

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

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## Abstract

1  
2 The maximum intrinsic rate of population increase  $r_{max}$  is a commonly estimated demo-  
3 graphic parameter used in assessments of extinction risk. In teleosts,  $r_{max}$  can be calculated  
4 using an estimate of spawners per spawner, but for chondrichthyans, most studies have used  
5 annual reproductive output  $b$  instead. This is problematic as it effectively assumes all juveniles  
6 survive to maturity. Here, we propose an updated  $r_{max}$  equation that uses a simple mortal-  
7 ity estimator which also accounts for survival to maturity: the reciprocal of average lifespan.  
8 For 94 chondrichthyans, we now estimate that  $r_{max}$  values are on average 10% lower than  
9 previously published. Our updated  $r_{max}$  estimates are lower than previously published for  
10 species that mature later relative to maximum age and those with high annual fecundity. The  
11 most extreme discrepancies in  $r_{max}$  values occur in species with low age at maturity and low  
12 annual reproductive output. Our results indicate that chondrichthyans that mature relatively  
13 later in life, and to a lesser extent those that are highly fecund, are less resilient to fishing than  
14 previously thought.

15 Keywords: elasmobranch, extinction risk, demography, data-poor, population growth rate,  
16 recovery potential

# 1 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 and Mertz, 1998; Myers et al., 1997). When population trajectories are lacking,  $r_{max}$  is useful for evaluating a species' relative risk of overexploitation (Dulvy et al., 2014) as it is equivalent to the fishing mortality that will drive a species to extinction,  $F_{ext}$  (Myers and Mertz, 1998).

A fundamental parameter in calculating  $r_{max}$  is the product of survival to maturity  $l_{\alpha_{mat}}$  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  $l_{\alpha_{mat}} b$ .

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 relationships, 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 (Dulvy et al., 2014; García et al., 2008; Hutchings et al., 2012). 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

46 updated method for estimating  $r_{max}$  that takes into account juvenile survival. Finally, we re-  
47 estimate  $r_{max}$  for 94 chondrichthyans using our updated equation and the same life history  
48 parameters used previously (see supplementary material in García et al., 2008), compare our  
49 updated  $r_{max}$  estimated with previous ones, and discuss which species'  $r_{max}$  were previously  
50 overestimated.

## 51 2 Methods

### 52 2.1 Original derivation of $r_{max}$

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

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

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

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

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

67 If we solve the summation we obtain the following (see Charnov and Schaffer, 1973; Myers

68 et al., 1997; and Supplementary material for a more detailed derivation)

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

69 which we can rearrange as

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

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

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

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

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

77 Hence, the previous equation of  $r_{max}$  for chondrichthyans assumed all individuals sur-  
78 vived until maturity. This formulation was used for chondrichthyans by García et al. (2008),  
79 Hutchings et al. (2012), and Dulvy et al. (2014), and is hereafter referred to as the “previous”  
80 equation.

81 The oversight in the previous formulation of  $r_{max}$  is comparable to an erroneous assump-  
82 tion in fisheries models where steepness — the productivity of the population — is held con-  
83 stant or set to 1 if data from stock-recruitment relationships are not available (reviewed in  
84 Mangel et al., 2010). Low-fecundity species such as chondrichthyans are assumed to have  
85 extremely high juvenile survival relative to teleost fishes, given that fecundity of sharks and  
86 rays is one or two orders of magnitude lower than most teleosts. However, steepness itself

87 is fundamentally a property of early life history traits (Mangel et al., 2010; Myers et al., 1999)  
88 and hence should be calculated from demographic data or life history relationships.

89 Furthermore, it is often assumed that density dependence acts mainly upon juvenile sur-  
90 vival. When estimating intrinsic rate of population increase, juvenile mortality is assumed  
91 to be lowest at very low population sizes, which may have justified its omission from earlier  
92 formulations of the  $r_{max}$  equation (E.L. Charnov, pers. comm.).

## 93 **2.2 Accounting for survival to maturity**

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

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

97 We chose to use a simple estimate of natural mortality  $M$  based on average lifespan. As-  
98 suming that the natural mortality rate of a cohort is exponentially distributed, the average  
99 mortality rate is the mean of that distribution, which is equivalent to the reciprocal of av-  
100 erage lifespan (Dulvy et al., 2004), such that  $M = 1/\omega$ , where  $\omega$  is an estimate of average  
101 lifespan, in years (See Supplementary Material). Since cohort data on average lifespan are  
102 difficult to obtain, we assume  $\omega = (\alpha_{max} + \alpha_{mat})/2$  – the midpoint between age at maturity  
103 and maximum age. We do this for three reasons: First, estimates of maximum age are readily  
104 available for many chondrichthyan species, and they are applicable to most chondrichthyan  
105 populations since they have truncated size class distributions due to prolonged fishing expo-  
106 sure (Law, 2000). Second, chondrichthyans have low fecundity and large offspring, which are  
107 much more likely to survive to maturity than species with very high fecundity. This means  
108 that the average lifespan and the maximum lifespan are likely much closer together for chon-  
109 drichthyans than for teleosts. Third, some of the common methods for estimating  $M$ , e.g.,  
110 Jensen (1996) or Hewitt and Hoenig (2005), result in unrealistic estimates of  $r_{max}$  for many  
111 species (i.e., zero or negative, see Fig. 5 in Supplementary Material) probably due to natural  
112 mortality being overestimated for many chondrichthyan species when using estimators based

113 mostly on teleost data. In preliminary analyses we found that when using these teleost-based  
114 mortality estimators, we could only obtain plausible estimates of  $r_{max}$  for all species when  
115 ignoring juvenile mortality.

116 One reason for the overestimation may be that the Hewitt and Hoenig (2005) equation  
117 coefficients are estimated from data on fish that have extremely low juvenile survival (mostly  
118 teleosts). By contrast, our method assumes that 36.8% of offspring reach average lifespan  
119 (see explanation and Supplementary Material in Hewitt and Hoenig, 2005). Put simply, for  
120 a species with an average lifespan of ten years, 9.5% of the population must die each year  
121 for there to be a 37% chance of surviving for ten years. While in teleosts average lifespan is  
122 probably less than the age of maturity, for chondrichthyans it is likely greater, which is why we  
123 assume it is the mean of age at maturity and maximum observed lifespan. We recalculate  $r_{max}$   
124 for 94 chondrichthyan species examined in García et al. (2008) and Dulvy et al. (2014) using  
125 our updated method that combines equations 4 and 7, as well as using the previous method  
126 that uses equation 6 and Jensen's (1996)  $M$  estimator. Finally, we compare  $r_{max}$  values from  
127 previous and updated methods and explore the relationship between life history parameters  
128 and discrepancies in  $r_{max}$  values.

### 129 **3 Results and Discussion**

130 Our updated estimates of maximum intrinsic population growth rates ( $r_{max}$ ) for chondrichthyans  
131 are on average 10% lower than previous estimates (Fig. 1). For the most fecund species ( $b > 10$   
132 female offspring per year) updated  $r_{max}$  estimates were always 10-20% lower than previous  
133 estimates. This means that for species with high fecundity,  $r_{max}$  has been overestimated in  
134 the past (see right side of Fig. 2a,b; large circles in Fig. 3). In contrast, for less fecund species  
135 ( $b < 5$  female offspring per year), discrepancy in  $r_{max}$  between updated and previous esti-  
136 mates varies from 30% lower to 80% higher (small circles in Fig. 3). Two of the most fecund  
137 chondrichthyans, the Big Skate (*Raja binoculata*) and the Whale Shark (*Rhincodon typus*), have  
138 lower intrinsic rates of population increase (see Fig. 3) and may be less resilient to fishing than  
139 previously thought.

140 The greatest positive and negative discrepancies in  $r_{max}$  values (extremes in percent dif-  
141 ference) occurred in species with very low annual fecundity and to a lesser extent low age at  
142 maturity (see lower left corner of Fig. 2a). The proportional difference between updated  $r_{max}$   
143 and previous estimates were greatest in species with low  $r_{max}$  values. Alternatively, greater  
144 fecundity, combined with late maturity “buffer” against variation in estimates of  $r_{max}$  (Fig. 2a,b  
145 right side of plots). When age at maturity is low relative to maximum age ( $\alpha_{mat}/\alpha_{max} < 0.3$ ),  
146 updated  $r_{max}$  estimates were much higher than previous estimates. For example, the updated  
147  $r_{max}$  estimate for the Lobed Stingaree (*Urolophus lobatus*) is 82% higher than its previous  $r_{max}$   
148 estimate, due to its early relative maturation ( $\alpha_{mat}/\alpha_{max} = 0.21$ , Fig. 3). Conversely, when  
149 age at maturity is high relative to maximum age ( $\alpha_{mat}/\alpha_{max} > 0.4$ ), updated  $r_{max}$  estimates  
150 were lower than previous estimates (Fig. 3). For example, the Velvet Belly Lanternshark (*Et-  
151 mopterus spinax*) and the Blacktip Shark (*Carcharhinus limbatus*) have relative maturation  
152 ratios of 0.71 and 0.65, respectively, and have updated  $r_{max}$  values that are 31% and 28% lower  
153 than previously estimated (see Fig. 3). While our study did not explore the relationship be-  
154 tween relative maturation (the  $\alpha_{mat}/\alpha_{max}$  ratio) and  $r_{max}$  values among species, a negative  
155 relationship between relative maturation and intrinsic rate of population increase has been  
156 previously pointed out in sharks (Liu et al., 2015) and skates (Barnett et al., 2013).

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

162 Our simple method to estimate survival to maturity requires no extra parameters but as-  
163 sumes that juvenile mortality is equal to adult mortality. This is likely to result in conservative  
164 estimates of  $M$  because juveniles tend to have higher mortality rates than adults (Cushing,  
165 1975). Future work could explore using age-specific mortality estimators to calculate survival  
166 to maturity, but we caution that these estimators are mostly based on teleost fishes and re-  
167 quire additional data such as on Bertalanffy growth parameters (Chen and Watanabe, 1989)  
168 or weight-at-age relationships (Peterson and Wroblewski, 1984).

169 We found that species with high fecundity all had lower  $r_{max}$  values than previously es-  
170 timated, hence our method is more effective at representing higher juvenile mortality rates  
171 in species with high fecundity. Nonetheless, direct estimates of differential juvenile mortality  
172 are still missing from both models, and motivates further research on this topic (Heupel and  
173 Simpfendorfer, 2002). Our method undoubtedly ignores nuances related to absolute offspring  
174 size and litter size (Smith and Fretwell, 1974), but it is still likely to be an improvement over  
175 the previous assumption that all juveniles survive to maturity.

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

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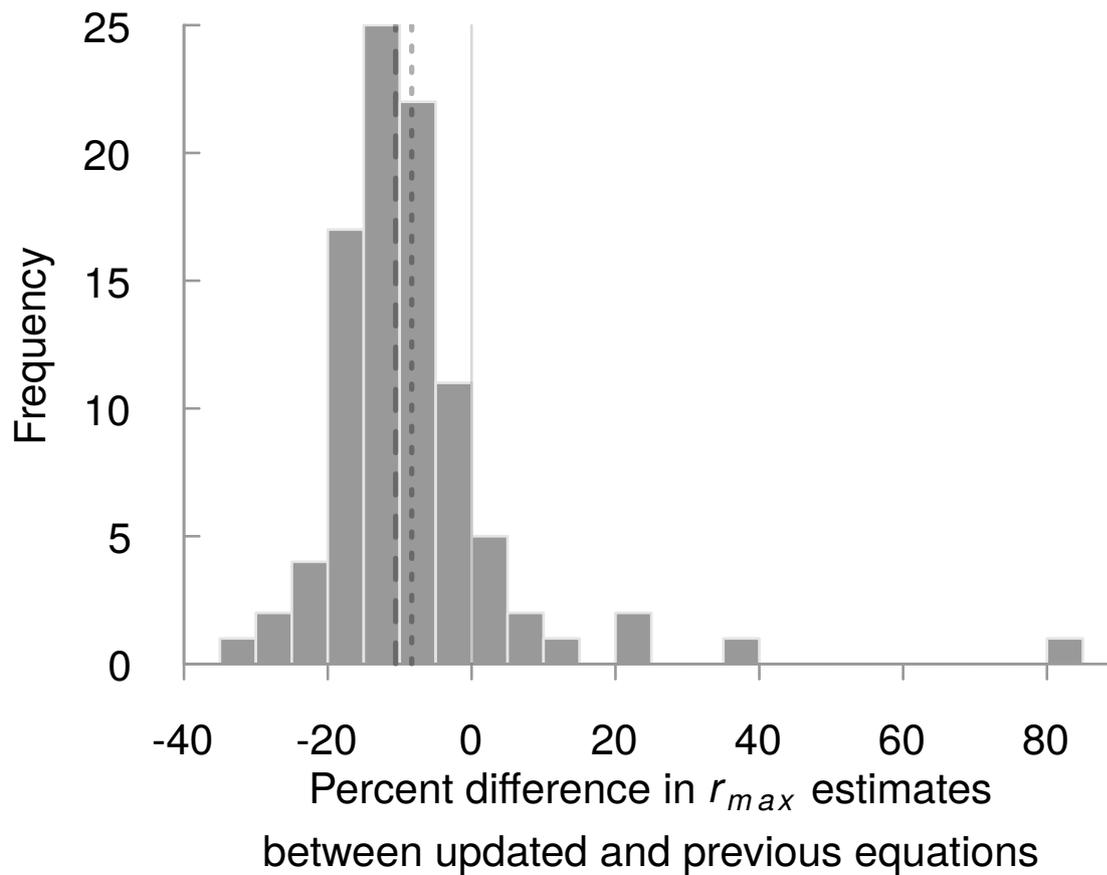


Figure 1: Histogram of percent difference between updated  $r_{max}$  values (this study) and previous ones (from García et al. 2008 and Dulvy et al. 2014). Dashed and dotted lines indicate median and mean values, respectively.

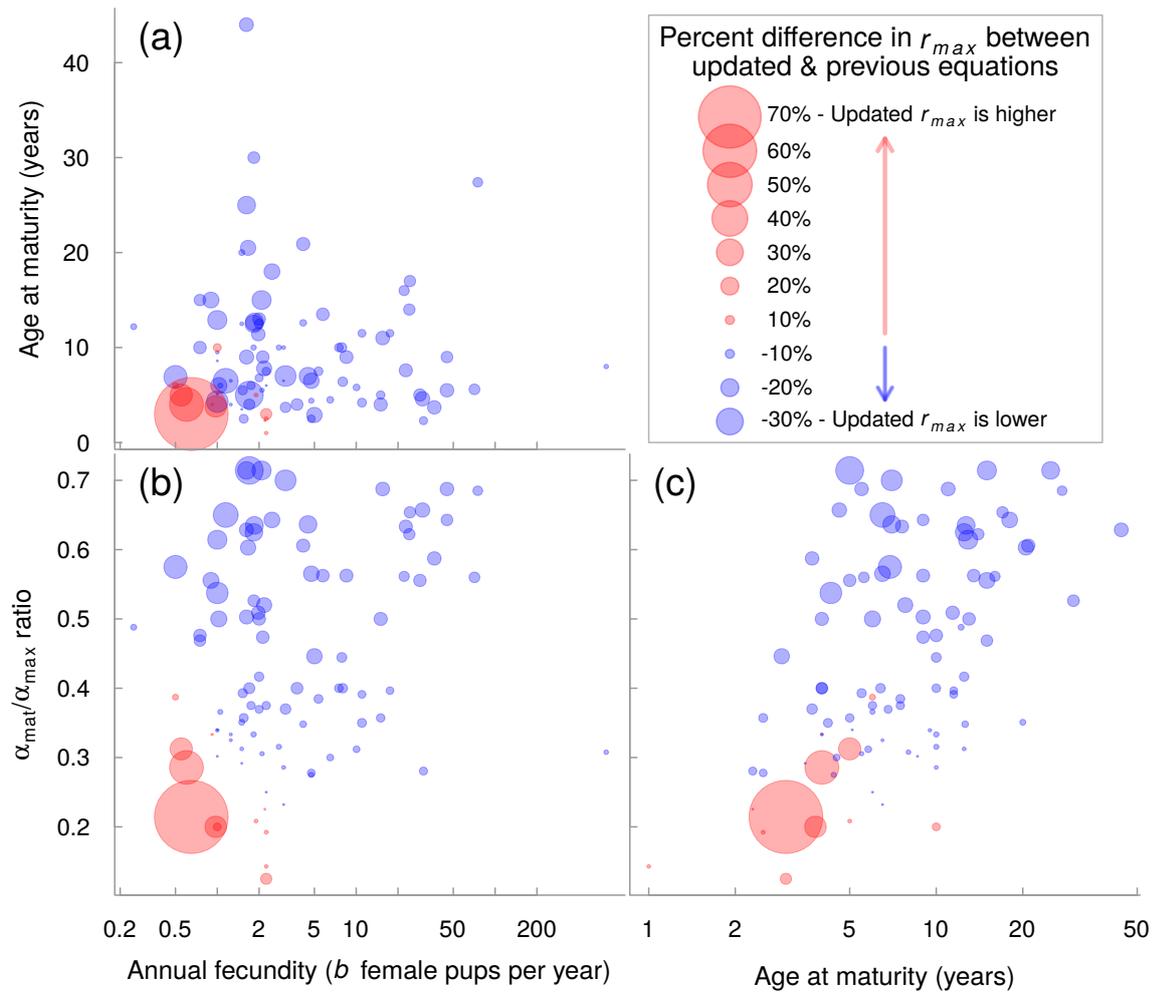


Figure 2: Annual fecundity ( $b$ , in log-scale) vs (a) age at maturity and (b) the  $\alpha_{mat}/\alpha_{max}$  ratio. (c) Age at maturity vs  $\alpha_{mat}/\alpha_{max}$  ratio. Colour indicates whether the updated model estimates a higher (red) or lower (blue)  $r_{max}$  than the previous formulation,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

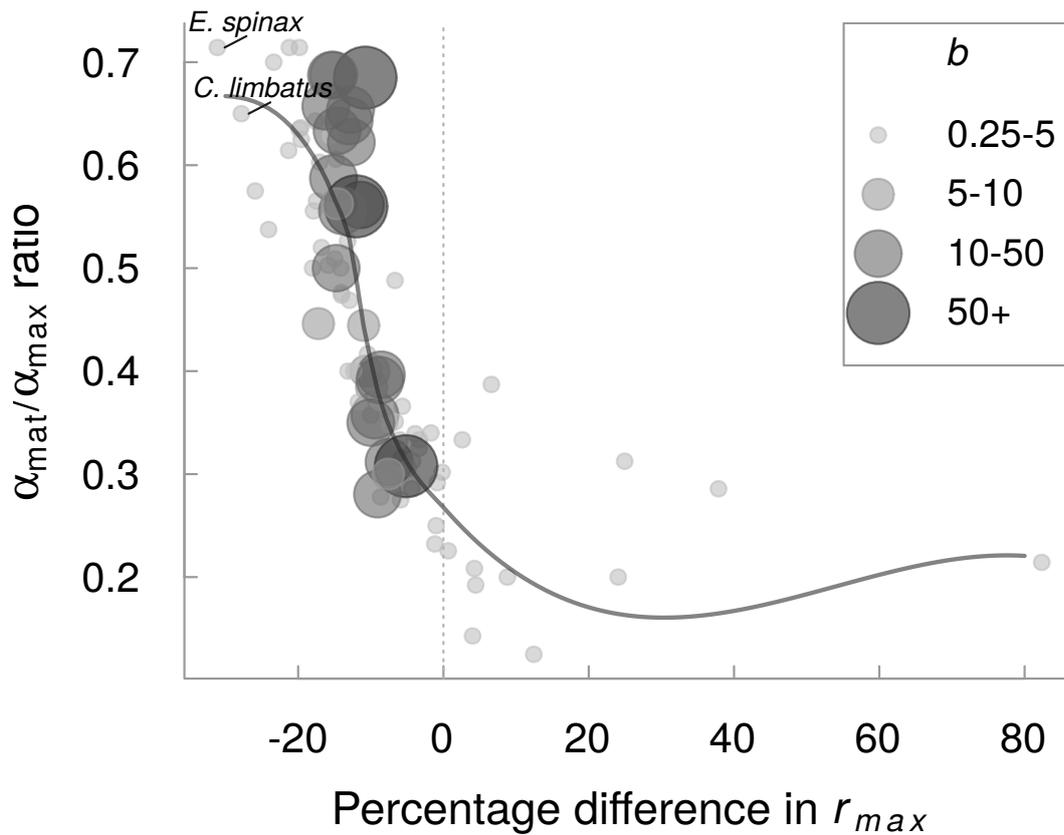


Figure 3: Comparison of percentage difference between updated and traditional  $r_{max}$  and the  $\alpha_{mat}/\alpha_{max}$  ratio across different values of annual reproductive output  $b$ . Darker grey and larger circles indicate a higher annual reproductive output ( $b$ ) value. The grey line is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

## 260 **Supplementary Material**

261 The Supplementary Material includes a more detailed account on deriving  $r_{max}$  which uses  
262 many of the same equations in the main text of the body (here repeated for clarity), details on  
263 the conversion of lifetime spawners per spawners to a yearly rate, explanation of why  $1/\omega$   
264 means that 37% of individuals reach average lifespan, and Supplementary Figures.

265 The raw data used for our analyses are available on figshare at [https://dx.doi.org/10.](https://dx.doi.org/10.6084/m9.figshare.3207697.v1i)  
266 [6084/m9.figshare.3207697.v1i](https://dx.doi.org/10.6084/m9.figshare.3207697.v1i).

### 267 **Detailed derivation of $r_{max}$**

268 The maximum rate of population increase  $r_{max}$  is typically derived from the Euler-Lotka equa-  
269 tion in discrete time (Myers et al., 1997):

$$\sum_{t=1}^{\omega} l_t m_t e^{-rt} = 1 \quad (8)$$

270 Where  $t$  is age,  $\omega$  is maximum age,  $l_t$  is the yearly survival at age  $t$ ,  $m_t$  is fecundity at age  $t$ ,  
271 and  $r$  is the rate of population increase. This rate changes with population density, but we are  
272 concerned with the maximum intrinsic rate of population increase  $r_{max}$ , which occurs a very  
273 low densities in the absense of density dependence. Assuming that after reaching maturity  
274 annual fecundity and annual survival are constant ( $b$  and  $p$ , respectively), we can estimate  
275 survival to year  $t$  as survival to maturity  $l_{\alpha_{mat}}$  times yearly adult survival  $p$  for the years after  
276 maturation (Myers et al., 1997):

$$\text{for}(t \geq \alpha_{mat}) \begin{cases} m_t = b \\ l_t = l_{\alpha_{mat}} p^{t-\alpha_{mat}} \end{cases} \quad (9)$$

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

$$l_{\alpha_{mat}} b \sum_{t=\alpha_{mat}}^{\omega} p^{t-\alpha_{mat}} e^{-r_{max}t} = 1 \quad (10)$$

281 If we assume that  $\omega = \infty$  we can then solve the geometric series by finding the common  
282 ratio. Let  $S$  be the sum:

$$S = \sum_{t=\alpha_{mat}}^{\infty} p^{t-\alpha_{mat}} e^{-r_{max}t} \quad (11)$$

283 We can break down the summation as:

$$S = p^0 e^{-r_{max}\alpha_{mat}} + p^1 e^{-r_{max}(\alpha_{mat}+1)} \quad (12)$$

$$+ p^2 e^{-r_{max}(\alpha_{mat}+2)} + \dots$$

284 which is equivalent to:

$$S = e^{-r_{max}\alpha_{mat}} + p e^{-r_{max}\alpha_{mat}} e^{-r_{max}} \quad (13)$$

$$+ p^2 e^{-r_{max}\alpha_{mat}} (e^{-r_{max}})^2 + \dots$$

285 The value that would convert the first item of the sum into the second one, the second item  
286 into the third one and so on, is the common ratio, which in this case is  $p e^{-r_{max}}$ . Multiplying  
287 everything by  $p e^{-r_{max}}$  gives us:

$$S p e^{-r_{max}} = p e^{-r_{max}\alpha_{mat}} e^{-r_{max}} \quad (14)$$

$$+ p^2 e^{-r_{max}\alpha_{mat}} (e^{-r_{max}})^2$$

$$+ p^3 e^{-r_{max}\alpha_{mat}} (e^{-r_{max}})^3 + \dots$$

288 Therefore, the product of  $S$  and  $p e^{-r_{max}}$  is equal to  $S$  minus the first item of the series,  
289  $e^{-r_{max}\alpha_{mat}}$ . We can then subtract this second series ( $S p e^{-r_{max}}$ ) from  $S$ :

$$S - S p e^{-r_{max}} = e^{-r_{max}\alpha_{mat}} \quad (15)$$

290 Which allows for estimating  $S$  as:

$$S = \frac{e^{-r_{max}\alpha_{mat}}}{1 - pe^{-r_{max}}} \quad (16)$$

291 We then replace the summation back in the modified Euler-Lotka equation:

$$l_{\alpha_{mat}} b \frac{e^{-r_{max}\alpha_{mat}}}{1 - pe^{-r_{max}}} = 1 \quad (17)$$

292 and finally isolate  $l_{\alpha_{mat}} b$  and rearrange:

$$\begin{aligned} l_{\alpha_{mat}} b &= \frac{1}{e^{-r_{max}\alpha_{mat}}} - \frac{pe^{-r_{max}}}{e^{-r_{max}\alpha_{mat}}} \\ &= e^{r_{max}\alpha_{mat}} - \frac{pe^{r_{max}\alpha_{mat}}}{e^{r_{max}}} \\ &= e^{r_{max}\alpha_{mat}} - pe^{r_{max}\alpha_{mat} - r_{max}} \\ &= e^{r_{max}\alpha_{mat}} - pe^{r_{max}(\alpha_{mat} - 1)} \\ &= e^{r_{max}\alpha_{mat}} - p(e^{r_{max}})^{\alpha_{mat} - 1} \end{aligned} \quad (18)$$

293 This results in the same equation used by Hutchings et al. (2012), and is mathematically  
294 equivalent to the equation used by García et al. (2008) in the case where age of selectivity into  
295 the fishery  $\alpha_{sel} = 1$ . Equation 18 shows that survival to maturity is only encapsulated in  $l_{\alpha_{mat}}$   
296 and that its omission effectively assumes that all recruits survive to maturity.

297 **Understanding why spawners per spawners per year  $\tilde{\alpha}$  has been equated**  
298 **with annual fecundity  $b$**

299 All calculations of spawners per spawner are derived from the lifetime spawners per span-  
300 wner,  $\hat{\alpha}$ . The correct description of  $\tilde{\alpha}$  is given in Myers et al. (1997), where it is described as  
301 “the number of spawners produced by each spawner per year (after a lag of  $\alpha_{mat}$  years, where  
302  $\alpha_{mat}$  is age at maturity)”. Accounting for that lag is key, as then the lifetime spawners per  
303 spawner are divided by the years of sexual maturity, and therefore it is roughly analogous to  
304 annual fecundity in females times survival to maturity. The correct way of calculating  $\tilde{\alpha}$  is by  
305 solving

$$\hat{\alpha} = \sum_{t=\alpha_{mat}}^{\infty} p^t \tilde{\alpha} \quad (19)$$

306 Nonetheless, it has previously been calculated without including the lag of  $\alpha_{mat}$  years,  
307 hereafter defined as  $\tilde{\alpha}'$ , and has been estimated by solving  $\hat{\alpha} = \sum_{t=0}^{\infty} p^t \tilde{\alpha}'$ , which is the equa-  
308 tion used in Myers et al. (1999, 1997) and Goodwin et al. (2006). When using this equation, we  
309 are not removing the years before maturity effectively resulting in a metric more akin average  
310 yearly spawners per spawner across all age classes. Solving this geometric series without the  
311 lag yields:

$$\tilde{\alpha}' = \hat{\alpha}(1 - p) \quad (20)$$

312 However, as shown in equation 19, we can rewrite the geometric series so that it effec-  
313 tively removes immature age classes. Assuming that after reaching maturity annual survival is  
314 constant:

$$\begin{aligned} \hat{\alpha} &= \sum_{t=\alpha_{mat}}^{\infty} l_{\alpha_{mat}} p^{t-\alpha_{mat}} \tilde{\alpha} \\ &= l_{\alpha_{mat}} \tilde{\alpha} \sum_{t=\alpha_{mat}}^{\infty} p^{t-\alpha_{mat}} \end{aligned} \quad (21)$$

315 By solving it we obtain the following:

$$\tilde{\alpha} = \frac{\hat{\alpha}(1-p)}{l_{\alpha_{mat}}} \quad (22)$$

316 which is analogous to average yearly spawners per spawner across adult age classes, and  
317 therefore can be used to estimate  $r_{max}$  instead of  $l_{\alpha_{mat}} b$ . It also becomes apparent that  $\tilde{\alpha} =$   
318  $\tilde{\alpha}'/l_{\alpha_{mat}}$ . Given that this estimate of  $\tilde{\alpha}$  is divided by a proportion, it is larger than the  
319 previous estimate; this is expected as lifetime spawners per spawner are partitioned between  
320 only by mature age classes ( $\tilde{\alpha}$ ) instead of all age classes ( $\tilde{\alpha}'$ ).

321 **Assumptions of  $M = 1/\omega$**

322 As already mentioned, we assume that natural mortality rate of a cohort is exponentially  
323 distributed, thus the mean of that distribution is the reciprocal of that rate. Estimating in-  
324 stantaneous natural mortality  $M$  as the reciprocal of average lifespan  $\omega$  is mathematically  
325 equivalent to a given percentage of the population reaching  $\omega$ . As previously shown by He-  
326 witt and Hoenig (2005) using their equation as an example, we can calculate that by using  $M$   
327 as  $1/\omega$ , we are assuming that, on average, 36.8% of the population reaches average lifespan:

$$M = 1/\omega \quad (23)$$

328 We then rearrange and exponentiate:

$$\begin{aligned} M * \omega &= 1 \\ e^{-M\omega} &= e^{-1} \end{aligned} \quad (24)$$

329 The term  $e^{-M\omega}$  is equivalent to the survival to age  $\omega$ , or  $l_\omega$ . By then calculating the value  
330 of  $e^{-1}$  we can see that:

$$e^{-M\omega} = l_\omega = 0.3678 \quad (25)$$

331 Therefore using our method, the average survival to average lifespan is 36.8%, or roughly  
332 one out of three individuals.

333 **Supplementary Figures**

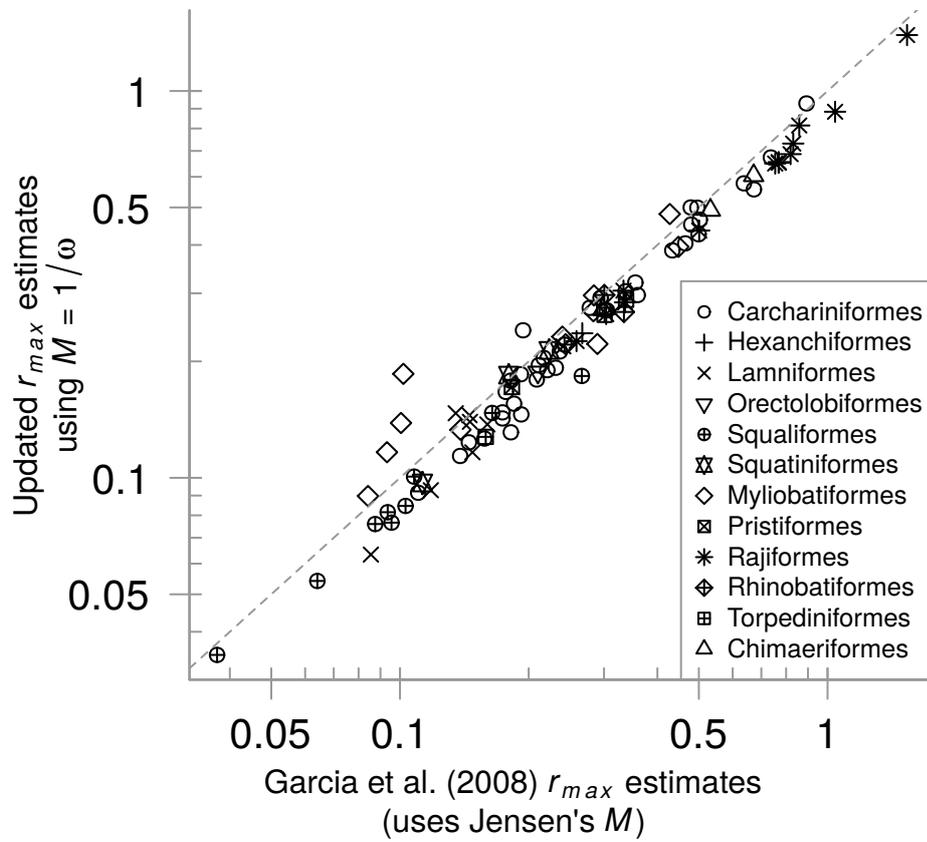


Figure 4: Comparison of previous  $r_{max}$  estimates of the model used in García et al. (2008) (recalculated using the method outlined in their paper) with our updated estimates. Different symbols denote different chondrichthyan orders. Note that the axes are log-transformed.

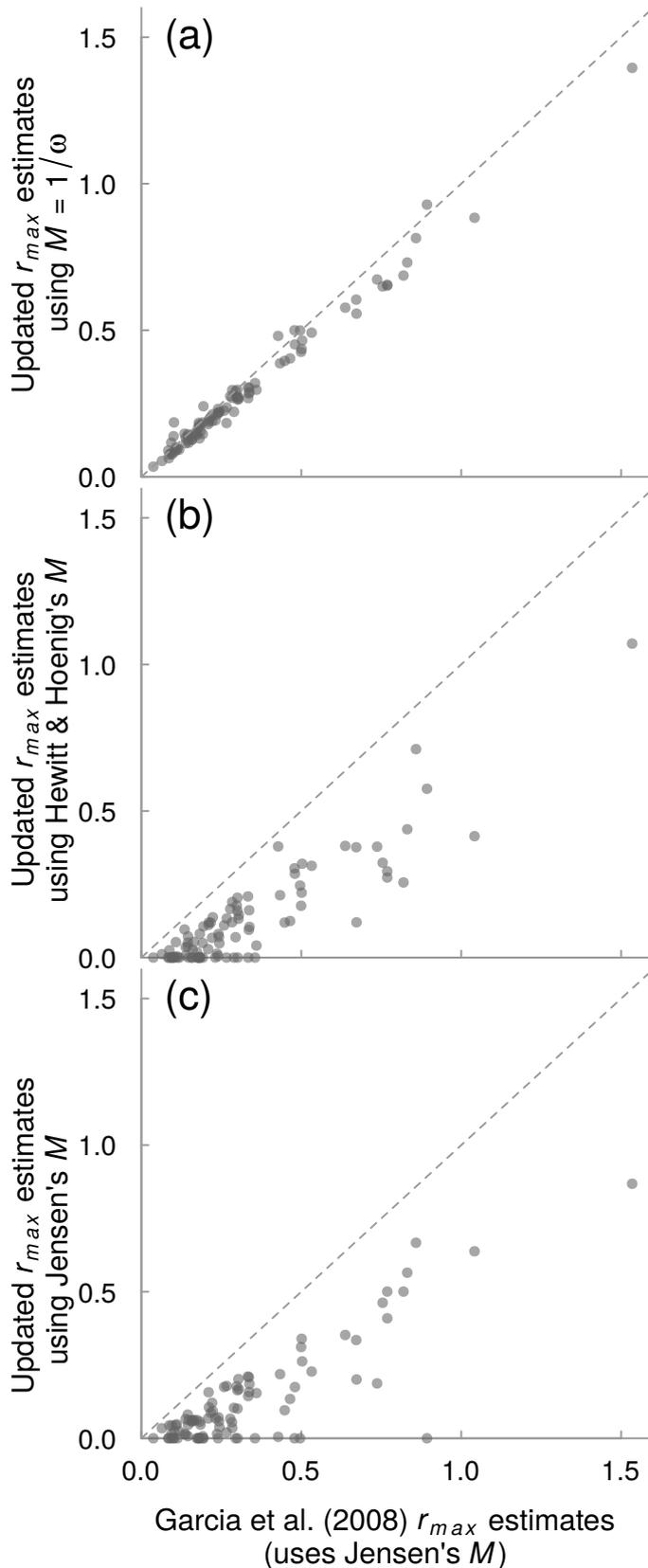


Figure 5: Comparison between updated  $r_{max}$  values with natural mortality estimated from (a) reciprocal of average lifespan, (b) Hewitt and Hoenig (2005), and (c) Jensen (1996). The dashed line represents the 1:1 relationship. Note that only the updated method using the reciprocal of average lifespan (a) shows similar values to the previous  $r_{max}$  estimates, while (b) and (c) often produce  $r_{max}$  estimates equal to zero or negative (both represented here by zeros).

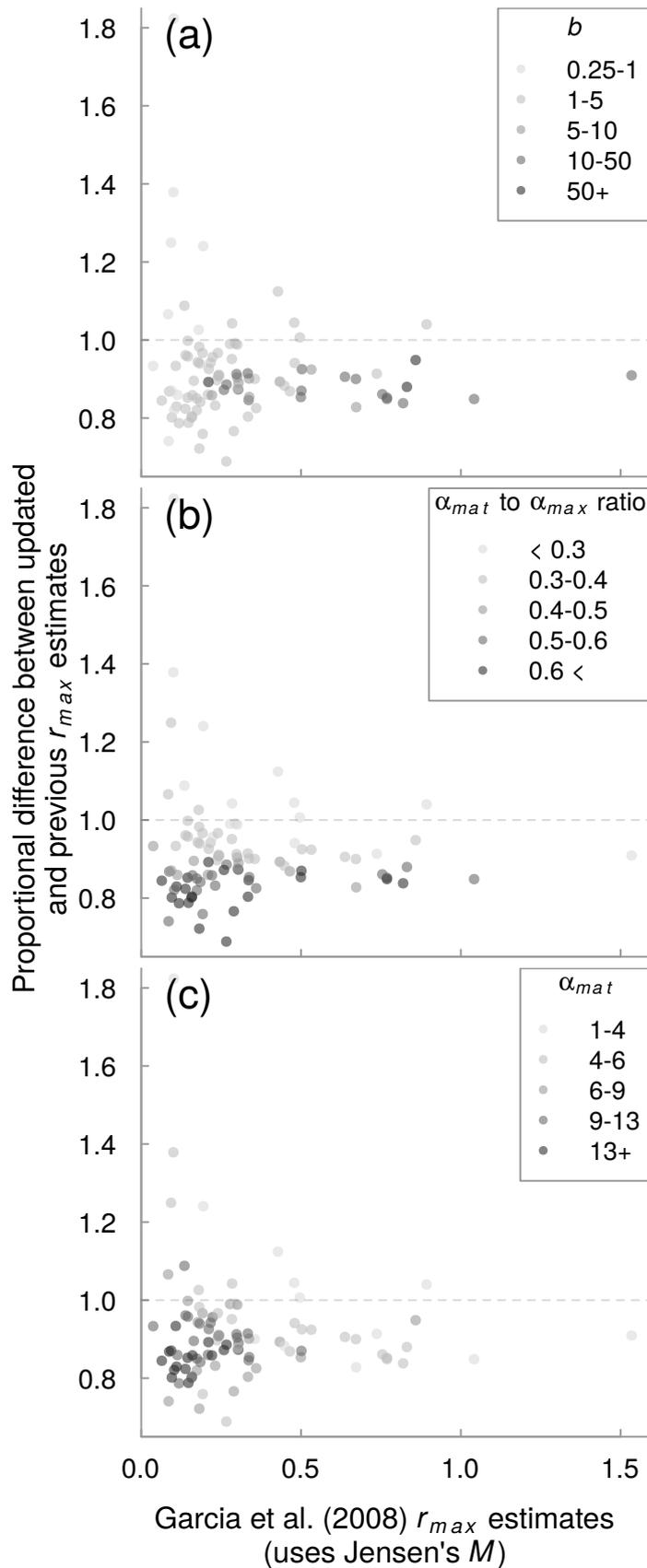


Figure 6: Proportional difference between updated and previous  $r_{max}$  estimates contrasted with (a) annual reproductive output of daughters, (b)  $\alpha_{mat}/\alpha_{max}$  ratio and (c) age at maturity. The dashed line represents no difference between updated and previous estimates.