Communications

Life-history correlates of extinction risk and recovery potential

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Abstract. Extinction risk is inversely associated with maximum per capita population growth rate (r_{max}). However, this parameter is not known for most threatened species, underscoring the value in identifying correlates of r_{max} that, in the absence of demographic data, would indirectly allow one to identify species and populations at elevated risk of extinction and their associated recovery potential. We undertook a comparative life-history analysis of 199 species from three taxonomic classes: Chondrichthyes (e.g., sharks; $n = 82$), Actinopterygii (teleost or bony fishes; $n = 47$), and Mammalia ($n = 70$, including 16 marine species). Median r_{max} was highest for (and similar between) terrestrial mammals (0.71) and teleosts (0.43), significantly lower among chondrichthyans (0.26), and lower still in marine mammals (0.07). Age at maturity was the primary (and negative) correlate of r_{max}. In contrast, although body size was negatively correlated with r_{max} in chondrichthyans and mammals, evidence of an association in teleosts was equivocal, and fecundity was not related to r_{max} in fishes, despite recurring assertions to the contrary. Our analyses suggest that age at maturity can serve as a universal predictor of extinction risk in fishes and mammals when r_{max} itself is unknown. Moreover, in contrast to what is generally expected, the recovery potential of teleost fishes does not differ from that of terrestrial mammals. Our findings are supportive of the application of extinction-risk criteria that are based on generation time and that are independent of taxonomic affinity.

Key words: age at maturity; body size; Chondrichthyes; conservation; marine; population growth rate; sharks; teleosts.

INTRODUCTION

From a conservation perspective, historically unprecedented reductions in abundance have hastened efforts to identify correlates of extinction risk in a variety of taxa (Mace et al. 2008). For most potentially threatened species, however, data on demographic parameters that might allow one to model population viability (e.g., Beissinger and McCullough 2002) are lacking. A similar challenge is faced by agencies tasked with adopting a precautionary approach to fisheries management, as fisheries scientists are under considerable pressure to assess the status of data-poor fish stocks (Patrick et al. 2010). Various proxies of extinction risk and population viability have been proposed that would allow one to evaluate the status of species and populations for which abundance or distributional data are sparse, unreliable, or unavailable (e.g., Ross 1992, Reed and Shine 2002, Pilgrim et al. 2004, Hero et al. 2005, Thomas et al. 2006, García et al. 2008, Patrick et al. 2010).

Suggested life-history correlates of increased extinction risk have included large body size (Gaston and Blackburn 1995, Bennett and Owens 1997, Denney et al. 2002), long life span (Smith et al. 1998, Stevens et al. 2000), and delayed age at maturity (Reynolds et al. 2005). Among potential life-history correlates, perhaps none has a longer history than that of fecundity. The annual production of hundreds of thousands, often millions, of eggs per female provided the basis for Thomas Huxley's prediction in 1883 that "all the great sea-fisheries are inexhaustible" (Smith 1994). Indeed, the hypothesis that high fecundity confers low extinction risk and high recovery potential is one of several empirically suspect assertions that have contributed to the perception that the threat of extinction for marine fishes is lower than that of other vertebrates (Musick

1999, DeMaster et al. 2004). Studies continue to incorporate the assumption that recovery potential is positively associated with fecundity across vertebrates (Patrick et al. 2010, Prugh et al. 2010).

One important limitation characteristic of most analyses of extinction-risk correlates is that the metric of extinction probability typically examined is that of species status category (e.g., endangered, threatened, vulnerable), the assignment of which is unavoidably encumbered by a level of subjectivity that almost certainly varies among species and among species status assessors. A second limitation is that these categories yield, by necessity, a categorical rather than a continuous metric of extinction risk, which constrains analyses that attempt to detect correlations between extinction risk and quantitative species- or population-specific traits, such as body size and fecundity. Continuous metrics of population persistence are also needed when providing advice on the harvest control rules in fisheries management, i.e., sets of conditions that govern how fishing mortality should change with breeding population size.

To address these limitations, we undertook a study of how a continuous, quantitative, and unequivocal metric of depicting extinction risk is associated with life history. All else being equal, this metric, maximum per-capita population growth rate, or r_{max}, is negatively associated with extinction probability (Lande 1993, Dulvy et al. 2004, Mace et al. 2008) and is positively associated with the instantaneous rate of mortality required to drive a species to extinction, $F_{extinct}$ (Dulvy et al. 2004, García et al. 2008). However, in the absence of detailed demographic information, data that are frequently lacking for potentially threatened species, r_{max} itself cannot be determined. However, if r_{max} is correlated with specific life-history traits that are typically known, r_{max} could then be predicted based on such life-history correlates. More generally, knowledge of such correlations between life-history traits and r_{max} would also be useful in identifying species that are more likely to have low r_{max} and, thus, to be an increased risk of extinction.

The objectives of this study are threefold. The first is to estimate and then compare r_{max} for three classes of vertebrates (Chondrichthyes, Actinopterygii, and Mammalia; $n = 199$ species) to evaluate the degree to which extinction risk differs between fishes and mammals ceteris paribus. The second objective is to quantify potential correlations between r_{max} and each of three life-history traits for which data on at least one trait tend to be readily available: fecundity, maximum body size, and age at maturity. Our third objective is to test the null hypothesis that correlations between each of these traits and r_{max} do not differ among the three vertebrate classes examined here.

Materials and Methods

Estimation of r_{max}

Following established methods (Goodman 1984, Myers et al. 1997, 1999, Myers and Worm 2005),

estimates of r_{max} for teleost fish were derived from the Euler-Lotka equation in which survival to age at first reproduction (l_α), adult survival (p), and annual fecundity (measured in daughters, b) are assumed constant at low population size, from maturity ($t = \alpha$), until age at senescence ($t = \omega$), so that

$$l_\alpha b \sum\nolimits_{t=\alpha}^{\omega} e^{(-r_{max}t)} p^{(t-\alpha)} = 1. \qquad (1)$$

To estimate l_α at low population size, we fit data on annual offspring production and adult reproductive biomass for each population to a Ricker stock-recruitment function (Myers et al. 1997, 1999), a model in which instantaneous juvenile survival ($\log l_\alpha$) is a linear function of offspring production. For chondrichthyans and mammals, r_{max} was also estimated from the Euler-Lotka equation, but using data on age at maturity, fecundity, and natural mortality obtained from the literature (Appendix). (The r_{max} values differ among populations either because of population-level differences in l_α, age at maturity, or natural mortality.)

Given that the number of daughters produced annually by each female ($\tilde{\alpha}$) equals $l_\alpha b$, Eq. 1 can be rearranged (following Myers et al. 1997) so that it takes the following form:

$$\tilde{\alpha} = (e^{r_{max}})^\alpha - p(e^{r_{max}})^{\alpha-1} \qquad (2)$$

where $\tilde{\alpha}$ is the maximum annual number of female individuals produced per reproducing female, α is the age at maturity, or first parturition in mammals, and p is the adult annual survival rate. For chondrichthyans and mammals, $\tilde{\alpha}$ was calculated as $f/i \times 0.5$, where f and i represent maximum litter size and interbirth interval, respectively. In all cases, r_{max} was calculated iteratively using the optim function available in the R statistical software, v. 2.3.0 (R Development Core Team 2006).

Data

Using data collected in an online database by R. Myers, estimates of life-history traits for teleost fishes were collated for 47 species, encompassing 19 families and eight orders, ranging in body size from 0.040 kg to 684 kg (Appendix). Population-level data for some traits were available for 29 species. Fecundity data, obtained from Fishbase, were assigned at the species level, rather than at the level of population (data *available online*).[6] (Although fecundity varies with body size in teleosts, there is a lack of population-specific information on fecundity–body-size relationships and on the proportional representation of body sizes within populations.)

Data on chondrichthyans were collated for 82 species (23 families and 12 orders), ranging in body size from 0.473 to 3600 kg. Population-level data for some traits were available for 23 species. Most data were obtained from primary literature sources (Appendix). However, when estimates of litter size, interbirth interval, or body

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[6] http://www.fishbase.org

mass were not available for a particular population, the values from other populations of the same species were used instead. Due to the paucity of direct estimates of adult annual mortality (M_a) for chondrichthyans, M_a was estimated from Jensen's (1996) equation relating mortality rate and α ($M_a = 1.65/\alpha$). Although arguably not ideal, the use of this statistical relationship to estimate natural mortality (a fundamental component of r_{max}) allows us to include this understudied class of vertebrates in our analysis and is an approach that has been applied in many other analyses (e.g., Hisano et al. 2011).

Data on mammals were obtained for 70 species, including 29 families and 10 orders, ranging from 0.006 to 50 000 kg in body mass (Appendix). Data on marine mammal populations were those collated by Whitehead and Mann (2000). Terrestrial mammal data were those compiled by Purvis and Harvey (1995) with litter size estimates obtained from their original sources whenever available. Annual mortality (M_a) was derived from Purvis and Harvey's (1995) formulation in which monthly adult mortality (M_m) was calculated as $M_a = -\ln((e^{-M_m})^{12})$.

Analyses

If r_{max} is associated with a life-history trait for which data are typically available for a particular species or population, it is important to know the strength of such univariate associations. Although a multivariate analysis might also be considered, the general applicability of such an approach would be hindered by a lack of readily available data for all three life-history traits, in addition to the strong correlations known to exist among these traits (Roff 2002). Thus, our aim was to detect pairwise correlations between r_{max} and each considered life-history trait.

We modeled log-transformed r_{max} with three linear mixed-effect models (LMEs), where log-transformed maximum number of eggs produced per breeding season (i.e., fecundity), log-transformed body mass, or age at maturity was considered as a fixed covariate together with taxonomic class (factor) and its interaction with the life-history covariate. Taxonomic hierarchy was included as a nested random effect to control for associations among related species resulting from their common phylogenetic history. Analyses were performed at the species level. Among fishes for which population level data were available, species-level estimates for the trait under consideration were obtained as averages of the population-specific estimates of the same species. To also utilize the population-level information available for fishes, we further investigated the effects of the three life-history traits on log(r_{max}) in teleosts and chondrichthyans separately, assigning species to the innermost level among the nested random effects. Model selection was done through stepwise model reductions, based on likelihood ratio tests, as suggested by Crawley
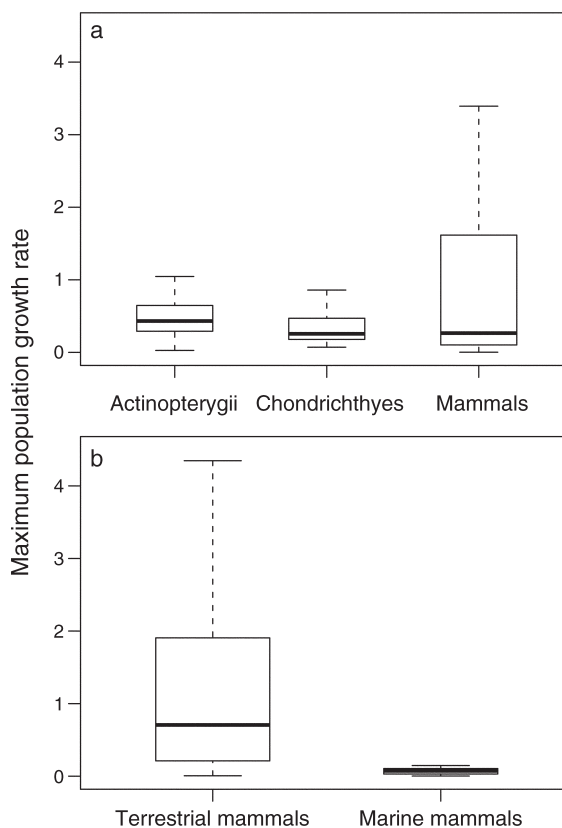

FIG. 1. Maximum population growth rates for (a) teleost fishes, chondrichthyan fishes, and mammals and (b) terrestrial and marine mammals separately. The central line of the boxplots indicates the median, boxes span the interquartile range, and whiskers encompass values less than 1.5 box lengths away from the box. Outliers are excluded from the figure.

(2007). Analyses were performed in R 2.10.1 (R Development Core Team 2009).

RESULTS

Maximum population growth rates differed among teleosts, chondrichthyans, and mammals (Fig. 1a). At the level of taxonomic class, and based on the observation that their bootstrapped confidence levels (CIs) did not overlap, the median r_{max} of teleosts (0.432 [CI 0.354–0.531]) exceeded that of chondrichthyans (0.256 [CI 0.207–0.298]). Although the r_{max} of mammals (0.266) was much less than that of teleosts, the confidence interval about the median was extremely wide (0.138–0.706) and overlapped the CI for teleosts. Partitioning mammals into terrestrial ($n = 54$) and aquatic ($n = 16$) species, the median r_{max} for terrestrial mammals was 0.706 (CI 0.270–1.286) while that for marine mammals was 0.073 (CI 0.030–0.095) (Fig. 1b). Thus, based on their median estimates and degree of CI overlap, r_{max} was highest among teleosts and terrestrial mammals, significantly lower among chondrichthyans, and lower still among marine mammals.
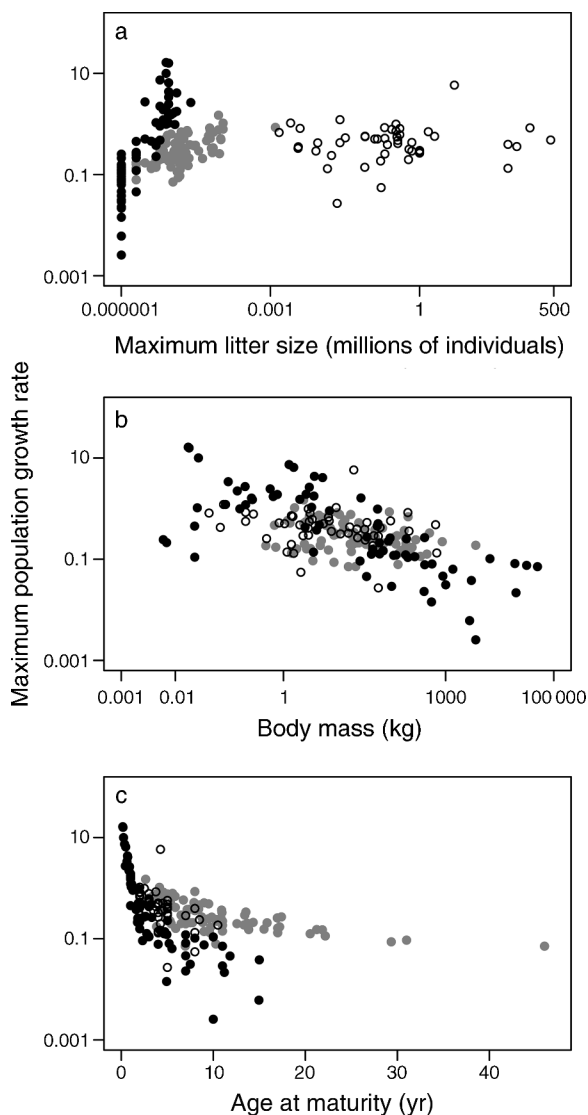
FIG. 2. Relationships between maximum population growth rate and (a) maximum litter size, (b) body mass, and (c) age at maturity for 47 species of teleost or bony fishes (open symbols), 82 chondrichthyan fishes (sharks, skates, rays, chimaeras; gray symbols), and 70 species of mammals (black symbols). Note the log scale for all axes except the *x*-axis in panel (c).

Maximum population growth rate was significantly affected by interactions with both the life-history trait under consideration (Fig. 2) and taxonomic class in all three models ($P < 0.001$ in all likelihood ratio tests for model reduction). The main effect of taxonomic class (i.e., its effect on the intercept) could be reduced in the model for which body size was the considered life-history covariate (likelihood ratio = 1.574, $P = 0.455$), but not in the other models ($P < 0.001$ in all likelihood ratio tests). Fecundity was not correlated with r_{max} in fishes, although a positive association was evident in mammals (Table 1, Fig. 2a). Body size was negatively

correlated with maximum population growth rate in chondrichthyans and mammals, whereas in teleosts the negative correlation was not significant (Table 1, Fig. 2c). Age at maturity was strongly and negatively correlated with r_{max} within each taxonomic class (Table 1, Fig. 2c). None of the variance in r_{max} could be attributed to subclass or superorder, whereas some variability was encompassed by order (27.9–34.4%), family (24.0–31.2%), and genus (13.4–28.9%) (Table 1); 17.8–27.4% of the variation in r_{max} remained among species within genera.

Population-level analyses in teleost fishes did not reveal any new trends relative to those documented by the species-level analyses, such that age at maturity remained negatively correlated with r_{max} (coefficient for the life-history covariate = -0.203, $t_{13} = -7.85$, $P < 0.001$), and the effects of fecundity (coefficient for the life-history covariate = -0.012, $t_{13} = -0.250$, $P = 0.807$) and body size (-0.078, $t_{13} = -1.613$, $P = 0.131$) on maximum population growth rate remained nonsignificant (Table 1). In the population-level analyses for chondrichthyans, both age at maturity (-0.048, $t_{34} = -11.986$, $P < 0.001$) and body size (-0.107, $t_{34} = -3.509$, $P = 0.001$) retained the negative associations with r_{max} that had been documented previously (Table 1). However, in contrast to the species-level analysis, fecundity appeared to be significantly associated with r_{max} when the data were analyzed at the population level (0.243, $t_{34} = 4.132$, $P < 0.001$).

DISCUSSION

Our comparative analysis reveals three primary findings. First, by providing quantitative estimates of r_{max}, our work shows that maximum population growth rate and, thus, extinction probability (which also depends on magnitude of exposure to a specific threat) differs among taxonomic classes of vertebrates. Second, we find that population growth rate is highly correlated with age at maturity across taxa, suggesting that this life-history metric might be the most reliable predictor of r_{max} within and among the vertebrate classes considered here. This finding is consistent with early theoretical work (e.g., Cole 1954), with numerous empirical studies of much narrower taxonomic breadth (e.g., Purvis et al. 2000, Denney et al. 2002), and with efforts to apply risk-of-extinction criteria that are based on generation time (which is highly correlated with age at maturity; Roff 2002) to populations and species independently of their taxonomic affiliation (Mace et al. 2008). Third, one particularly novel aspect of our study is the specification of regression models that can be used to predict maximum population growth rate when data for only one significant life-history correlate of r_{max} are available. These models can be used in support of efforts to apply life-history criteria to species conservation and management.

Comparison of r_{max} among the vertebrate classes confirms empirically the prediction (Holden 1973, Dulvy et al. 2003, Myers and Worm 2005) that the maximum

TABLE 1. Effects of taxonomical class and three considered life-history traits and on the log of maximum per capita population growth rate ($\log[r_{max}]$), as estimated by linear mixed effect models ($n = 199$).

Life-history covariate and taxonomic class	Intercept	Covariate coefficient	t_{64}	P
log(maximum litter size)†				
Fish	−1.041	−0.0004	−0.008	0.993
Sharks	−1.727	0.137	1.506	0.137
Mammals	−2.524	1.352	9.869	0.001
log(weight)‡				
Fish	−0.783	−0.102	−1.894	0.060
Sharks	−0.783	−0.123	−2.896	0.006
Mammals	−0.783	−0.317	−7.013	0.001
Age at maturity§				
Fish	−0.213	−0.209	−6.089	0.001
Sharks	−0.823	−0.049	−5.817	0.001
Mammals	−0.284	−0.355	−10.050	0.001

† Variance components associated with subclass, superorder, order, family, genus, and residuals: 0.0%, 0.0%, 27.9%, 31.2%, 13.4%, and 27.4%, respectively.

‡ Variance components associated with subclass, superorder, order, family, genus, and residuals: 0.0%, 0.0%, 34.4%, 29.5%, 16.5%, and 19.6%, respectively.

§ Variance components associated to subclass, superorder, order, family, genus, and residuals: 0.0%, 0.0%, 29.2%, 24.0%, 28.9%, and 17.8 %, respectively.

population growth rate, and thus recovery potential, of sharks, skates, rays, and chimaeras is, on average, significantly lower (reflecting increased extinction risk) than that of teleosts. Our analysis indicates that this difference in r_{max} can likely be attributed to the larger body size and older age at maturity characteristic of chondrichthyans. However, notwithstanding this difference between classes of fishes, our work also indicates that the r_{max} of terrestrial mammals does not differ, on average, from that of teleost fishes. Given the positive association between r_{max} and $F_{extinct}$ (Dulvy et al. 2004, García et al. 2008), the logical extension of this finding is that, all else being equal, the probability of extinction among teleosts is similar to that of terrestrial mammals.

We find no support for the hypothesis that increased fecundity confers lower extinction threat and increased resilience in fishes. Despite a lack of theoretical support (Cole 1954, Hutchings 2001, Sadovy 2001), coupled with empirical analysis (Denney et al. 2002, Dulvy et al. 2003), the premise that high fecundity lowers extinction risk has been prominent, particularly for marine teleost fishes. For example, the UN's Food and Agricultural Organization argued that "greater potential fecundity and dispersion would tend to make aquatic species more resilient to depletion and result in a lower risk of extinction" (FAO 2002). Based on work by Mace and Sissenwine (1993), a U.S. National Marine Fisheries Service working group predicted that Atlantic cod (*Gadus morhua*) should have the greatest resilience to fishing because of its high fecundity (NMFS 2001). However, as a consequence of serial over-exploitation, this prediction has been tested repeatedly throughout much of the North Atlantic and found wanting; despite significant reductions in fishing mortality, many cod populations have shown few signs of recovery (Swain and Chouinard 2008, Hutchings and Rangeley 2011). It

has further been recommended that high-fecundity species be permitted to decline to lower levels than low-fecundity species before consideration for listing under: CITES (the Convention on International Trade in Endangered Species of Wild Fauna and Flora) (Mace et al. 2002); the U.S. Endangered Species Act (DeMaster et al. 2004); and the American Fisheries Society (Musick 1999). Our results suggest otherwise.

It is not surprising that fecundity is unrelated to r_{max} (as noted by Cole 1954), given that it is only one of many traits that contribute to an individual's fitness (and thus population growth rate) and given that various trade-offs (reflected by negative associations among traits) often prevent selection from increasing the value of one fitness-related trait without diminishing the value of another (Roff 2002). Nonetheless, we do note the positive species-level association between fecundity and r_{max} within mammals, which might be attributable to the relatively narrow range in fecundity within this class.

At the species level, the functional relationships between life-history traits and r_{max} differed among chondrichthyans, teleosts, and mammals. For the models of age at maturity, in addition to class-level differences in intercept, the negative slopes differed among classes, being lowest for chondrichthyans and highest for mammals. The observation that r_{max} scales negatively with body size in chondrichthyans and in mammals (albeit at a significantly lower rate for chondrichthyans) is consistent with previous work on mammals (Fenchel 1974, Blueweiss et al. 1978, Hennemann 1983) and with predictions for sharks, skates, and rays (Reynolds et al. 2005). The low P value (0.06; Table 1) associated with the negative model coefficient in teleosts in the present study, while suggestive of a link with extinction risk, might be indicative of an equivocal link between body size and r_{max}, or at least a weaker link

than that for chondrichthyans and mammals when examined across broad taxonomic scales.

Ginzberg et al. (2010) recently examined the question of whether body size was associated with a metric of maximum population growth rate slightly different from that used here (they defined r_{max} to be the net reproductive rate in the absence of density-dependent feedbacks, thus representing a maximum potential generational growth rate). They found no association between r_{max} and body size in either teleost fishes or mammals (although they did report a negative association in birds). Given that their estimates of r_{max} for non-chondrichthyan fishes were the same as those presented previously by one of us (Myers et al. 1999) and that the present study incorporated a greater number of species (47 vs. 38), one might conclude that the lack of association between r_{max} and body size in teleosts is relatively robust. The differences between our and Ginzberg et al.'s (2010) results for mammals may be attributable to the latter's exclusion of cetaceans.

Notwithstanding the strong statistical associations documented here, caution is warranted in the application of our results, a caveat characteristic of studies that encompass broad taxonomic breadth. The scatter of data in Fig. 2c, for example, suggests that even if one has knowledge on age at maturity, there remains uncertainty in one's estimate of r_{max} for a given species, an uncertainty that can be magnified by environmental stochasticity. Bearing these caveats in mind, it is likely that the application of our results will improve overall predictability in forecasting species or population viability and their risk of depletion or extinction.

In summary, we find that (1) maximum population growth rate (r_{max}), a metric that is directly related to extinction risk and recovery potential, is similar between teleost fishes and terrestrial mammals, significantly lower for chondrichthyans, and lower still for marine mammals; (2) age at maturity is the primary correlate of r_{max} in three classes of vertebrates (including the most speciose); (3) negative relationships between r_{max} and both age at maturity and body size differ functionally among classes; and (4) fecundity is not related to r_{max} in fishes. Our analyses specify regression models that can be used to predict maximum population growth rate when data for only one significant life-history correlate of r_{max} are available; they also provide guidance on the type of life-history data that are most important to collect to predict species extinction risk. Our work indicates that age at maturity can serve as a universal predictor of extinction risk in fishes and mammals when r_{max} is unknown. These findings are thus supportive of the application of extinction-risk and population-status criteria that are based on generation time and that are independent of taxonomic affinity (Mace et al. 2008).

LITERATURE CITED

Beissinger, S. R., and R. D. McCullough. 2002. Population viability analysis. University of Chicago Press, Chicago, Illinois, USA.

Bennett, P. M., and I. P. F. Owens. 1997. Variation in extinction risk among birds: Chance or evolutionary predisposition? Proceedings of the Royal Society B 264:401–408.

Blueweiss, L., H. Fox, V. Kudzma, D. Nakashima, R. Peters, and S. Sams. 1978. Relationships between body size and some life history parameters. Oecologia 37:257–272.

Cole, L. C. 1954. The population consequences of life history phenomena. Quarterly Review of Biology 29:103–137.

Crawley, M. J. 2007. The R book. John Wiley, Chichester, UK.

DeMaster, D., R. Angliss, J. Cochrane, P. Mace, R. Merrick, M. Miller, S. Rumsey, B. Taylor, G. Thompson, and R. Waples. 2004. Recommendations to NOAA fisheries: ESA listing criteria by the Quantitative Working Group. Technical memorandum NMFS-F/SPO-67. National Oceanic and Atmospheric Administration, Washington, D.C., USA.

Denney, N. H., S. Jennings, and J. D. Reynolds. 2002. Life-history correlates of maximum population growth rates in marine fishes. Proceedings of the Royal Society B 269:2229–2237.

Dulvy, N. K., J. R. Ellis, N. B. Goodwin, A. Grant, J. D. Reynolds, and S. Jennings. 2004. Methods of assessing extinction risk in marine fishes. Fish and Fisheries 5:255–276.

Dulvy, N. K., Y. Sadovy, and J. D. Reynolds. 2003. Extinction vulnerability in marine populations. Fish and Fisheries 4:25–64.

FAO. 2002. Report of the second technical consultation on the suitability of the CITES criteria for listing commercially-exploited aquatic species. FAO Fisheries Report No. 667. Untied Nations Food and Agriculture Organization, Rome, Italy.

Fenchel, T. 1974. Intrinsic rate of nature increase: the relationship with body size. Oecologia 14:317–326.

García, V. B., L. O. Lucifora, and R. A. Myers. 2008. The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. Proceedings of the Royal Society B 275:83–89.

Gaston, K. J., and T. M. Blackburn. 1995. Mapping biodiversity using surrogates for species richness: macroscales and New World birds. Proceedings of the Royal Society B 262:335–341.

Ginzberg, L. R., O. Burger, and J. Damuth. 2010. The May threshold and life-history allometry. Biology Letters 6:850–853.

Goodman, D. 1984. Risk spreading as an adaptive strategy in iteroparous life histories. Theoretical Population Biology 25:1–20.

Hennemann, W. W. 1983. Relationship among body mass, metabolic rate and the intrinsic rate of natural increase in mammals. Oecologia 56:104–108.

Hero, J. M., S. E. Williams, and W. E. Magnusson. 2005. Ecological traits of declining amphibians in upland areas of eastern Australia. Journal of Zoology 267:221–232.

Hisano, M., S. R. Connolly, and W. D. Robbins. 2011. Population growth rates of reef sharks with and without fishing on the Great Barrier Reef: robust estimation with multiple models. PLoS ONE 6:e25028.

Holden, M. J. 1973. Are long-term sustainable fisheries for elasmobranchs possible? Rapports et Proces-verbaux des

Communications

Réunions. Conseil International pour l'Éxploration de la Mer 164:360–367.

Hutchings, J. A. 2001. Influence of population decline, fishing, and spawner variability on the recovery of marine fishes. Journal of Fish Biology (Supplement A) 59:306–322.

Hutchings, J. A., and R. W. Rangeley. 2011. Correlates of recovery for Canadian Atlantic cod. Canadian Journal of Zoology 89:386–400.

Jensen, A. L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences 53:820–822.

Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. American Naturalist 142:911–927.

Mace, G. M., N. J. Collar, K. J. Gaston, C. Hilton-Taylor, H. R. Akçakaya, N. Leader-Williams, E. J. Milner-Gulland, and S. N. Stuart. 2008. Quantification of extinction risk: IUCN's system for classifying threatened species. Conservation Biology 22:1424–1442.

Mace, P. M., et al. 2002. NMFS/Interagency Working Group evaluation of CITES criteria and guidelines. NOAA Technical Memorandum NMFS-F/SPO-58. U.S. Department of Commerce, NOAA, Silver Springs, Maryland, USA.

Mace, P. M., and M. P. Sissenwine. 1993. How much spawning per recruit is enough? Canadian Special Publication in Fisheries and Aquatic Sciences 120:101–118.

Musick, J. A. 1999. Criteria to define extinction risk in marine fishes. Fisheries 24:6–12.

Myers, R. A., K. G. Bowen, and N. J. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences 56:2404–2419.

Myers, R. A., G. Mertz, and P. S. Fowlow. 1997. Maximum population growth rates and recovery times for Atlantic cod (*Gadus morhua*). Fishery Bulletin 95:762–772.

Myers, R. A., and B. Worm. 2005. Extinction, survival or recovery of large predatory fishes. Proceedings of the Royal Society B 360:13–20.

NMFS. 2001. Report of the NMFS CITES Criteria Working Group. Preliminary Draft 16 May 2001. NOAA National Marine Fisheries Service, Woods Hole, Massachusetts, USA.

Patrick, W. S., P. Spencer, J. Link, J. Cope, J. J. Field, D. Kobayashi, P. Lawson, T. Gedamke, E. Cortés, O. Ormseth, K. Bigelow, and W. Overholtz. 2010. Using productivity and susceptibility indices to assess the vulnerability of United States fish stocks to overfishing. Fishery Bulletin 108:305–322.

Pilgrim, E. S., M. J. Crawley, and K. Dolphin. 2004. Patterns of rarity in the native British flora. Biological Conservation 120:161–190.

Prugh, L. R., A. R. E. Sinclair, K. E. Hodges, A. L. Jacob, and D. S. Wilcove. 2010. Reducing threats to species: threat reversibility and links to industry. Conservation Letters 3:267–276.

Purvis, A., and P. H. Harvey. 1995. Mammal life-history evolution—a comparative test of Charnov's model. Journal of Zoology 237:259–283.

Purvis, A., K. Jones, and G. Mace. 2000. Extinction. Bioessays 22:1123–1133.

R Development Core Team. 2009. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. www.R-project.org

Reed, R. N., and R. Shine. 2002. Lying in wait for extinction: ecological correlates of conservation status among Australian elapid snakes. Conservation Biology 16:451–461.

Reynolds, J. D., N. K. Dulvy, N. B. Goodwin, and J. A. Hutchings. 2005. Biology of extinction risk in marine fishes. Proceedings of the Royal Society B 272:2337–2344.

Roff, D. A. 2002. Life history evolution. Sinauer, Sunderland, Massachusetts, USA.

Ross, C. 1992. Environmental correlates of the intrinsic rate of natural increase in primates. Oecologia 90:383–390.

Sadovy, Y. 2001. The threat of fishing to highly fecund fishes. Journal of Fish Biology (Supplement A) 59:90–108.

Smith, S. E., D. W. Au, and C. Show. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. Marine and Freshwater Research 49:663–678.

Smith, T. D. 1994. Scaling fisheries: the science of measuring the effects of fishing, 1855–1955. Cambridge University Press, Cambridge, Massachusetts, USA.

Stevens, J. D., R. Bonfil, N. K. Dulvy, and P. A. Walker. 2000. The effects of fishing on sharks, rays, and chimaeras (chondrichthyans), and the implications for marine ecosystems. ICES Journal of Marine Science 57:476–494.

Swain, D. P., and G. A. Chouinard. 2008. Predicted extirpation of the dominant demersal fish in a large marine ecosystem: Atlantic cod (*Gadus morhua*) in the southern Gulf of St. Lawrence. Canadian Journal of Fisheries and Aquatic Sciences 65:2315–2319.

Thomas, G. H., R. B. Lanctot, and T. Szekely. 2006. Can intrinsic factors explain population declines in North American breeding shorebirds? A comparative analysis. Animal Conservation 9:252–258.

Whitehead, H. A., and J. Mann. 2000. Female reproductive strategies of cetaceans: life histories and calf care. Pages 219–246 *in* J. C. Mann, R. C. Connor, P. L. Tyack, and H. Whitehead, editors. Cetacean societies: field studies of dolphins and whales. University of Chicago Press, Chicago, Illinois, USA.

Communications

Supplemental Material

Appendix

Reference sources for the data used in preparing the raw data available in the Supplement (*Ecological Archives* A022-059-A1).

Supplement

Raw species-specific data on life-history traits and population growth rate (*Ecological Archives* A022-059-S1).