not assessed.)

geographical range	no. marine fish species	no. species assessed for extinction risk status	% of total species assessed	no. of threatened species	% of species threatened	no. listed in CITES Appendix I or II	threatened species on regional legal list	species assessed for fishery resource status
global	> 15 482 ^a	487 ^b	<3.2	131	27	44		
Canada	834 ^c –950 ^d	15 ^e	1.6–1.8	8	53	3	3 ^f	17 ^g
United States	2150 ^{h,i}	82 ^j	3.8	52	63	10	2 ^k	~ 140–150 ^l
Caribbean	1552 ^h	52 ^m	3.4	38	73	3		
Mexico	1777 ^h			13 ⁿ –16 ^j		7		
Brazil	1080 ^h			22 ^o		5		
Australia	3800 ^p	114 ^{p,q}	3	18	16	26	9 ^r	67 ^{s,t}
New Zealand	964 ^u	196 ^v	20.3	51	26	4		57 ^w
India	1400 ^x	52 ^x	3.7	11	21	5		

^a Census of marine life (www.coml.org); ^b Baillie *et al.* (2004); ^c Reist (1997); ^d Coad (1995); ^e www.cosewic.gc.ca; ^f Species at Risk Act (www.sararegistry.gc.ca); ^g Department of Fisheries and Oceans (www.dfo-mpo.gc.ca); ^h FishBase (www.fishbase.org); ⁱ Mecklenburg *et al.* (2002); ^j Musick *et al.* (2000); ^k Endangered Species Act (www.nmfs.noaa.gov); ^l NMFS (2004); ^m Caribbean Fishes Specialist Group (based on slightly larger area than defined by reference h, <http://caribbeanfish.org/tf.html>); ⁿ www.conabio.gob.mx (nom-059-SEMARNAT-2001); ^o www.biodiversitas.org.br; ^p Pogonoski *et al.* (2002); ^q Cavanagh *et al.* (2003); ^r Environment Protection and Biodiversity Conservation Act (www.deh.gov.au); ^s Caton (2003); ^t Kailola *et al.* (1993); ^u www.biodiversity.govt.nz; ^v Hitchmough (2002); ^w Status of Stocks Reports 2003–2004 (www.fish.govt.nz); ^x Kapoor *et al.* (2002) (mangrove species).

underwater. The Census of Marine Life project, which has overseen some of the most recent biological explorations of the seas, has reported the discovery of approximately 400 new fish species in its first two years (<http://www.coml.org>).

Table 1 summarizes formal assessments of marine fish species that have been undertaken in several regions. Many of the holes in this table reflect difficulties in obtaining information about how many species were assessed by the various bodies responsible. These include assessments of risk of extinction as well as stock assessments by fisheries agencies. With the exception of New Zealand, for which documented assessments are available for 20% of marine species, most countries and regions have documented the status of only 1–4% of species. Of the 850–950 marine fish species in Canadian waters (Coad 1995; Reist 1997), time series abundance data are available for only about 30 species (Hutchings & Baum 2005). Of the 2150 species of marine fish in the waters off the USA excluding Alaska, the National Marine Fisheries Service has assessed the fishery status of approximately 140–150 species (NMFS 2004).

Of the species that have been examined in the sub-global assessments, approximately 35% have been listed as threatened. This does not, of course, mean that 35% of the world's marine fishes are threatened with extinction. Documentation is often lacking for species that were considered in some way, but deemed not to be at risk. This strong documentation bias greatly hampers attempts at extrapolation. Another bias stems from the fact that assessments tend to focus on groups of species considered *a priori* to be under the greatest threat. For example, IUCN Species Specialist Groups have made elasmobranchs (sharks, skates and rays) and groupers and wrasses high priorities because of well known problems faced by these taxa. At the time of writing one-third (373) of the world's elasmobranchs and 8% (74) of groupers and

wrasses have been assessed to date. Thus, while the list in table 1 is very preliminary, it does reflect a true lack of knowledge concerning the status of marine species, as well as the bias towards assessments by countries that can afford them.

The abundance of some marine fishes has fluctuated considerably over the past half-century, while that of others has increased following population decline; these fishes tend to be lower-trophic, pelagic (mid-water) species, although some demersal (bottom-dwelling) species have also exhibited some recovery, possibly due to declines in the abundance of their predators (Dulvy *et al.* 2004a,b; Daan *et al.* 2005; Hutchings & Baum 2005). By and large, however, known declines experienced by marine fishes have been substantial. By 2001, based on data for 98 populations for which estimates of breeding population size were available for a minimum of 25 years, marine fishes had declined by a median 65%, and 29% had declined by more than 80% (figure 1). The duration of the time series was not significantly associated with magnitude of decline ($r^2=0.02$, $p=0.21$). Analyses of historical data as well as ecosystem reconstructions suggest that such declines are not uncommon throughout most of the world's oceans (Myers & Worm 2005). For example, it has been estimated that more than 97% of the biomass of large (4–66 kg) fishes has been removed from the North Sea (Jennings & Blanchard 2004).

3. CAUSES OF DECLINES AND THREATENED STATUS

The primary threats to marine fishes are over-exploitation and habitat degradation and loss (figure 2a). Fishing and habitat loss have also been implicated in most of the world's extinctions at local, regional and global scales (figure 2b). It is important to note that only three of these

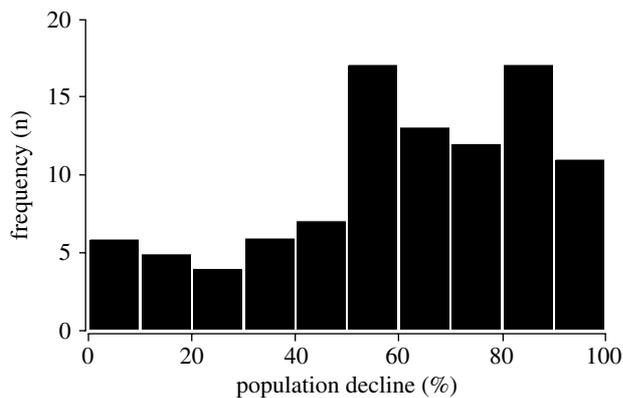


Figure 1. Frequency distribution of population declines experienced by marine fish populations. Percentage decline was calculated by comparing a metric of adult population size in 2001 relative to that population's estimated historical maximum based on stock assessments. In 83% of cases the data are based on spawning stock biomass; the rest are from catch rates by survey vessels. Data shown are for 98 marine fish populations in the North Atlantic and northeast Pacific for which a minimum of 25 years of data were available (range = 25–55 years; mean = 33.9 ± 8.9 s.d. years). These populations include those assessed by the International Council for the Exploration of the Sea, the Department of Fisheries and Oceans Canada, and by the US National Marine Fisheries Service off New England.

cases involve global extinction of entire species, though there are good reasons to expect that this is a considerable under-estimate (Dulvy *et al.* 2003).

There is no longer any question about the vulnerability to extinction of marine fish at smaller scales. Many inshore sub-populations of Atlantic herring (*Clupea harengus*) and Atlantic cod (*Gadus morhua*) have either been driven extinct or have yet to recover from historically unprecedented depletions (Smedbol & Stephenson 2001). For example, genetic evidence suggests that one of the four North Sea cod populations has disappeared since the 1950s (Hutchinson *et al.* 2003). The mean number of potentially mature cod in the Flamborough Head population was 3.1 million individuals, yet the effective population size (N_e) was estimated to be just 121 individuals (51–426, 95% CI) between 1960 and 1970. This population comprised approximately one-tenth of the North Sea cod stock prior to its decline in the 1970s, with subsequent replacement by the nearby German Bight population (Hutchinson *et al.* 2003). It is notable that many disappearances went undetected until long after they occurred. This is not surprising given that most extinctions have been detected retrospectively using indirect methods and even our best population census techniques often have little power (Roberts & Hawkins 1999; Dulvy *et al.* 2003; Maxwell & Jennings 2005).

Extrapolation from local disappearances to global extinction risk is a matter of scaling up the probabilities of sequential population extinction, allowing for any source–sink dynamics or rescue effects that may occur. There can be perverse interactions with fisheries management. For example, use of closed areas to allow fish populations to re-build is gaining in popularity. However, this needs to be combined with a reduction in overall fishing effort, to avoid displacing effort to adjacent populations (Dinmore *et al.* 2003; Myers & Worm

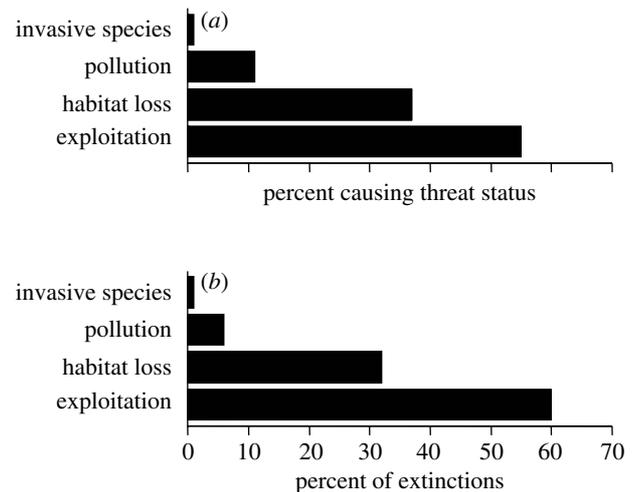


Figure 2. Causes of threat to marine fish populations and species. The figures include cases where more than one cause of threat has been identified for a given population or species. (a) North American species threatened with extinction ($n=82$), including those considered Vulnerable, Endangered or Critically Endangered (Musick *et al.* 2000). (b) Local, regional and global marine fish extinctions ($n=65$; data from Dulvy *et al.* 2003). In all cases exploitation and habitat loss were the primary causes of threat.

2005). There is an urgent need to learn more about inter-population processes, and how these interact with human behaviour (Hutton *et al.* 2004). Given the losses that have been documented so far, including strong ecosystem shifts (Pinnegar *et al.* 2000; Jackson *et al.* 2001; Dulvy *et al.* 2004a,b), and the potential for negative population growth at small sizes (the Allee effect, also known as depensation in fisheries), there is little reason to be complacent (Liermann & Hilborn 2001; Rowe & Hutchings 2003; Gascoigne & Lipcius 2004). At present, the best we can say is that of the several hundred commercially important species with populations being monitored by fisheries agencies worldwide, none has become globally extinct, despite the strong population declines summarized in figure 1.

While the declines of most threatened populations and species have been predicated by over-exploitation, the perceived pre-eminence of fishing as a threat is biased by the fact that we know the most about the status of commercially exploited species. Recent assessments of tropical coral reef species, for example, indicate that many have small, restricted population sizes, which may render them highly vulnerable to human activities (Hawkins *et al.* 2000). In most parts of the world, coral reefs are declining rapidly, with 20% of the world's reefs having been destroyed with little prospect for recovery in the near future (Wilkinson 2004). This trend is expected to accelerate in the future due to coastal development, sedimentation and global warming (Côté & Reynolds *in press*). Thus, extinction threats attributable to habitat loss might easily rival fishing as a cause of extinction risk in marine fishes (Kappel 2005).

4. CORRELATES OF VULNERABILITY

Vulnerability depends on the interaction between extrinsic threats and intrinsic ability of populations to meet the challenges that are imposed. For example, large-bodied

Table 2. Empirical comparative analyses of biological correlates of vulnerability in fishes.

taxa	location	traits considered	mortality controlled?	vulnerability metric	trait correlated with vulnerability	references
various: 18 stocks	NE Atlantic	size, age mature, growth, fecundity	yes	population trend	large size, late maturity	Jennings <i>et al.</i> (1998)
various: 23 species	global North Sea	trophic level size, age mature, growth, fecundity	no no	changes in landings population trend	high trophic level large size, late maturity, slow growth	Pauly <i>et al.</i> (1998) Jennings <i>et al.</i> (1999a)
various: 90 stocks	global	demersal versus pelagic	no	population recovery	demersal behaviour	Hutchings (2000)
various: 90 stocks	global	demersal versus pelagic	yes	population recovery	demersal behaviour	Hutchings (2001)
reef species: 2 MPAs	Philippines	size	no	population trend	large size	Russ & Alcala (1998)
reef species: 3 families	Fiji	size, age mature, growth	no	population trend	late maturity, slow growth, large size	Jennings <i>et al.</i> (1999b)
reef species: 12 MPAs	global	size	no	differences in abundance	large size	Mosqueira <i>et al.</i> (2000)
sharks: 26 species	Pacific	size, age mature, max age	yes	rebound potential at MSY (index of <i>r</i>)	late maturity, large size, high max age	Smith <i>et al.</i> (1998)
sharks: 20 species	Pacific	size, age mature, fecundity, max age	yes	rebound potential at MSY (index of <i>r</i>)	late maturity, high max age	Stevens <i>et al.</i> (2000)
skates: 8 species	North Sea	size, age mature	no	population trend	large size, late maturity	Walker & Heessen (1996)
skates: 7 species	w. UK	size, growth, length mature	yes	population trend	large size	Dulvy <i>et al.</i> (2000)
skates: 230 species	global	size, range size	no	local extinction	large size	Dulvy & Reynolds (2002)
teleosts: 63 stocks	NE Atlantic	size, age mature, growth, fecundity	yes	low recruitment in small pop. (index of <i>r</i>)	large size, demersal ecology	Denney <i>et al.</i> (2002)
Atlantic cod: 20 stocks	N. Atlantic	age mature, temperature	yes	low recruitment in small pop. (index of <i>r</i>)	late maturity	Myers <i>et al.</i> (1997)

Abbreviations: MPAs, marine protected areas; MSY, maximum stable yield.

fishes are usually targeted most heavily due to their high value and catchability (Jennings *et al.* 2001). As with any exploited species, the degree to which additional mortality reduces the probability of persistence is expected to depend on life history traits and on the magnitude of compensatory growth and/or survival responses to reductions in population density. In addition, habitat loss implies a reduction in carrying capacity whose impacts will be greatest on species that have low dispersal capability and small range sizes. These ecological traits need not be correlated with any particular suite of life history traits.

A key feature of the indeterminate growth patterns of fishes is that fundamental aspects of life histories are tied strongly to body size (Beverton & Holt 1959; Charnov 1993). Maximum body size is linked to growth, which in turn is correlated with natural mortality rates, and hence longevity, age at maturity and reproductive output. Large-bodied species with long life spans and repeated breeding are able to bet-hedge against variable and unpredictable environments for offspring survival by producing large numbers of small eggs (Hutchings 2002). Some researchers have focused on high fecundity as a predictor of resilience—one lucky female cod could repopulate the sea with her five million eggs. However, such a prediction is strikingly inconsistent with a considerable body of life history and demographic theory which predicts that fecundity will have a low impact on population growth rates compared with traits such as age at maturity and adult survival (Cole 1954; Heppell *et al.* 1999; Caswell 2001). Large-bodied species are indeed highly fecund, but they also have low maximum rates of population increase at small population size and strong density dependence in recruit production at larger population sizes, resulting in much lower reproductive output than would be expected from fecundity measures (Myers *et al.* 1997; Denney *et al.* 2002; Goodwin *et al.* in press).

Table 2 summarizes comparative analyses of biological correlates of decline, low recovery and threat status of marine fishes. These studies, nearly all of which have focused on life history traits, have found repeatedly that larger-bodied fish species have lower resilience than do smaller species, for which fishing poses the major threat to persistence. This is not simply because large-bodied species are killed more often. These species also tend to have advanced ages at maturity, and hence their populations have low rates of intrinsic population growth from small numbers, r (Myers *et al.* 1997; Denney *et al.* 2002). The same life history correlates of vulnerability apply to terrestrial species for which hunting constitutes the primary threat to persistence (Reynolds 2003). One example in fishes was shown by Jennings *et al.* (1998), who controlled for mortality differences among commercially exploited fish stocks in the northeast Atlantic, and found that larger-bodied, late maturing species still declined more rapidly than related stocks or species that were smaller. A similar effect was documented for species of skates and rays west of Britain (Dulvy *et al.* 2000). Body size is also a trait that can be readily and accurately measured, giving it a practical advantage over other traits in statistical analyses.

Most studies that have examined age at maturity have confirmed the prediction that late maturity would be correlated with vulnerability (table 2). Slow-growing

fishes have occasionally been found to be more vulnerable as well. Unfortunately, these traits, as well as body size, tend to be so inter-correlated that it has been difficult to disentangle their separate contributions.

Ecology and behaviour do not feature as strongly in the comparative analyses listed in table 2 as do life history traits. Studies of fishes have lagged behind studies of terrestrial animals in this regard. We need to know more about links between behaviour, ecology and risk of extinction. For example, there is evidence that marine fishes may have more sophisticated mating systems than previously suspected, which when combined with a tendency to gather in large, easily fished spawning aggregations, is thought to result in greater risk of extinction (Vincent & Sadovy 1998; Reynolds & Jennings 2000; Rowe & Hutchings 2003).

5. RELEVANCE TO EXTINCTION RISK ASSESSMENT

An understanding of the pattern and process of vulnerability in fishes can enhance our ability to prioritize species for conservation assessments and help improve the accuracy of those assessments. As the data summarized here show, we have barely begun to assess the status of the world's marine fishes. Furthermore, many of the assessments that have been undertaken have been called into question because of debates about the biology of vulnerability. This is not merely an academic matter, as many countries have legislation that compels them to identify and protect threatened species. Biologists who conduct these assessments are under increasing pressure to make their reasoning more defensible and transparent. An understanding of the biology of vulnerability illuminates four key controversies in such assessments.

First, it has been argued that highly fecund species should be able to withstand higher population declines, as illustrated by the incorporation of fecundity into assessments of threat status by some organizations (see below). Neither the theory nor the empirical evidence reviewed here support this. Yet, we have found this pervasive myth hard to dispel despite the widespread evidence that highly fecund fishes tend to be large-bodied with 'slow' life histories and include some of the most vulnerable species (reviewed in Sadovy 2001).

Second, it has been suggested that many fish populations exhibit high natural fluctuations in population size, which confound efforts to attribute steep declines to conservation problems (Powles *et al.* 2000; Mace *et al.* 2002). While this is true for many species in the family Clupeidae (herrings, sardines), comparative studies have shown that in general, fish species do not exhibit greater temporal fluctuations in adult population sizes than birds and terrestrial mammals (Hutchings 2001; Dulvy *et al.* 2003). On a related note, comparative studies have found little relationship between high fecundity of teleost fishes and inter-annual variation in recruitment (Mertz & Myers 1996; Rickman *et al.* 2000; Einum *et al.* 2003).

Third, there has been strong debate about whether the thresholds specified by threat criteria are prone to false alarms when applied to commercially exploited species. Hypothetically, a well managed fishery could aim for a level of mortality that would reduce the population by 50% in a few years, but this could trigger a status of 'Endangered' by

the IUCN. To avoid this anomaly, in 2001 the IUCN devised an additional series of thresholds for species in which 'the causes of the reduction in population size are clearly reversible, and understood and have ceased' (IUCN 2001). Where these conditions are met (are they ever?), the decline thresholds are higher. However, most of the populations in figure 1 would still be listed as threatened if IUCN criteria are applied. The key question from a management point of view is whether such threat criteria are in conflict with the standard reference point criteria used in fisheries management. A recent empirical analysis of European fisheries suggests that the answer is no—there is no conflict for declines of $\geq 50\%$ within the greater of 10 years or 3 generations (Dulvy *et al.* in press). At this threshold, IUCN criteria consider stocks to be 'vulnerable to extinction' and European fisheries management bodies consider them to be 'outside safe biological limits'. In other words, the aims of conservationists concerned with extinction risk need not conflict with the aims of fisheries managers—keeping fish stocks within safe biological limits should keep them safe from extinction. Indeed, the steepest decline thresholds permitted under some circumstances by the American Fisheries Society and CITES (99 and 95%), are not sufficiently precautionary as they risk postponing threat listings of populations and species until their probability of extinction is unduly high or their probability of recovery unduly low (Dulvy *et al.* in press).

A final outstanding issue concerning extinction risk is whether species that have undergone declines sufficient to qualify as threatened are really at risk of extinction when they may still number in the millions of adults (Hutchings & Reynolds 2004). For example, a small shark, *Squalus acanthias*, known as the spurdog in Europe and the spiny dogfish in North America, has declined by $> 78\%$ in the North East Atlantic over approximately three generations. This decline would be sufficient to qualify the species for Endangered status, according to the IUCN's criterion for decline, yet there are still tens of millions of adults (Mace 2004). The same is true for many species. In our view, this is the most difficult question to answer. We require a far better understanding of minimum viable population sizes, from both the genetic and demographic perspectives, before we can honestly predict whether they are truly facing a strong risk of extinction. Thus, while life histories and ecology can explain much of the variation among fish species in declines, we still have much to learn about how they interact to influence persistence and recovery.

Three fundamentally different approaches have been taken in putting the information discussed above directly into practice when assessing population status: (i) prioritization of which species to assess, (ii) adjustment of the outcomes of quantitative assessments and (iii) direct integration into quantitative assessments. We will briefly consider each of these in turn.

The information summarized in table 2 points to simple rules that can be used to screen species rapidly to set priorities for conducting more formal assessments. An example would be, 'if the species is big and individuals are being killed by fisheries, it is more apt to be in trouble than related species that are smaller'. This logic can work surprisingly well, as in the case of a study of body size and geographic range, which helped to identify skates (Rajidae) that might be vulnerable to extinction (Dulvy & Reynolds 2002). An impressive recent advance has used a

sophisticated fuzzy logic expert system to combine various vulnerability correlates in order to estimate intrinsic extinction vulnerabilities of fishes (Cheung *et al.* 2005). This method was validated against some of the studies in table 2, and proved very successful at predicting population status without using formal stock assessments.

An example of the second approach, using life histories to adjust formal quantitative assessments, is provided by Canada's national science advisory body on species at risk, COSEWIC (Committee on the Status of Endangered Wildlife in Canada). They use IUCN quantitative criteria as guidelines, rather than as strict status-determining thresholds. This allows for 'sober second thought', by considering the effects of age at maturity, body size and dispersal on extinction risk. This process can lead to a downgrading or, occasionally, an upgrading of threat status, based on life histories and ecology. While this introduces additional subjectivity into the quantitative criteria, the consensus is that as long as documentation is clear, the costs of subjectivity are out-weighed by the value of using expert opinion to consider a wider range of evidence. The comparative evidence reviewed in table 2 supports COSEWIC's use of body size and age at maturity to modulate their listings. Measures of habitat specificity of fishes and importance of dispersal characteristics for persistence and recovery would also be valuable.

The strongest use of life histories involves direct integration into quantitative assessments, as implemented by the American Fisheries Society (AFS) and by CITES. These are more controversial because of difficulties in estimating key parameters of productivity or intrinsic rates of increase, r , which are part of the process. For example, the AFS assigns species or populations to a productivity category based on intrinsic rates of natural increase for the population (r), age at maturity, body growth rate, lifespan or fecundity (Musick 1999). Populations that are deemed highly productive are allowed to decline by up to 99% before being considered vulnerable to extinction. This is strikingly less precautionary than IUCN criteria. Based on the information reviewed here, we would also assert that fecundity should be excluded from criteria used to assess extinction risk. The new CITES criteria are similar to the AFS criteria, in that the choice of decline threshold depends upon life history—with the lowest threshold reserved for species with the highest maximum rate of intrinsic growth or productivity (FAO 2002; Mace *et al.* 2002).

Although the status of most of the world's marine fishes has yet to be assessed, we still know a great deal more about them than we do for most of the world's biota. Fishes occupy a middle ground between better known vertebrates and lesser known 'everything else'. But having been belatedly swept up in the conservation movement, since the 1990s, they have often found themselves the subjects of bitter custody battles between resource managers concerned with stock recovery and conservationists concerned with extinction risk. Recent debates about extinction risk should not distract from the serious disruptions that have occurred to the ecology of the oceans as a result of human activities, about which there is no disagreement. The work reviewed here suggests that marine fishes are not fundamentally different from other taxa in the manner in which their populations respond to the interaction between extrinsic threats and intrinsic life history traits. The extraordinary declines that have

occurred under fishing pressure are almost certainly leading to local extinctions in a manner that can be predicted from intrinsic aspects of their biology. A better understanding of these processes will lead to an enhanced ability to assess the status of marine fishes and to set priorities for conservation action.

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