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Small fish, big fish, red fish, blue fish: size-biased extinction risk of the world's freshwater and marine fishes

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ABSTRACT

Aim In light of the current biodiversity crisis, there is a need to identify and protect species at greatest risk of extinction. Ecological theory and global-scale analyses of bird and mammal faunas suggest that small-bodied species are less vulnerable to extinction, yet this hypothesis remains untested for the largest group of vertebrates, fish. Here, we compare body-size distributions of freshwater and marine fishes under different levels of global extinction risk (i.e. listed as vulnerable, endangered or critically endangered according to the *IUCN Red List of Threatened Species*) from different major sources of threat (habitat loss/degradation, human harvesting, invasive species and pollution).

Location Global, freshwater and marine.

Methods We collated maximum body length data for 22,800 freshwater and marine fishes and compared body-size frequency distributions after controlling for phylogeny.

Results We found that large-bodied marine fishes are under greater threat of global extinction, whereas both small- and large-bodied freshwater species are more likely to be at risk. Our results support the notion that commercial fishing activities disproportionately threaten large-bodied marine and freshwater species, whereas habitat degradation and loss threaten smaller-bodied marine fishes.

Main conclusions Our study provides compelling evidence that global fish extinction risk does not universally scale with body size. Given the central role of body size for trophic position and the functioning of food webs, human activities may have strikingly different effects on community organization and food web structure in freshwater and marine systems.

Keywords

Biological traits, body size, fish, invasive species, life-history strategies, overfishing, Red List, threatened species.

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INTRODUCTION

Fish are among the world's most important natural resources, providing humans with numerous ecosystem goods and services, including an annual harvest of over 100 million tonnes of wild biomass worldwide (Hilborn *et al.*, 2003). The 27,977 fish species described (Nelson, 2006) comprise almost one-half of the global vertebrate diversity, and current evidence suggests that aquatic species, in particular freshwater fishes, are at much greater extinction risk than their terrestrial counterparts (Jenkins, 2003). Of the many threats, habitat loss and degradation, invasive species, overexploitation, pollution, climate change and disease, are of

major concern (Pauly *et al.*, 2002; Hilborn *et al.*, 2003; Allan *et al.*, 2005; Xenopoulos *et al.*, 2005; Dudgeon *et al.*, 2006).

In the light of these concerns, a paramount challenge for conservation biology is to identify and protect those species facing the greatest risk of extinction (Purvis *et al.*, 2000). Life histories underscore the demography of fish populations and therefore dictate intrinsic vulnerability to decline, recovery potential and, ultimately, extinction risk (Winemiller, 2005). Body size is a fundamental ecological parameter correlated with growth, which in turn is associated with natural mortality rates, longevity, age at maturity and reproductive output (Pimm, 1982; Peters, 1983). A number of regional studies have shown that maximum body

size is predictive of extinction threat for freshwater and marine species. For marine fishes, where the most significant threat is associated with direct mortality from human fishing activities (Jennings *et al.*, 1998; Dulvy *et al.*, 2003; Reynolds *et al.*, 2005a), large body size and slow population growth rates are associated with species declines. In contrast, linkages between fish body size and conservation status in freshwater ecosystems are less clear, owing to the fact that fish species are subjected to a greater range of threats (Angermeier, 1995; Duncan & Lockwood, 2001; Reynolds *et al.*, 2005b; Olden *et al.*, 2006).

Vulnerability to extinction depends on the interaction between extrinsic threats and the intrinsic ability of populations to respond to environmental change (Purvis *et al.*, 2000). Recent research has shown that linkages between extinction threat and species life histories are both complex and specific to the source of the threat. Owens & Bennett (2000) found that the extinction risk for avian families incurred through persecution and introduced predators was associated with large body size and long generation time, whereas the extinction risk incurred through habitat loss was associated with habitat specialization and small body size. For terrestrial mammals, the global extinction risk for large-bodied species was driven by intrinsic and environmental factors, whereas small-bodied species were primarily threatened by environmental factors (Cardillo *et al.*, 2005).

While the relationship between body size and extinction risk is complex, a considerable body of ecological theory predicts that small-bodied species are less vulnerable to extinction (McKinney, 1997; Cardillo, 2003; and references therein). Support for this hypothesis at the global scale comes primarily from analyses conducted for large, taxonomically inclusive faunas, including birds (Blackburn & Gaston, 1994; 1996; Owens & Bennett, 2000) and mammals (Blackburn & Gaston, 1998; Cardillo *et al.*, 2005), yet this hypothesis remains untested for the largest group of vertebrates, namely fish. In this study, we assembled maximum total body length data for 22,800 species to test the hypothesis that size–frequency distributions for globally at-risk freshwater and marine fishes are biased towards large-bodied species. We examine how maximum body length varies with different levels of global extinction risk (internationally classified as vulnerable, endangered or critically endangered) and major sources of extinction threat (habitat loss/degradation, human harvesting, invasive species and pollution), and discuss the implications of these findings for the conservation of freshwater and marine fishes.

MATERIALS AND METHODS

Body-length data

We collated data on maximum total body length for 22,800 fish species from FishBase (available at <http://www.fishbase.org>, accessed on March 2006): an information system providing an unparalleled source of data for global fishes. Our data included species and subspecies (hereafter called species) that occur primarily in freshwater ($n = 10,323$) and marine ecosystems ($n = 12,477$), which together constitute > 80% of the 27,977

Table 1 Summary of data used in the analysis. Values represent the number of fish species in each category. The footnote indicates the number of species whose body length was measured as total length defined as the length from the most anterior part of the fish to the tip of the longest caudal fin rays, standard length defined as the length from the tip of the upper jaw (typically the most anterior part of the fish) to the posterior end of the hypural plate (i.e. an array of altered vertebral elements that support the rays of the caudal fin), and fork length defined as the length from the most anterior part of the fish to the tip of the median caudal fin rays.

Category	Freshwater	Marine
Total	10,323*	12,477†
Extinction risk		
Vulnerable	277	82
Endangered	89	30
Critically endangered	118	20
Major threat types‡		
Habitat loss/degradation	85	8
Harvesting	137	8
Invasive species	73	2
Pollution	123	7
Not listed	9766	12,345
Total described species§	11,952	16,025

* $n = 4591$ total length, $n = 5696$ standard length, and $n = 36$ fork length.

† $n = 7773$ total length, $n = 4570$ standard length, and $n = 134$ fork length.

‡Values are tallied across all levels of extinction risk. Species were assigned to all major threat types that were identified, therefore the sum of these values do not equal the total number of at-risk species.

§From Nelson (2006).

described fish species of the world (Nelson, 2006). We included body-length data based on total, standard and fork length measurements for male (or if unavailable, female) specimens (Table 1). Although we recognize that this will introduce variation into our data, we consider it to be extremely small compared to the difference of more than four orders of magnitude in body length among the entire species pool. Throughout this study we use maximum body length as a measure of body size, and \log_{10} -transform all data prior to statistical analyses.

Risk and threats to global extinction

We followed the international standard for species extinction risk according to the *Red List of Threatened Species* of the World Conservation Union (IUCN) (Baillie *et al.*, 2004). The IUCN Red List is widely recognized as the most objective and authoritative listing of species that are globally at risk of extinction; species are assigned to Red List categories according to a detailed assessment of information based on standard, quantitative criteria by thousands of scientists (Lamoreux *et al.*, 2003). Body size data were available for 616 'at risk' fish species (132 marine species and 484 freshwater species) as assessed according to the critically endangered (CR), endangered (EN) and vulnerable (VU) categories of the Red List (Table 1). Species categorized as 'non-listed'

include near threatened, least concern, data-deficient and species that have not been listed by the IUCN, but this category does not include species that are extinct or extinct in the wild. Although we recognize the potential biases and limitations of the IUCN listing procedure for fishes (e.g. Musick, 1999; Hutchings, 2001), it is the most comprehensive and accurate account of the threatened status of fishes across the globe.

Recently, the IUCN developed a hierarchical classification of the major causes of species decline responsible for triggering the Red List decisions (Baillie *et al.*, 2004). To date, efforts have focused on collating threat data for amphibian, bird and mammal species, whereas considerably fewer data have been collected for other taxonomic groups. Based on the available data, we were able to assign Red Listed freshwater and marine fishes to four major sources of threat: habitat loss/degradation (associated with agricultural land-use, natural resource extraction, human infrastructure); harvesting (for food, medicine, fuel or materials); invasive species (associated with competition, predation, hybridization or pathogens/parasites); and pollution (contained in the atmosphere, land or water) (Table 1). Small sample sizes for other threat categories precluded their inclusion in the analysis. We assigned species to all major threat sources that were identified, owing to the fact that most species are threatened by multiple factors. Notably, we consider this to be a preliminarily investigation of body size differences among major threat types because the IUCN's coverage for fishes is still very sparse. Lastly, we used the Fisheries Information System of the Food and Agriculture Organization (available at <http://www.fao.org/fi>, accessed July 2006) to classify freshwater and marine species as either important or not important in global commercial or subsistence fisheries.

Statistical analysis

To address whether the body size distribution of globally threatened fish species represents a non-random sample of the world's species pool, we calculated the skew (g_1) of log-transformed maximum body length for freshwater and marine species classified according to extinction risk (critically endangered, endangered or vulnerable) and major source of extinction threat (habitat loss/degradation, harvesting, invasive species or pollution). Analyses of threat categories within levels of extinction risk were not possible due to small sample sizes. Skewness measures the deviation of the distribution from symmetry and is calculated as

$$\frac{n}{(n-1)(n-2)} \sum (x_i - \bar{x})^3,$$

where x_i is the log-transformed maximum body length for species i , and n is the number of species. A positive g_1 indicates a right-skewed distribution with a greater frequency of small-bodied species, and a negative g_1 indicates a left-skewed distribution with a greater frequency of large-bodied species, while a g_1 of zero indicates a uniform distribution. The statistical significance of g_1 from zero was calculated according to Sokal & Rohlf (1995).

Taxonomically related species share many aspects of biology as a result of inheritance from common ancestors. We used a bootstrap approach to test for statistical differences in g_1 between categories of extinction risk and major threat, and a null species pool that controlled for the effect of shared ancestry among species. Specifically, the bootstrap test was designed to account for two factors that may confound the relationship between fish body size and extinction risk. First, the degree of skew in body size–frequency distribution varies phylogenetically (Knouft, 2004). Second, there is taxonomic selectivity in the vulnerability to extinction (Duncan & Lockwood, 2001; del Monte-Luna & Lluh-Belda, 2003). The bootstrap test comprised randomly selecting X species from the entire species pool (either freshwater or marine) represented only by the set of families that are listed under risk/threat category Y , where X equals the total number of species listed under category Y (one of either three levels of extinction risk or four sources of major threat) (see Table 1). Next, we calculated g_1 , and repeated the entire bootstrap procedure 9999 times. Statistical significance was calculated by comparing the observed g_1 to the null distribution of g_1 values from the bootstrap samples, where the P value equals the proportion of bootstrap g_1 values (including the observed) that were more extreme (either positive or negative) than the observed g_1 . Notably, we used the bootstrap approach instead of independent contrasts because a composite phylogeny of 22,800 fish species was not available or feasible to construct.

The dip test of unimodality was used to assess the shape of the body size–frequency distribution for different Red List categories (Hartigan & Hartigan, 1985). The dip statistic measures departure of a sample from unimodality. Asymptotically, the dip for samples from a unimodal distribution approaches zero and that for samples from any multimodal distribution approaches a positive constant.

RESULTS

Maximum body size (total length) spanned more than four orders of magnitude, from the world's smallest fish species recently found in highly acidic peat swamps (*Paedocypris progenetica*) with a maximum length of 7.9 mm (Kottelat *et al.*, 2006), to the world's largest fish species, the whale shark (*Rhincodon typus*), with a maximum length of 20,000 mm or 20 m. The global fish fauna exhibited a characteristic positive or right-skewed body size–frequency distribution (Fig. 1); a pattern that was stronger for freshwater fishes ($g_1 = 0.54$, $t = 22.29$, d.f. = 10,322, $P < 0.001$) than for marine fishes ($g_1 = 0.12$, $t = 5.91$, d.f. = 12,476, $P < 0.001$). Right-skewness has been observed for many taxonomic groups, illustrating that small-bodied species tend to greatly outnumber large-bodied species.

Extinction risk

The body-size distribution of at-risk freshwater fishes (classified here as globally vulnerable, endangered or critically endangered) was highly right-skewed ($g_1 = 1.27$, $t = 11.41$, d.f. = 483, $P < 0.001$) at a magnitude significantly greater than the global

Figure 1 Body size–frequency distributions (log-transformed) for global freshwater and marine fish faunas. Results are presented for all freshwater (a) and marine fish species (b), and those freshwater (c) and marine fish species (d) classified as vulnerable, endangered or critically endangered according to the IUCN Red List. The skewness coefficient (g_1) was calculated for log-transformed values of maximum body length. A positive g_1 indicates a right-skewed distribution with a greater frequency of small-bodied species, and a negative g_1 indicates a left-skewed distribution with a greater frequency of large-bodied species, while a g_1 of zero indicates a uniform distribution. Sample sizes are presented in Table 1.

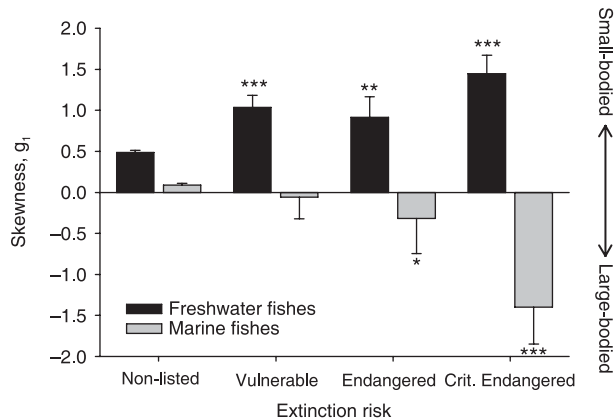
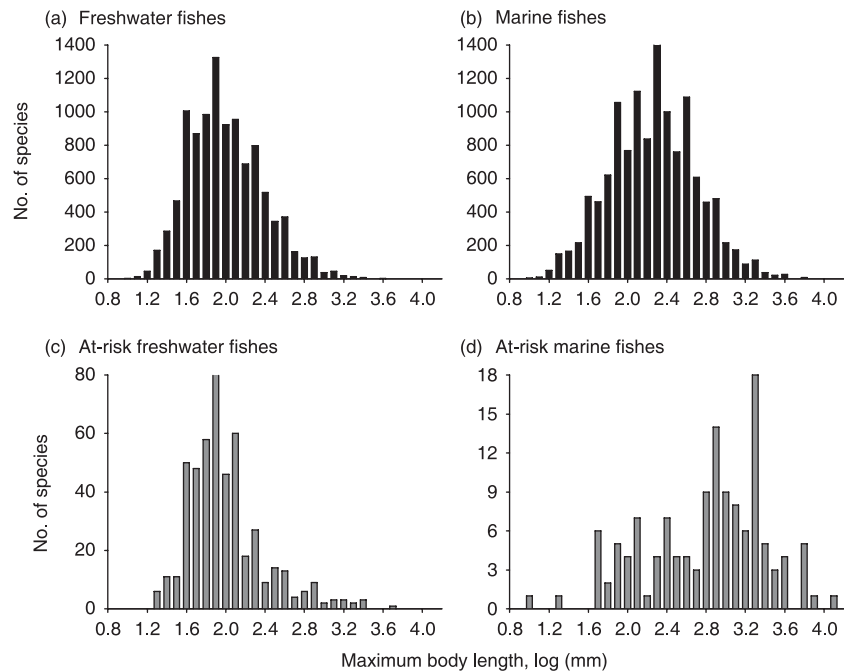


Figure 2 Skewness (g_1) in body size–frequency distributions for freshwater and marine fish species along a gradient of increasing extinction risk according to the IUCN Red List. Statistical significance from random is based on a bootstrap test that accounts for the higher-order influence of phylogeny on body size: * $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$ (see Materials and Methods). Sample sizes are presented in Table 1.

freshwater species pool ($t = 8.39$, d.f. = 10,321, $P < 0.001$) even after controlling for phylogeny (bootstrap test: $P < 0.001$). This indicates that threatened freshwater species tend to be smaller-bodied representatives of the global species pool. The opposite is true for at-risk marine fishes, where the body-size distribution was strongly left-skewed ($g_1 = -0.44$, d.f. = 131, $t = -2.07$, $P = 0.040$); a value that exceeded all marine fishes ($t = -2.96$, d.f. = 12 475, $P < 0.001$) and closely related species (bootstrap phylogeny test: $P < 0.001$). Threatened species in marine environments are therefore more likely to be larger-bodied representatives of the global species pool.

Body size–frequency distributions varied with the level of global imperilment (Fig. 2). Freshwater fishes under increasing risk of extinction, from vulnerable to endangered to critically endangered, were characterized by significantly greater right-skew body size distributions (bootstrap test for all extinction levels: $P < 0.05$). These results suggest that for global freshwater fishes there is a general tendency for smaller-bodied species to exhibit increasingly greater risk of extinction compared to closely related species. By contrast, greater levels of extinction risk for marine fishes were associated with increasingly larger body size distributions or greater left-skewed distributions (bootstrap test for critically endangered: $P < 0.01$; endangered: $P < 0.10$; Fig. 2). The difference in size-biased extinction risk between freshwater and marine fishes is best illustrated by the comparison of body size distributions for critically endangered species, in which the magnitude of skew is nearly identical, but in opposite directions (freshwater fishes $g_1 = 1.45$; marine fishes $g_1 = -1.41$).

Body size–frequency distributions (based on percentage of species in different body-length size classes) for at-risk species provide further evidence for differential size-biased extinction risk between freshwater and marine fishes. For freshwater fishes we found a significant bidirectional size bias where both small- and large-bodied species were more likely to be facing a global extinction risk (Fig. 3a, dip statistic = 0.12, d.f. = 14, $P = 0.042$). This supports a bimodal size–frequency distribution for threatened freshwater fishes even after accounting for the high proportion of small-bodied fishes in the global species pool. At-risk marine fishes, on the other hand, showed no evidence for bimodality, with large-bodied species more likely to be threatened (Fig. 3b, dip statistic = 0.07, d.f. = 16, $P = 0.889$), although small-bodied fishes still exhibited elevated risk. Subsequent analyses revealed that the results from the dip test were independent of histogram class size: freshwater (dip statistic = 0.13, d.f. = 28, $P = 0.035$)

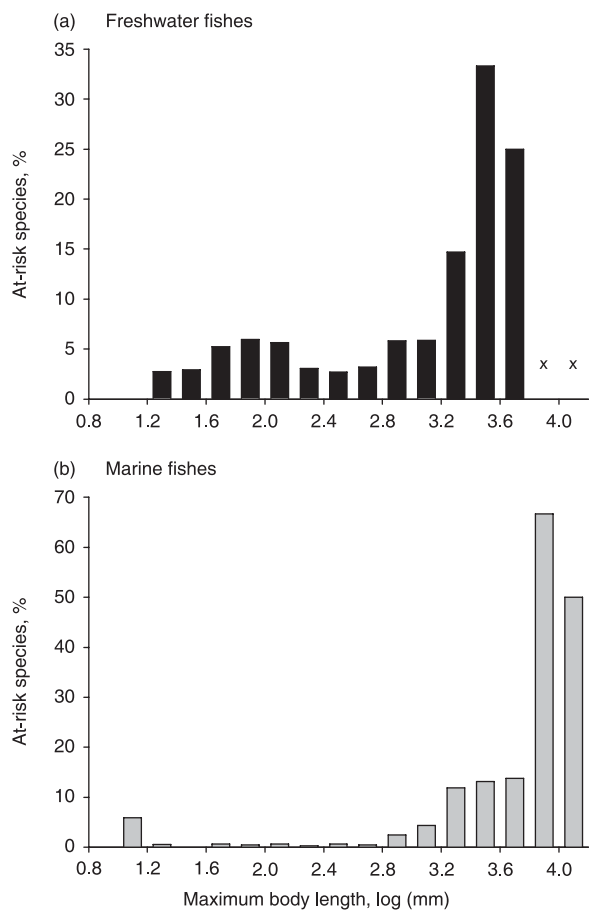


Figure 3 Body size–frequency distributions for at-risk freshwater (a) and marine fish species (b) classified as vulnerable, endangered or critically endangered according to the IUCN Red List. Results are presented as the percentage of species in different body-length size classes (X indicates no species).

and marine (dip statistic = 0.07, d.f. = 32, $P = 0.775$) for a class size of 0.05 (log mm); freshwater (dip statistic = 0.12, d.f. = 56, $P = 0.032$) and marine (dip statistic = 0.08, d.f. = 64, $P = 0.642$) for a class size of 0.10 (log mm).

Major threats to extinction

Body size–frequency distributions of at-risk species (all risk categories combined) differed depending on the major source of extinction threat (Fig. 4). Freshwater fishes were characterized by significantly greater right-skew body size distributions for all threat sources (bootstrap test for all extinction levels: $P < 0.01$), corroborating the previous result that smaller-bodied freshwater species exhibit greater risk of extinction compared to closely related species. We found no major differences in body-size distributions among the sources of threat. By contrast, at-risk marine fishes from harvesting exhibited a highly left-skewed distribution, or in other words a greater frequency of large-bodied species were at-risk ($g_1 = -0.73$, bootstrap test $P < 0.01$), followed by fishes threatened by pollution ($g_1 = -0.69$, bootstrap test

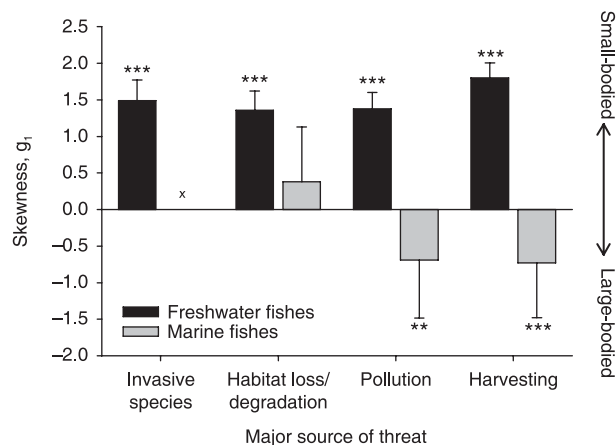


Figure 4 Skewness (g_1) in body size–frequency distributions for at-risk freshwater and marine fish species under extinction risk from four major sources of threat according to the IUCN Red List. Threat types are presented in order of increasing sample size (see Table 1). Statistical significance from random is based on a bootstrap test that accounts for the higher-order influence of phylogeny on body size: * $P < 0.10$; ** $P < 0.05$; *** $P < 0.01$ (see Materials and Methods). X indicates that sample size was too small to calculate g_1 .

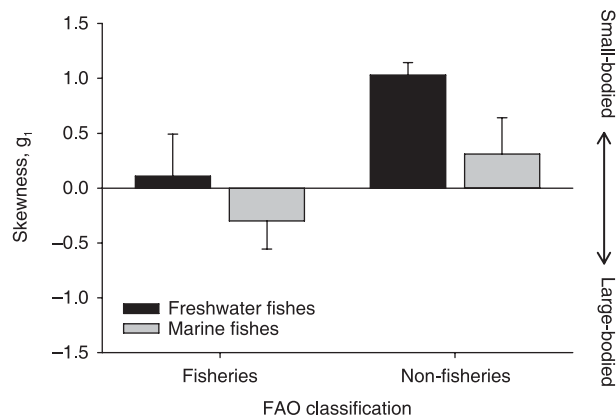


Figure 5 Skewness (g_1) in body size–frequency distributions for at-risk freshwater and marine fish species classified as either important or not important in global commercial or subsistence fisheries according to the Fisheries Information System of the Food and Agriculture Organization.

$P < 0.05$) (Fig. 4). Marine species imperilled by habitat loss/degradation showed the opposite pattern and were considerably smaller-bodied compared to other at-risk species ($g_1 = 0.38$); however, this value was not significantly different than that for closely related species (bootstrap test $P < 0.36$).

Size-biased extinction risk associated with human harvesting was supported by comparisons of at-risk freshwater and marine species classified as either important or not important in global commercial or subsistence fisheries (Fig. 5). At-risk marine fishes that are considered important to commercial or subsistence fisheries were significantly more left-skewed (i.e. larger-bodied) than at-risk non-fisheries marine species ($t = 9.23$, d.f. = 138,

$P < 0.001$). Similarly, we found a greater frequency of at-risk large-bodied fishes that are considered important to commercial or subsistence freshwater fisheries compared to at-risk non-fisheries species ($t = 12.33$, d.f. = 489, $P < 0.001$).

DISCUSSION

Ecological theory and data suggest that species with fast life histories, i.e. short generation times and associated traits such as small body size, should be able to persist better and recover more rapidly from human activities. In contrast, slow life histories — characterized by long-lived species that grow slowly, have late maturity and attain large body sizes — are linked to low maximum rates of population growth and are intrinsically more vulnerable to environmental change and, ultimately, extinction (Pimm *et al.*, 1988; Reynolds, 2003). Evidence from global bird and mammal species supports the hypothesis that large-bodied species are more vulnerable to extinction. Our study is the first to show that this prediction is not universally true for the world's largest group of vertebrates, fish. At the global scale, our results corroborate previous comprehensive studies illustrating the disproportionate risk of extinction faced by large-bodied marine fishes (Jennings *et al.*, 1998; Duly *et al.*, 2003; Reynolds *et al.*, 2005a). By contrast, body-size distributions of at-risk freshwater fishes are bimodal, suggesting that both small- and large-bodied freshwater species are more likely to be threatened by global extinction. This result agrees with the continental analysis of Reynolds *et al.* (2005b), who found that threatened freshwater fishes in Europe were smaller-bodied than related species at lower risk, whereas the inclusion of anadromous species (i.e. larger-bodied species primarily at-risk from over-exploitation) caused the relationship to reverse.

Size-bias extinction risk for fishes is a result of a number of mechanisms that are both directly and indirectly linked to body size (Winemiller, 2005). Despite the many challenges of examining the relationship between sources of extinction threat and body size for the global fish species pool (species-specific threats are currently available for only a limited number of IUCN Red Listed fishes, and the results reported here should be regarded as preliminary), we expect that particular threats may differentially endanger fish species of different sizes.

Over-exploitation and habitat loss and degradation are the leading drivers of extinction threat for marine fishes (Reynolds *et al.*, 2005). Our results support the observation that commercial fishing activities disproportionately threaten at-risk large-bodied marine species via selective harvesting practices (Dulvy *et al.*, 2003; Kappel, 2005). Species groups such as the chondrichthyan fishes (sharks, skates and rays) are examples of large-bodied fishes that show greater susceptibility to over-harvesting and limited potential for recovery (Jennings *et al.*, 1998; Musick *et al.*, 2000; Hutchings & Reynolds, 2004). Interestingly, marine fishes threatened by habitat loss and degradation were considerably smaller than those under extinction risk from other threats. These included coral reef species such as angelfishes (Pomacanthidae), wrasses (Labridae) and damselfishes (Pomacentridae), which are characterized by small body sizes and are faced with

the 'triple jeopardy' of extinction risk associated with small geographical ranges, small population sizes and specialized habitat requirements (Munday & Jones, 1998). The extensive habitat degradation that is occurring on coral reefs continues to have profound consequences for the existence of small-bodied reef fishes across the world (Munday, 2004).

For global fresh waters, small-bodied species groups, such as pupfishes (Cyprinodontidae), darters (Percidae) and live-bearers (Poeciliidae), and large-bodied species groups, such as sturgeons (Acipenseridae) and shark catfishes (Pangasiidae), are highly susceptible to global extinction. However, in contrast to marine ecosystems, the panoply of threats in fresh waters and their relation to the dynamic aquatic–terrestrial interface (i.e. river basins as integrators of the landscape: Dudgeon *et al.*, 2006) is expected to affect different sized species in a manner that is both complex and particular to species and locations. In support of this, we found minimal differences in body-size distributions among freshwater fishes endangered by different threats, with one notable exception. Our findings showed that at-risk freshwater fishes that are considered important to commercial or subsistence fisheries are much larger than non-fisheries freshwater species that are similarly threatened by global extinction. While we expect that size-selective harvesting efforts of freshwater fishes may be less prominent compared to marine fisheries, our findings do suggest that the size-biased effects of human fisheries may exist in both freshwater and marine ecosystems (Hogan *et al.*, 2004; Allan *et al.*, 2005). In general, although the effects of multiple threats on the extinction risk of freshwater fishes may not be easily predicted at regional and global scales, we disagree with the notion that life histories may simply be irrelevant for this group of species (Duncan & Lockwood, 2001). Rather, we expect species extinction risk to vary nonlinearly with individual life-history traits (our study) and only be predictable by considering coevolving complexes of multiple traits (Olden *et al.*, 2006).

We suggest that a number of fundamental differences between how humans (and the terrestrial systems we inhabit) interact with marine and freshwater systems may influence the different global body size–extinction risk relationship found in our study. Because trophic position often increases with body size within a given food web (e.g. Cohen *et al.*, 1993), human activities that threaten fish species of different sizes in freshwater and marine systems may translate into strikingly different effects on community organization and food web structure and function (Layman *et al.*, 2005). Recent research for other major taxonomic groups showing that body size may be linked to different levels of extinction risk from particular sources of threat (Owens & Bennett, 2000; Cardillo *et al.*, 2005) highlights the need for a comprehensive assessment and better understanding of the population status and threats to vulnerable populations of the world's fishes.

Our study provides compelling evidence that global fish extinction risk does not universally scale with body size. This result is especially relevant in the context of a human society that attaches special importance to charismatic megafauna. Of immediate concern is our finding that a substantial number of small-bodied freshwater fishes are threatened by global extinction. These species may reside in environments where few people ever

see or study them, thus making it difficult to muster public attention and conservation funding. These findings highlight a potential, and likely significant, disparity between the numerous small-bodied freshwater fishes that are at high risk of global extinction and the research, management and education efforts that focus predominantly on imperilled large fishes, or small marine fishes inhabiting tropical coral reefs. More generally, our study underscores the need to understand the differential selectivity and mechanisms of fish declines in freshwater and marine ecosystems to facilitate a more proactive science for triaging threatened species before global extinction occurs.

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