

# Maximum intrinsic rate of population increase in sharks, rays, and chimaeras: the importance of survival to maturity

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**Abstract:** The maximum intrinsic rate of population increase ( $r_{\max}$ ) is a commonly estimated demographic parameter used in assessments of extinction risk. In teleosts,  $r_{\max}$  can be calculated using an estimate of spawners per spawner, but for chondrichthyans, most studies have used annual reproductive output ( $b$ ) instead. This is problematic as it effectively assumes all juveniles survive to maturity. Here, we propose an updated  $r_{\max}$  equation that uses a simple mortality estimator that also accounts for survival to maturity: the reciprocal of average life-span. For 94 chondrichthyans, we now estimate that  $r_{\max}$  values are on average 10% lower than previously published. Our updated  $r_{\max}$  estimates are lower than previously published for species that mature later relative to maximum age and those with high annual fecundity. The most extreme discrepancies in  $r_{\max}$  values occur in species with low age at maturity and low annual reproductive output. Our results indicate that chondrichthyans that mature relatively later in life, and to a lesser extent those that are highly fecund, are less resilient to fishing than previously thought.

**Résumé :** Le taux intrinsèque maximum d'accroissement de la population ( $r_{\max}$ ) est un paramètre démographique couramment estimé, utilisé dans les évaluations du risque de disparition. Pour les téléostéens,  $r_{\max}$  peut être calculé en utilisant le nombre estimé de géniteurs par géniteur, mais pour les chondrichthyens, la plupart des études ont plutôt utilisé l'efficacité de la reproduction annuelle ( $b$ ). Cette approche pose problème parce qu'elle présuppose que tous les juvéniles survivent jusqu'à la maturité. Nous proposons une équation révisée pour  $r_{\max}$  qui utilise un estimateur de la mortalité simple qui tient également compte de la survie jusqu'à la maturité, soit la réciproque de la longévité moyenne. Pour 94 chondrichthyens, nous estimons que les nouvelles valeurs de  $r_{\max}$  sont en moyenne 10 % plus faibles que les valeurs déjà publiées. Nos estimations révisées de  $r_{\max}$  sont plus faibles que les valeurs déjà publiées pour les espèces qui atteignent la maturité plus tard par rapport à l'âge maximum et les espèces à forte fécondité annuelle. Les écarts les plus grands des valeurs de  $r_{\max}$  sont observés pour les espèces qui atteignent la maturité en bas âge et dont l'efficacité de la reproduction annuelle est faible. Nos résultats indiquent que les chondrichthyens qui atteignent la maturité plus tard et, dans une moindre mesure, qui sont très féconds, ont une moins grande résilience à la pêche que ce qui était présumé auparavant. [Traduit par la Rédaction]

## Introduction

The rate of increase is a fundamental property of populations that arises from birth and death rates. A commonly used metric for guiding assessments of extinction risk and setting limit reference points is the maximum intrinsic rate of population increase ( $r_{\max}$ ); it reflects the productivity of depleted populations where density-dependent regulation is absent (Myers et al. 1997; Myers and Mertz 1998). When population trajectories are lacking,  $r_{\max}$  is useful for evaluating a species' relative risk of overexploitation (e.g., Dulvy et al. 2014), as it is equivalent to the fishing mortality that will drive a species to extinction ( $F_{\text{ext}}$ ; Myers and Mertz 1998).

A fundamental parameter in calculating  $r_{\max}$  is the product of survival to maturity ( $l_{\alpha_{\text{mat}}}$ ) and annual fecundity ( $b$ ). Fisheries biologists studying teleost fishes often calculate it based on lifetime spawners per spawner ( $\hat{\alpha}$ ), which is related to the slope near the origin of a stock–recruitment relationship (Denney et al. 2002; Dulvy et al. 2004; Hutchings et al. 2012). In other words, the spawners per spawner incorporates juvenile survival and approximates  $l_{\alpha_{\text{mat}}}$ .

Surprisingly, survival to maturity has not been incorporated into calculations of  $r_{\max}$  for chondrichthyans (sharks, rays, and chimaeras). As most of these species lack stock–recruitment rela-

tionships, survival to maturity at low population sizes has been assumed to be very high and hence set to one because they have high investment per offspring (García et al. 2008; Hutchings et al. 2012; Dulvy et al. 2014). In other words, species with one or hundreds of offspring annually were assumed to have the same survival through the juvenile life stage. However, juvenile survival is likely to vary among chondrichthyans even in the absence of density dependence, as they have a wide variety of reproductive modes (ranging from egg-laying to placental live-bearing), including some of the longest gestation periods in the animal kingdom (Branstetter 1990). Sensitivity analyses of age- and stage-structured models show that juvenile survival is a key determinant of population growth ( $\lambda$ ), especially for species with low  $r_{\max}$  (Cortés 2002; Frisk et al. 2005; Kindsvater et al. 2016).

To correct for the assumption that all juveniles survive to maturity, here we show how the commonly used equation to estimate  $r_{\max}$  was derived and then indicate where juvenile survival is accounted for in the model but has been overlooked. We then introduce a simple updated method for estimating  $r_{\max}$  that takes into account juvenile survival. Finally, we re-estimate  $r_{\max}$  for 94 chondrichthyans using our updated equation and the same life

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history parameters used previously (see supplementary material in García et al. 2008), compare our updated  $r_{\max}$  estimated with previous ones, and discuss which species'  $r_{\max}$  were previously overestimated.

## Methods

### Original derivation of $r_{\max}$

The maximum rate of population increase ( $r_{\max}$ ) can be derived from the Euler-Lotka equation in discrete time:

$$(1) \quad \sum_{t=1}^{\omega} l_t b_t e^{-rt} = 1$$

where  $t$  is age,  $\omega$  is maximum age,  $l_t$  is the proportion of individuals that survive to age  $t$ ,  $b_t$  is fecundity at age  $t$ , and  $r$  is the rate of population increase. This rate changes with population density, but we are concerned with the maximum intrinsic rate of population increase ( $r_{\max}$ ), which occurs at very low densities in the absence of density dependence. If we assume that after reaching maturity at age  $\alpha_{\text{mat}}$  annual fecundity and annual survival are constant ( $b$  and  $p$ , respectively), we can estimate the probability of survival to ages  $t > \alpha_{\text{mat}}$  as survival to maturity  $l_{\alpha_{\text{mat}}} p^{t-\alpha_{\text{mat}}}$ , where  $l_{\alpha_{\text{mat}}}$  is the proportion of individuals surviving to maturity (Myers et al. 1997).

Annual survival of adults is calculated as  $p = e^{-M}$ , where  $M$  is the species-specific instantaneous natural mortality rate. This allows for survival to maturity ( $l_{\alpha_{\text{mat}}}$ ) and annual fecundity ( $b$ ) to be removed from the sum and the equation to be rewritten as follows (eq. 6 in Myers et al. 1997):

$$(2) \quad l_{\alpha_{\text{mat}}} b \sum_{t=\alpha_{\text{mat}}}^{\omega} p^{t-\alpha_{\text{mat}}} e^{-r_{\max} t} = 1$$

If we solve the summation, we obtain the following (see Charnov and Schaffer 1973; Myers et al. 1997; also see online Supplementary Material<sup>1</sup> for a more detailed derivation):

$$(3) \quad l_{\alpha_{\text{mat}}} b \frac{e^{-r_{\max} \alpha_{\text{mat}}}}{1 - p e^{-r_{\max}}} = 1$$

which we can rearrange as

$$(4) \quad l_{\alpha_{\text{mat}}} b = e^{r_{\max} \alpha_{\text{mat}}} - p(e^{r_{\max}})^{\alpha_{\text{mat}}-1}$$

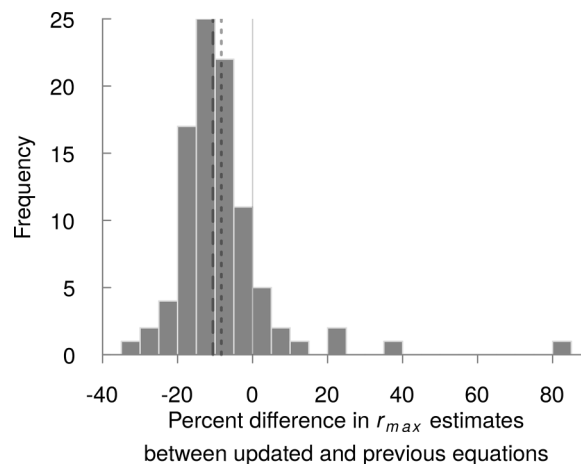
The term outside of the sum ( $l_{\alpha_{\text{mat}}} b$ ) has been equated to the maximum spawners per spawner ( $\tilde{\alpha}$ ); thus, we can rewrite the equation as

$$(5) \quad \tilde{\alpha} = e^{r_{\max} \alpha_{\text{mat}}} - p(e^{r_{\max}})^{\alpha_{\text{mat}}-1}$$

This is the same equation used by Hutchings et al. (2012) to solve for  $r_{\max}$  when estimates of  $\tilde{\alpha}$  are available and is mathematically equivalent to the equation used by García et al. (2008) in the case where age of selectivity into the fishery ( $\alpha_{\text{sel}}$ ) equals 1. Equation 2 shows that survival to maturity is only accounted for in  $l_{\alpha_{\text{mat}}}$ . Calculations of  $\tilde{\alpha}$  for chondrichthyans have ignored  $l_{\alpha_{\text{mat}}}$ , effectively equating it to 1, assuming  $\tilde{\alpha} = b$ :

$$(6) \quad b = e^{r_{\max} \alpha_{\text{mat}}} - p(e^{r_{\max}})^{\alpha_{\text{mat}}-1}$$

**Fig. 1.** Histogram of percent difference between updated  $r_{\max}$  values (this study) and previous ones (from García et al. 2008 and Dulvy et al. 2014). Dashed and dotted lines indicate median and mean values, respectively.



Hence, the previous equation of  $r_{\max}$  for chondrichthyans assumed all individuals survived until maturity. This formulation was used for chondrichthyans by García et al. (2008), Hutchings et al. (2012), and Dulvy et al. (2014) and is hereinafter referred to as the “previous” equation.

The oversight in the previous formulation of  $r_{\max}$  is comparable to an erroneous assumption in fisheries models where steepness — the productivity of the population — is held constant or set to 1 if data from stock–recruitment relationships are not available (reviewed in Mangel et al. 2010). Low-fecundity species such as chondrichthyans are assumed to have extremely high juvenile survival relative to teleost fishes, given that fecundity of sharks and rays is one or two orders of magnitude lower than that of most teleosts. However, steepness itself is fundamentally a property of early life history traits (Myers et al. 1999; Mangel et al. 2010) and hence should be calculated from demographic data or life history relationships.

Furthermore, it is often assumed that density dependence acts mainly upon juvenile survival. When estimating intrinsic rate of population increase, juvenile mortality is assumed to be lowest at very low population sizes, which may have justified its omission from earlier formulations of the  $r_{\max}$  equation (E.L. Charnov, personal communication).

### Accounting for survival to maturity

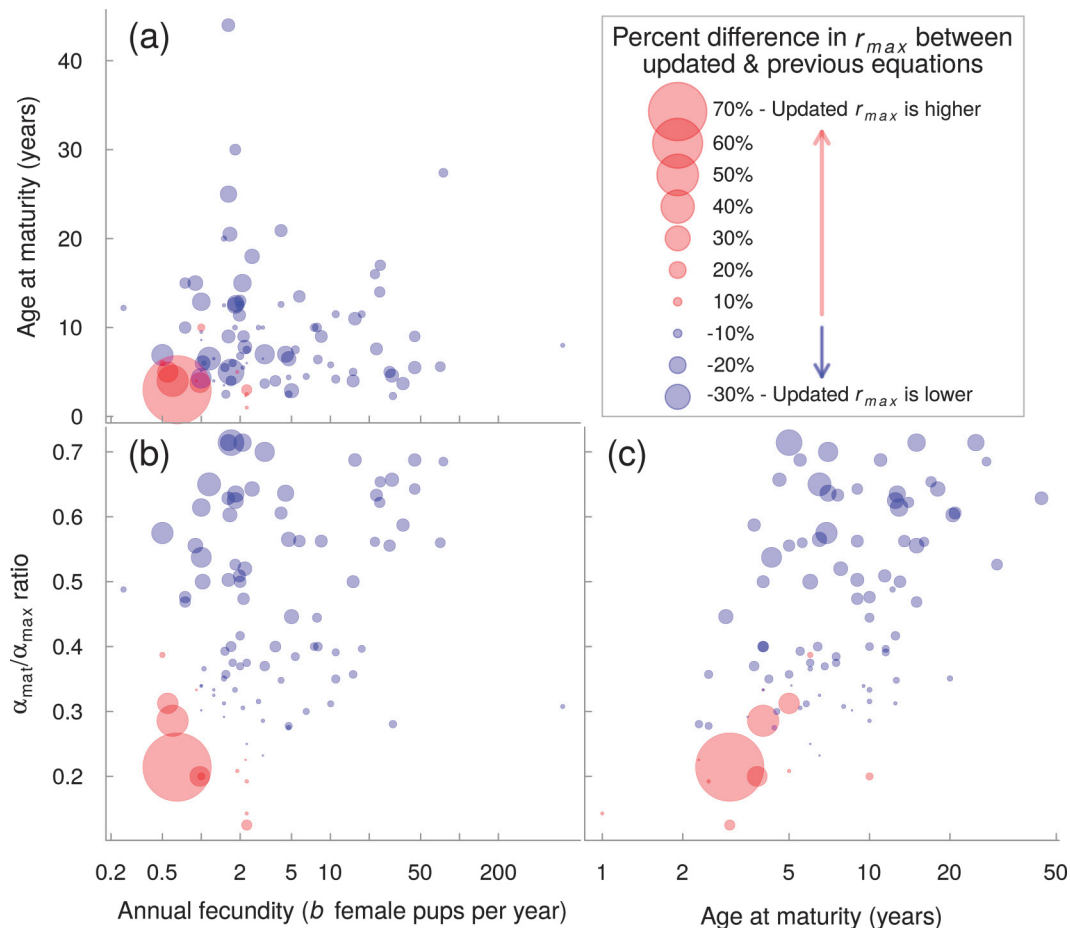
We revise the previous method by incorporating an estimate of juvenile survival that depends on age at maturity and species-specific natural mortality. We calculate the proportion of individuals surviving until maturity with the following equation:

$$(7) \quad l_{\alpha_{\text{mat}}} = (e^{-M})^{\alpha_{\text{mat}}}$$

We chose to use a simple estimate of natural mortality ( $M$ ) based on average life-span. Assuming that the natural mortality rate of a cohort is exponentially distributed, the average mortality rate is the mean of that distribution, which is equivalent to the reciprocal of average life-span (Dulvy et al. 2004), such that  $M = 1/\omega$ , where  $\omega$  is an estimate of average life-span, in years (see Supplementary Material<sup>1</sup>). Since cohort data on average life-span are difficult to obtain, we assume  $\omega = (\alpha_{\text{max}} + \alpha_{\text{mat}}) / 2$  — the midpoint between age at maturity and maximum age. We do this for three reasons:

<sup>1</sup>Supplementary materials are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfas-2016-0069>.

**Fig. 2.** Annual fecundity ( $b$  female pups per year, in log-scale) versus (a) age at maturity and (b) the  $\alpha_{\text{mat}} / \alpha_{\text{max}}$  ratio. (c) Age at maturity versus  $\alpha_{\text{mat}} / \alpha_{\text{max}}$  ratio. Colour indicates whether the updated model estimates a higher (red) or lower (blue)  $r_{\text{max}}$  than the previous formulation, while point size indicates percent difference in  $r_{\text{max}}$  estimates between updated and previous models.



First, estimates of maximum age are readily available for many chondrichthyan species, and they are applicable to most chondrichthyan populations since they have truncated size class distributions due to prolonged fishing exposure (Law 2000). Second, chondrichthyans have low fecundity and large offspring, which are much more likely to survive to maturity than species with very high fecundity. This means that the average life-span and the maximum life-span are likely much closer together for chondrichthyans than for teleosts. Third, some of the common methods for estimating  $M$  (e.g., Jensen 1996 or Hewitt and Hoenig 2005) result in unrealistic estimates of  $r_{\text{max}}$  for many species (i.e., zero or negative; see Fig. S2 in Supplementary Material<sup>1</sup>), probably due to natural mortality being overestimated for many chondrichthyan species when using estimators based mostly on teleost data. In preliminary analyses, we found that when using these teleost-based mortality estimators, we could only obtain plausible estimates of  $r_{\text{max}}$  for all species when ignoring juvenile mortality.

One reason for the overestimation may be that the Hewitt and Hoenig (2005) equation coefficients are estimated from data on fish that have extremely low juvenile survival (mostly teleosts). By contrast, our method assumes that 36.8% of offspring reach average life-span (see explanation and supplementary material in Hewitt and Hoenig 2005). Put simply, for a species with an average life-span of 10 years, 9.5% of the population must die each year for there to be a 37% chance of surviving for 10 years. While in teleosts average life-span is probably less than the age of maturity, for chondrichthyans it is likely greater, which is why we assume it is the mean of age at maturity and maximum observed life-span. We

recalculate  $r_{\text{max}}$  for 94 chondrichthyan species examined in García et al. (2008) and Dulvy et al. (2014) using our updated method that combines eqs. 4 and 7, as well as using the previous method that uses eq. 6 and Jensen's (1996)  $M$  estimator. Finally, we compare  $r_{\text{max}}$  values from previous and updated methods and explore the relationship between life history parameters and discrepancies in  $r_{\text{max}}$  values.

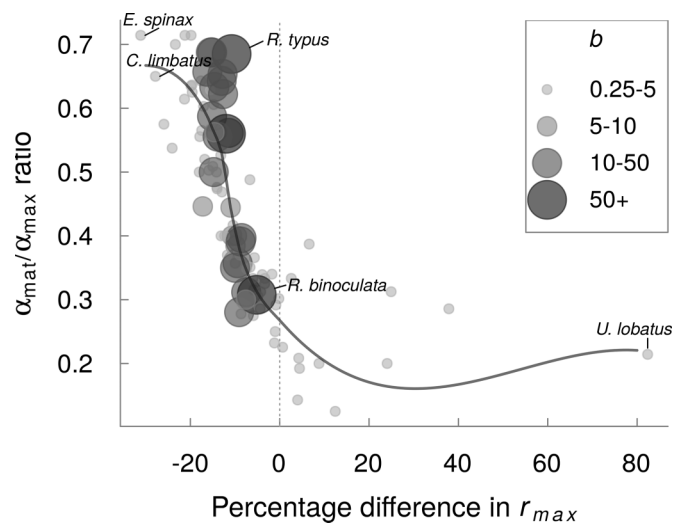
## Results and discussion

Our updated estimates of maximum intrinsic population growth rates ( $r_{\text{max}}$ ) for chondrichthyans are on average 10% lower than previous estimates (Fig. 1). For the most fecund species ( $b > 10$  female offspring per year), updated  $r_{\text{max}}$  estimates were always 10%–20% lower than previous estimates. This means that for species with high fecundity,  $r_{\text{max}}$  has been overestimated in the past (see right side of Figs. 2a, 2b; large circles in Fig. 3). In contrast, for less fecund species ( $b < 5$  female offspring per year), discrepancy in  $r_{\text{max}}$  between updated and previous estimates varies from 30% lower to 80% higher (small circles in Fig. 3). Two of the most fecund chondrichthyans, the big skate (*Raja binoculata*) and the whale shark (*Rhincodon typus*), have lower intrinsic rates of population increase (see Fig. 3) and may be less resilient to fishing than previously thought.

The greatest positive and negative discrepancies in  $r_{\text{max}}$  values (extremes in percent difference) occurred in species with very low annual fecundity and to a lesser extent low age at maturity (see lower left corner of Fig. 2a). The proportional difference between



**Fig. 3.** Comparison of percentage difference between updated and traditional  $r_{\max}$  and the  $\alpha_{\text{mat}}/\alpha_{\text{max}}$  ratio across different values of annual reproductive output  $b$ . Darker grey and larger circles indicate a higher annual reproductive output ( $b$ ) value. The grey line is the lowest-smoothed curve. Species highlighted are as follows: *E. spinax* = *Etmopterus spinax*, *C. limbatus* = *Carcharhinus limbatus*, *R. binoculata* = *Raja binoculata*, *R. typus* = *Rhincodon typus*, and *U. lobatus* = *Urolophus lobatus*.



updated  $r_{\max}$  and previous estimates were greatest in species with low  $r_{\max}$  values. Alternatively, greater fecundity, combined with late maturity “buffer” against variation in estimates of  $r_{\max}$  (Figs. 2a, 2b, right side of plots). When age at maturity is low relative to maximum age ( $\alpha_{\text{mat}}/\alpha_{\text{max}} < 0.3$ ), updated  $r_{\max}$  estimates were much higher than previous estimates. For example, the updated  $r_{\max}$  estimate for the lobed stingaree (*Urolophus lobatus*) is 82% higher than its previous  $r_{\max}$  estimate, owing to its early relative maturation ( $\alpha_{\text{mat}}/\alpha_{\text{max}} = 0.21$ ; Fig. 3). Conversely, when age at maturity is high relative to maximum age ( $\alpha_{\text{mat}}/\alpha_{\text{max}} > 0.4$ ), updated  $r_{\max}$  estimates were lower than previous estimates (Fig. 3). For example, the velvet belly lanternshark (*Etmopterus spinax*) and the blacktip shark (*Carcharhinus limbatus*) have relative maturation ratios of 0.71 and 0.65, respectively, and have updated  $r_{\max}$  values that are 31% and 28% lower than previously estimated, respectively (see Fig. 3). While our study did not explore the relationship between relative maturation (the  $\alpha_{\text{mat}}/\alpha_{\text{max}}$  ratio) and  $r_{\max}$  values among species, a negative relationship between relative maturation and intrinsic rate of population increase has been previously pointed out in sharks (Liu et al. 2015) and skates (Barnett et al. 2013).

Previous work comparing chondrichthyan life histories often overestimated the maximum rate of population increase by not accounting for the species-specific juvenile mortality rate (García et al. 2008; Hutchings et al. 2012). Juvenile survival was overestimated for all species, particularly for highly fecund and late-maturing species, which inflated their estimated maximum intrinsic population growth rates.

Our simple method to estimate survival to maturity requires no extra parameters but assumes that juvenile mortality is equal to adult mortality. This is likely to result in conservative estimates of  $M$  because juveniles tend to have higher mortality rates than adults (Cushing, 1975). Future work could explore using age-specific mortality estimators to calculate survival to maturity, but we caution that these estimators are mostly based on teleost fishes and require additional data such as von Bertalanffy growth parameters (Chen and Watanabe 1989) or weight-at-age relationships (Peterson and Wroblewski 1984).

We found that species with high fecundity all had lower  $r_{\max}$  values than previously estimated; hence, our method is more ef-

fective at representing higher juvenile mortality rates in species with high fecundity. Nonetheless, direct estimates of differential juvenile mortality are still missing from both models, and this motivates further research on this topic (Heupel and Simpfendorfer 2002). Our method undoubtedly ignores nuances related to absolute offspring size and litter size (Smith and Fretwell 1974), but it is still likely to be an improvement over the previous assumption that all juveniles survive to maturity.

These new insights into the maximum intrinsic rates of increase are relevant for the management of data-poor chondrichthyans. We recommend that scientist and managers using chondrichthyan  $r_{\max}$  estimates reevaluate them using our updated equation, emphasizing species whose  $r_{\max}$  values have been consistently overestimated in previous studies: highly fecund species, often thought to be more resilient to fishing (Sadovy 2001), and species that only reproduce during a short span of their total lifetime. To generalize management and conservation implications beyond the species in our study, future work needs to revisit our understanding of life history and ecological correlates of  $r_{\max}$ . Previous work suggest species in deeper (colder) habitat (García et al. 2008) as well as those with late age at maturity (Hutchings et al. 2012) have lower  $r_{\max}$  values. These and other correlates of  $r_{\max}$  can now be reevaluated with these updated estimates and used in ecological risk assessments and other forms of management priority setting.

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## References

- Barnett, L.A.K., Winton, M.V., Ainsley, S.M., Cailliet, G.M., and Ebert, D.A. 2013. Comparative demography of skates: life-history correlates of productivity and implications for management. *PLoS ONE*, 8(5): e65000. doi:10.1371/journal.pone.0065000.
- Branstetter, S. 1990. Early life-history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. In *Elasmobranchs as living resources: advances in the biology ecology systematics and the status of the fisheries*. Vol. 90. Edited by H.L.J. Pratt, S.H. Gruber, and T. Taniuchi. NOAA Technical Report NMFS 90. pp. 17–28.
- Charnov, E.L., and Schaffer, W.M. 1973. Life-history consequences of natural selection: Cole's result revisited. *Am. Nat.* 107(958): 791–793. doi:10.1086/282877.
- Chen, S., and Watanabe, S. 1989. Age dependence of natural mortality coefficient in fish population dynamics. *Nippon Suisan Gakkaishi*, 55: 205–208. doi:10.2331/suisan.55.205.
- Cortés, E. 2002. Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. *Conserv. Biol.* 16(4): 1048–1062. doi:10.1046/j.1523-1739.2002.00423.x.
- Cushing, D.H. 1975. The natural mortality of the plaice. *ICES J. Mar. Sci.* 36(2): 150–157. doi:10.1093/icesjms/36.2.150.
- Denney, N.H., Jennings, S., and Reynolds, J.D. 2002. Life-history correlates of maximum population growth rates in marine fishes. *Proc. R. Soc. B Biol. Sci.* 269(1506): 2229–2237. doi:10.1098/rspb.2002.2138.
- Dulvy, N.K., Ellis, J.R., Goodwin, N.B., Grant, A., Reynolds, J.D., and Jennings, S. 2004. Methods of assessing extinction risk in marine fishes. *Fish Fish.* 5: 255–276. doi:10.1111/j.1467-2679.2004.00158.x.
- Dulvy, N.K., Pardo, S.A., Simpfendorfer, C.A., and Carlson, J.K. 2014. Diagnosing the dangerous demography of manta rays using life history theory. *PeerJ*, 2: e400. doi:10.7717/peerj.400.
- Frisk, M.G., Miller, T.J., and Dulvy, N.K. 2005. Life histories and vulnerability to exploitation of elasmobranchs: inferences from elasticity, perturbation and phylogenetic analyses. *J. Northw. Atl. Fish. Sci.* 37(October): 27–45. doi:10.2960/j.v35.m514.
- García, V.B., Lucifora, L.O., and Myers, R.A. 2008. The importance of habitat and life history to extinction risk in sharks, skates, rays and chimaeras. *Proc. R. Soc. B Biol. Sci.* 275: 83–89. doi:10.1098/rspb.2007.1295.
- Heupel, M.R., and Simpfendorfer, C.A. 2002. Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. *Can. J. Fish. Aquat. Sci.* 59(4): 624–632. doi:10.1139/f02-036.

- Hewitt, D.A., and Hoenig, J.M. 2005. Comparison of two approaches for estimating natural mortality based on longevity. *Fish. Bull.* **103**: 433–437.
- Hutchings, J.A., Myers, R.A., García, V.B., Lucifora, L.O., and Kuparinen, A. 2012. Life-history correlates of extinction risk and recovery potential. *Ecol. Appl.* **22**(4): 1061–1067. doi:10.1890/11-1313.1.
- Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Can. J. Fish. Aquat. Sci.* **53**(4): 820–822. doi:10.1139/f95-233.
- Kindsvater, H.K., Mangel, M., Reynolds, J.D., and Dulvy, N.K. 2016. Ten principles from evolutionary ecology essential for effective marine conservation. *Ecol. Evol.* **6**(7): 2125–2138. doi:10.1002/ece3.2012.
- Law, R. 2000. Fishing, selection, and phenotypic evolution. *ICES J. Mar. Sci.* **57**(3): 659–668. doi:10.1006/jmsc.2000.0731.
- Liu, K.M., Chin, C.P., Chen, C.H., and Chang, J.H. 2015. Estimating finite rate of population increase for sharks based on vital parameters. *PLoS ONE*, **10**(11): e0143008. doi:10.1371/journal.pone.0143008.
- Mangel, M., Brodziak, J., and DiNardo, G. 2010. Reproductive ecology and scientific inference of steepness: a fundamental metric of population dynamics and strategic fisheries management. *Fish. Fish.* **11**(1): 89–104. doi:10.1111/j.1467-2979.2009.00345.x.
- Myers, R.A., and Mertz, G. 1998. The limits of exploitation: a precautionary approach. *Ecol. Appl.* **8**(s1): s165–s169. doi:10.1890/1051-0761(1998)8[S165:TLOEAP]2.0.CO;2.
- Myers, R.A., Mertz, G., and Fowlow, P.S. 1997. Maximum population growth rates and recovery times for Atlantic cod, *Gadus morhua*. *Fish. Bull.* **95**: 762–772.
- Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.* **56**(12): 2404–2419. doi:10.1139/f99-201.
- Peterson, I., and Wroblewski, J.S. 1984. Mortality rate of fishes in the pelagic ecosystem. *Can. J. Fish. Aquat. Sci.* **41**(7): 1117–1120. doi:10.1139/f84-131.
- Sadovy, Y. 2001. The threat of fishing to highly fecund fishes. *J. Fish Biol.* **59**: 90–108. doi:10.1111/j.1095-8649.2001.tb01381.x.
- Smith, C.C., and Fretwell, S.D. 1974. The optimal balance between size and number of offspring. *Am. Nat.* **108**(962): 499–506. doi:10.1086/282929.