Supplementary Material

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

The raw data used for our analyses are available on figshare at `https://dx.doi.org/10.6084/m9.figshare.3207697.v1`.

Detailed derivation of r_{max}

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

$$\sum_{t=1}^{\omega} l_t m_t e^{-rt} = 1 \tag{1}$$

Where t is age, ω is maximum age, l_t is the yearly survival at age t, m_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 a very low densities in the absense of density dependence. Assuming that after reaching maturity annual fecundity and annual surival are constant (b and p, respectively), we can estimate survival to year t as survival to maturity $l_{\alpha_{mat}}$ times yearly adult survival p for the years after maturation (Myers et al., 1997):

$$\text{for}(t \geq \alpha_{mat}) \begin{cases} m_t = b \\ \\ l_t = l_{\alpha_{mat}} p^{t-\alpha_{mat}} \end{cases} \tag{2}$$

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

1

Myers et al., 1997)

$$l_{\alpha_{mat}} b \sum_{t=\alpha_{mat}}^{\omega} p^{t-\alpha_{mat}} e^{-r_{max}t} = 1 \tag{3}$$

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

$$S = \sum_{t=\alpha_{mat}}^{\infty} p^{t-\alpha_{mat}} e^{-r_{max}t} \tag{4}$$

We can break down the summation as:

$$S = p^0 e^{-r_{max}\alpha_{mat}} + p^1 e^{-r_{max}(\alpha_{mat}+1)} \tag{5}$$
$$+ p^2 e^{-r_{max}(\alpha_{mat}+2)} + \dots$$

which is equivalent to:

$$S = e^{-r_{max}\alpha_{mat}} + p e^{-r_{max}\alpha_{mat}} e^{-r_{max}} \tag{6}$$
$$+ p^2 e^{-r_{max}\alpha_{mat}} (e^{-r_{max}})^2 + \dots$$

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

$$S p e^{-r_{max}} = p e^{-r_{max}\alpha_{mat}} e^{-r_{max}} \tag{7}$$
$$+ p^2 e^{-r_{max}\alpha_{mat}} (e^{-r_{max}})^2$$
$$+ p^3 e^{-r_{max}\alpha_{mat}} (e^{-r_{max}})^3 + \dots$$

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

$$S - S p e^{-r_{max}} = e^{-r_{max}\alpha_{mat}} \tag{8}$$

Which allows for estimating S as:

$$S = \frac{e^{-r_{max}\alpha_{mat}}}{1 - pe^{-r_{max}}} \tag{9}$$

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

$$l_{\alpha_{mat}} b \frac{e^{-r_{max}\alpha_{mat}}}{1 - pe^{-r_{max}}} = 1 \tag{10}$$

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

$$
\begin{aligned}
l_{\alpha_{mat}} b &= \frac{1}{e^{-r_{max}\alpha_{mat}}} - \frac{pe^{-r_{max}}}{e^{-r_{max}\alpha_{mat}}} \\
&= e^{r_{max}\alpha_{mat}} - \frac{pe^{r_{max}\alpha_{mat}}}{e^{r_{max}}} \\
&= e^{r_{max}\alpha_{mat}} - pe^{r_{max}\alpha_{mat}-r_{max}} \\
&= e^{r_{max}\alpha_{mat}} - pe^{r_{max}(\alpha_{mat}-1)} \\
&= e^{r_{max}\alpha_{mat}} - p(e^{r_{max}})^{\alpha_{mat}-1}
\end{aligned} \tag{11}
$$

This results in the same equation used by Hutchings et al. (2012), and is mathematically equivalent to the equation used by García et al. (2008) in the case where age of selectivity into the fishery $\alpha_{sel} = 1$. Equation 11 shows that survival to maturity is only encapsulated in $l_{\alpha_{mat}}$ and that its omission effectively assumes that all recruits survive to maturity.

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

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

$$\hat{\alpha} = \sum_{t=\alpha_{mat}}^{\infty} p^t \tilde{\alpha} \tag{12}$$

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

$$\tilde{\alpha}' = \hat{\alpha}(1-p) \tag{13}$$

However, as shown in equation 12, we can rewrite the geometric series so that it effectively removes immature age classes. Assuming that after reaching maturity annual surival is constant:

$$
\begin{aligned}
\hat{\alpha} &= \sum_{t=\alpha_{mat}}^{\infty} l_{alpha_{mat}} p^{t-\alpha_{mat}} \tilde{\alpha} \\
&= l_{alpha_{mat}} \tilde{\alpha} \sum_{t=\alpha_{mat}}^{\infty} p^{t-\alpha_{mat}}
\end{aligned} \tag{14}
$$

By solving it we obtain the following:

$$\tilde{\alpha} = \frac{\hat{\alpha}(1-p)}{l_{alpha_{mat}}} \tag{15}$$

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

$$\tilde{\alpha} = \qquad 5$$

Assumptions of $M = 1/\omega$

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

$$M = 1/\omega \tag{16}$$

We then rearrange and exponentiate:

$$M * \omega = 1$$
$$e^{-M\omega} = e^{-1} \tag{17}$$

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

$$e^{-M\omega} = l_\omega = 0.3678 \tag{18}$$

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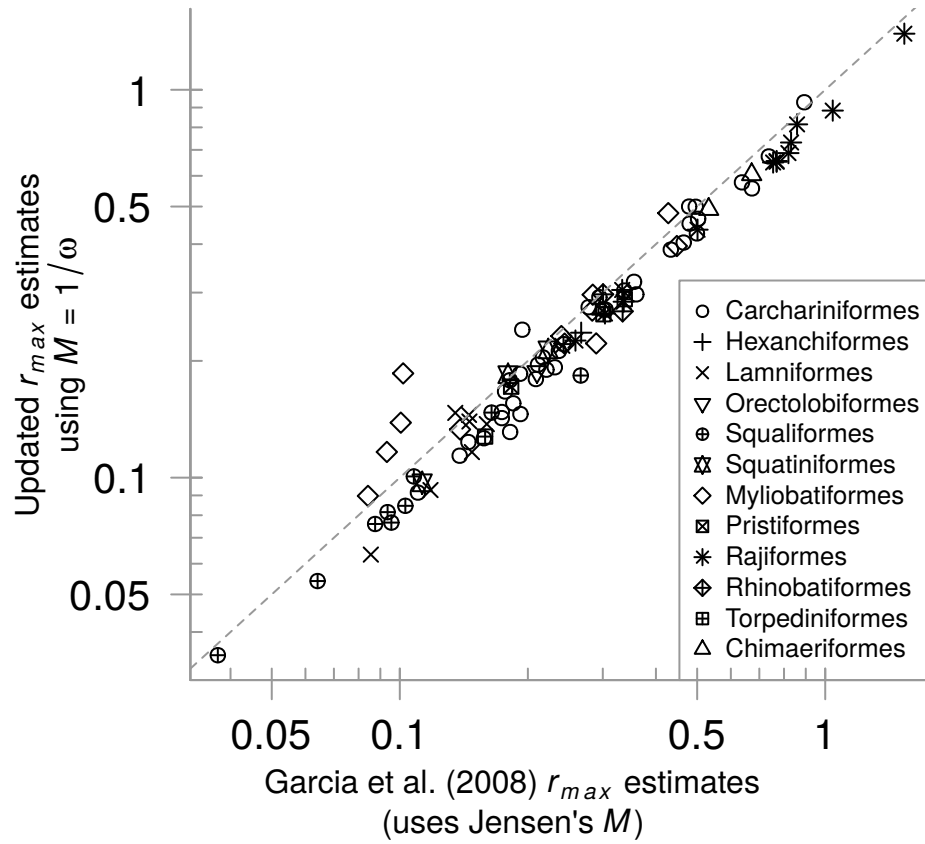
Supplementary Figures

Figure S1: 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.
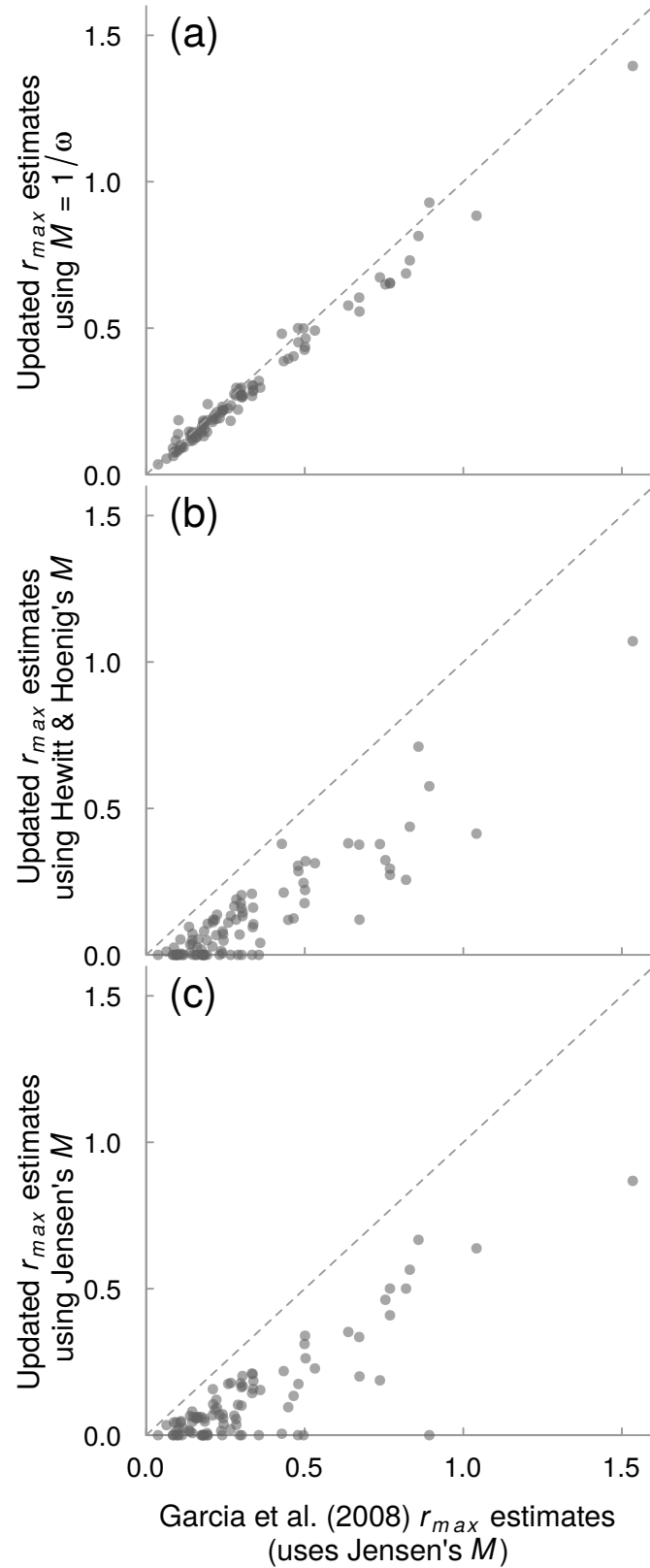
Figure S2: Comparison between updated r_{max} values with natural mortality estimated from (a) reciprocal of average lifespan, (b) Hewitt and Hoenig (2005), and (c) Jensen (1996). The dashed line represents the 1:1 relationship. Note that only the updated method using the reciprocal of average lifespan (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).
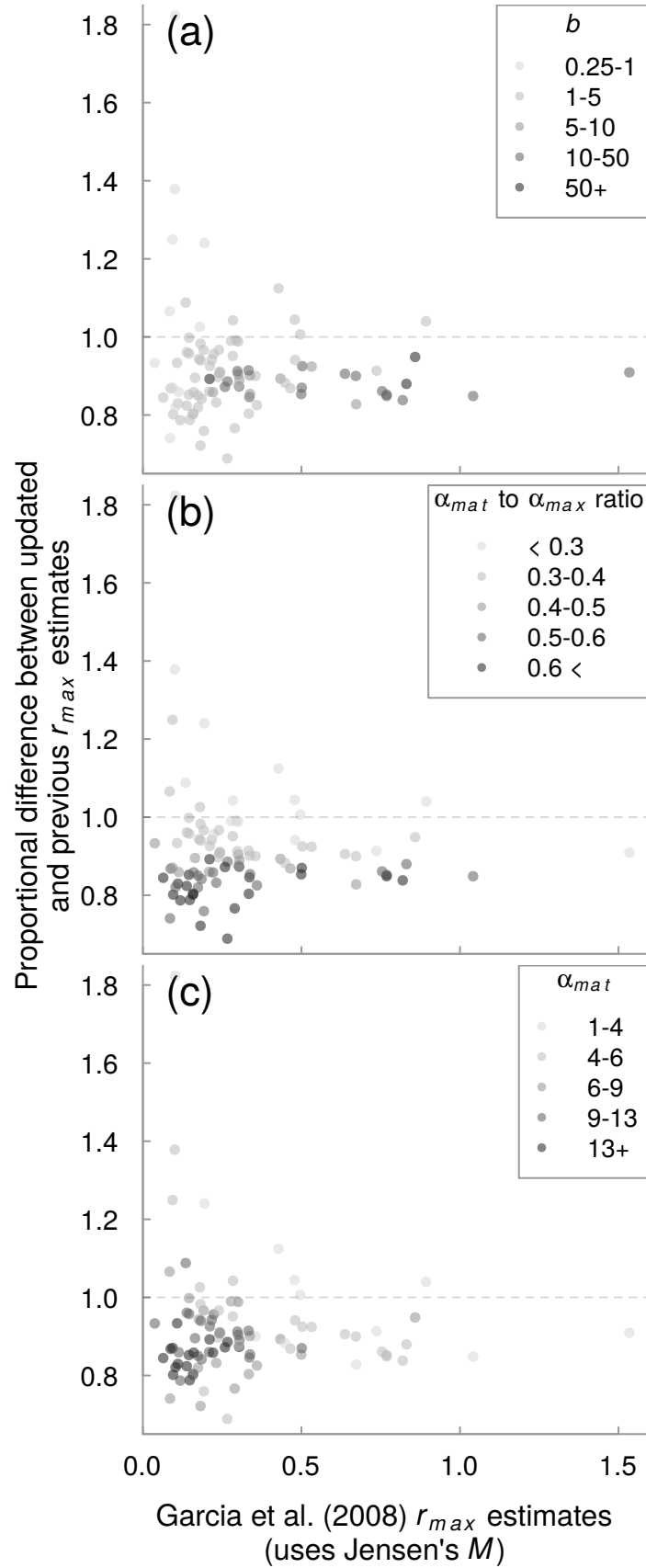
Figure S3: Proportional difference between updated and previous r_{max} estimates contrasted with (a) annual reproductive output of daughters, (b) $\alpha_{mat}/\alpha_{max}$ ratio and (c) age at maturity. The dashed line represents no difference between updated and previous estimates.

References

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. Proceedings of the Royal Society B **275**: 83–89. doi:10.1098/rspb.2007.1295.

Goodwin, N.B., Grant, A., Perry, A.L., Dulvy, N.K., and Reynolds, J.D. 2006. Life history correlates of density-dependent recruitment in marine fishes. Canadian Journal of Fisheries and Aquatic Sciences **63**(3): 494–509. doi:10.1139/f05-234.

Hewitt, D.A. and Hoenig, J.M. 2005. Comparison of two approaches for estimating natural mortality based on longevity. Fishery Bulletin **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. Ecological Applications **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. Canadian Journal of Fisheries and Aquatic Sciences **53**: 820–822.

Myers, R.A., Bowen, K.G., and Barrowman, N.J. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences **56**(12): 2404–2419. doi:10.1139/f99-201.

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