Unified natural mortality estimation for teleosts and elasmobranchs

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ABSTRACT: Natural mortality, $M$, is a key parameter for the assessment and management of living resources but is difficult to observe directly. Therefore, $M$ is often estimated indirectly from life history traits, and it is typically assumed to be invariant over size, age, and time. Such indirect estimators are particularly relevant for data-poor species, including many elasmobranchs (sharks, skates, and rays). However, as commonly used estimators were developed largely with teleost (bony fish) data, their performance for elasmobranchs is currently unknown. Here, we show that the relationship between observed maximum age, $t_{max}$, and mean adult $M$ is not significantly different between teleosts ($n = 105$) and elasmobranchs ($n = 15$). Furthermore, data on 16 teleosts and 2 elasmobranchs suggest that juvenile $M$ can be estimated from adult $M$ when juvenile $M$ is inversely proportional to body length and when a reference length can be provided. We introduce this reference length as the length at the age after which $M$ is assumed to be constant and demonstrate how it can be estimated using the von Bertalanffy growth function and the proportion surviving to $t_{max}$, which is shown to be approximately 1–2%. The data utilized here also suggest that if $t_{max}$ is unknown it can be estimated from growth information by assuming that 99% of the asymptotic maximum length is reached at $t_{max}$. Based on these life history parameters, the same indirect $M$ estimators can be utilized for teleosts and elasmobranchs, which may contribute to more reliable assessments of data-poor species.

KEY WORDS: Adult survival · Juvenile survival · Natural mortality · Life expectancy · Longevity · Growth · von Bertalanffy · Shark

1. INTRODUCTION

Globally, many overexploited marine species are lacking scientific assessments, which hampers sustainable use and effective conservation (Dulvy et al. 2014, Costello et al. 2016, Simpfendorfer & Dulvy 2017). This lack of information is also reflected by the proportion of species listed as Data Deficient on the IUCN’s Red List of Threatened Species for marine taxonomic groups that are of major conservation concern. Within these groups, elasmobranchs (sharks, skates, and rays) have the highest proportion of data deficiency, at 47% (Dulvy et al. 2014; www.iucn redlist.org). In such situations, one solution to gain knowledge critical for species’ assessments is to investigate whether common ecological principles across taxa allow for information to be shared between data-rich and data-poor species (Kindsvater et al. 2018). This is common practice, for example, when estimating the natural mortality rate, $M$ (Pauly 1980, Hoenig et al. 2016). $M$ is a highly influential parameter in many stock assessments and usually expressed

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as an instantaneous rate of decline within an exponential decay model:

\[ N_t = N_0 \times e^{-[(M + F) \times t]} \]  

(1)

where \( N_t \) is the number of individuals at time \( t \) (years), \( N_0 \) is the initial number of individuals, \( M \) is the instantaneous rate of natural mortality, and \( F \) is the instantaneous rate of fishing mortality (both \( M \) and \( F \) given in yr\(^{-1}\)), with the sum of \( M \) and \( F \) adding up to the total mortality rate, \( Z \). \( M \) is often required in the estimation of many important parameters, such as the prediction of catch and abundance (Haddon 2011) and the intrinsic rate of population increase (Simpfendorfer 2005, Pardo et al. 2018) or rebound potentials (Smith et al. 1998). In particular, \( M \) affects key reference parameters in fisheries, such as optimal exploitation rates, resilience, and productivity (Maunder & Wong 2011). For example, \( M \) has been widely used in fisheries management as a proxy for the level of \( F \) that produces maximum sustainable yield (Gulland 1971, Zhou et al. 2012). Furthermore, inaccurate rates of \( M \) can influence predicted stock size, especially when it is overestimated (Sims 1984, Johnson et al. 2015). Higher rates of \( M \) translate to higher estimated stock sizes (Cheilari & Rätz 2009) and reference points (Cheilari & Rätz 2009, Maunder & Wong 2011), and underestimated rates of \( F \) (Cheilari & Rätz 2009). Consequently, incorrect \( M \) estimates can result in biased estimates of stock status (Clark 1999), increasing the risk of mismanagement.

Ideally, \( M \) is estimated empirically via direct methods, i.e. from mark–recapture tagging data (Hoenig et al. 1998), telemetry data (Heupel & Simpfendorfer 2002, Knip et al. 2012), catch curves used to estimate \( Z \) in unexploited, newly exploited, or very lightly exploited populations (Simpfendorfer 1999), or by extrapolating \( M \) from \( Z \) and fishing effort (Pauly 1984). In very data-rich situations, \( M \) can also be estimated within stock assessments (Lee et al. 2011). However, these methods have limited applicability for data-poor groups, including many elasmobranchs.

Alternatively, indirect methods to estimate \( M \) have been developed, which utilize a relationship between the \( M \) and other life history traits. For example, Hoenig (1983) showed that in an unexploited population with no \( F \), Eq. (1) can be reformulated to yield the following linear predictive equation:

\[ \log_e(M) = \beta_0 + \beta_1 \times \log_e(t_{\text{max}}) \]  

(2)

where \( \beta_0 \) and \( \beta_1 \) are constants (the intercept and slope) to be estimated from a linear regression model, and \( t_{\text{max}} \) is the maximum age observed. Hence, a relationship can be developed empirically across species for which directly estimated rates of \( M \) (e.g. from catch curves in unexploited populations) and observed \( t_{\text{max}} \) are available. This relationship can then be used to obtain an estimate of \( M \) indirectly in species where \( M \) is unknown and cannot be estimated via direct methods, but for which \( t_{\text{max}} \), or any other life history parameter suitable to estimate \( M \), is known. Many of these indirect \( M \) estimators have been developed (see Kenchington 2014 for a review) and generally require information on \( t_{\text{max}} \) (Hoenig 1983, Then et al. 2015), age at maturity (\( t_m \)) (Jensen 1996), or growth (Pauly 1980, Jensen 1996, Then et al. 2015).

Additionally, many indirect methods typically assume that \( M \) is a constant that is independent of age, size, and time, which is also a common assumption in fisheries assessments (Vetter 1988). While age and size independence might well be a valid assumption during the adult phase (Brodziak et al. 2011, Deroba & Schueller 2013, Johnson et al. 2015), it may not hold for juveniles, which can experience substantially higher mortality rates than adults in both teleosts (bony fish) and elasmobranchs (Peterson & Wrobleski 1984, Chen & Watanabe 1989, Lorenzen 1996, 2000, Gruber et al. 2001, Gislason et al. 2010, Heupel & Simpfendorfer 2011). In response, indirect methods relating life history parameters to age- and size-dependent \( M \) rates have been developed (e.g. Peterson & Wrobleski 1984, Chen & Watanabe 1989, Lorenzen 1996, 2000, Gislason et al. 2010).

However, to date, both invariant and variant estimators for \( M \) have almost exclusively utilized information from teleosts, although the development of taxon-specific alternatives has been suggested (Kenchington 2014). In contrast to many teleosts, elasmobranchs are more generally characterized by low \( M \) rates, slow growth, late maturity, low fecundity, extended reproductive cycles, and longer lifespans (Hoenig & Gruber 1990, Camhi et al. 1998, Cortés 2000, Dulvy et al. 2014), similar to marine mammals (Smith et al. 1998). Therefore, it has been proposed that \( M \) estimators derived from cetacean (whales, dolphins, and porpoises) data can be used for elasmobranchs (Pardo et al. 2018), an approach that has been applied to several species (Cortés 1998, McAuley et al. 2007, Heupel & Simpfendorfer 2011, Hisano et al. 2011, Liu et al. 2015, Lessa et al. 2016, Yokoi et al. 2017, Queiroz et al. 2019). Yet the lack of adequate data has prevented detailed investigation of the performance of these indirect \( M \) estimators for elasmobranchs (Kenchington 2014).

Here, updated adult and juvenile databases for marine elasmobranchs and teleosts, with rates of \( M \) estimated from direct methods and associated life
history information, were assembled. Original sources were carefully checked before extracting the direct $M$ estimates. In addition, newly collected or previously unconsidered data were analyzed for elasmobranchs, combined with an extensive literature review, to obtain a larger sample of directly estimated $M$ rates for this group. On this basis, an empirically updated $M$ estimator was developed to investigate if taxon-specific estimators are required for teleosts and elasmobranchs. Furthermore, various indirect methods which estimate rates of $M$ from other life history parameters were compared to the direct estimates from the updated databases, for both juveniles and adults. Overall, our analyses aim to aid improved assessments and scientific management of data-poor species.

2. MATERIALS AND METHODS

2.1. Data

Two updated $M$ databases were developed: one for adult elasmobranchs and teleosts (see Table S1 in Supplement 1 at www.int-res.com/articles/suppl/m667p113_supp1.xlsx), and one for juveniles (Table S2). These databases contain direct estimates of $M$ as well as associated life history information required by many indirect estimators. All parameters were standardized to the same units. Rates are given in yr$^{-1}$, ages are given in years, and length is given in cm total length (TL) throughout. When TL was not available, it was estimated from length–length relationships using the provided length type.

2.1.1. Adult $M$ data

Adult $M$ is defined here as a constant average annual instantaneous mortality rate of adult individuals. For teleosts, direct estimates of $M$ were obtained from peer-reviewed literature by carefully checking and consulting the original sources utilized in a recently published extensive database (Then et al. 2015). The following selection criteria were applied: (1) only $M$ values from wild populations derived via direct methods in the original source, and from marine species for which the majority of data used to estimate $M$ came from adults, were considered; furthermore, estimates were excluded that (2) were unreliable (e.g. $Z$ was smaller than $M$); $M$ was based on expert opinion; $M$ was derived from mark–recapture methods that did not consider immigration and emigration, tag loss, reporting rate, or tagging mortality; (3) were considered unreliable or questionable by the authors in the original study; (4) were based on estimates of $Z$, and assumed $Z = M$, but the level of exploitation was unknown or the population was exploited and could not be considered very lightly exploited; and/or (5) had no estimate of corresponding $T_{\text{max}}$ available. If the authors of the present study were aware of revised $M$ estimates based on more and/or updated data, those estimates were used. Excluded references along with an explanation are provided in Table S3. Sex-specific $M$ estimates were preferred over combined estimates, given that the other life history parameters were also available for each sex. In the absence of sex-specific information, the average $M$ across both sexes was taken. If several direct methods were applied or the study gave several direct $M$ estimates and the authors did not specifically exclude the validity of a method or estimate, the average across methods or estimates was calculated. We also used the average when a study gave several $M$ estimates from a single unexploited population but from different areas.

For elasmobranchs, an extensive literature search including grey literature (such as government reports) was conducted to gather any additional information not yet included in previous work. Direct $M$ estimates for elasmobranchs were also obtained from newly collected data and published data not previously considered to estimate $M$. Published estimates for which updated information was available were re-analyzed. When sample size was sufficient, $M$ was estimated for males and females independently. One value of elasmobranch $M$ reported in Knip et al. (2012) that was extremely outlying was excluded from the analysis (see Fig. S1 in Supplement 2 at www.int-res.com/articles/suppl/m667p113_supp2.pdf).

2.1.2. Juvenile $M$ data

Juvenile $M$ is defined here as an annual instantaneous mortality rate estimated at a certain length, age, or weight representative for a juvenile individual. Direct estimates of juvenile $M$ were obtained from an extensive literature search, applying the same criteria as described above. In addition, only directly estimated mortality rates at a juvenile length, weight, or age and estimated per 1 yr (with units yr$^{-1}$) were included to avoid extrapolation. Juvenile $M$ estimates that were lower overall than adult $M$ estimates were not considered, because all tested methods assume a declining rate of $M$ with age, length, or
weight. Generally, the underlying samples consisted of juvenile individuals with various length or age classes, and therefore juvenile $M$ refers here to the instantaneous $M$ at a mean length. If not provided in the original source, the mean length at juvenile $M$ was calculated as the mean between the minimum and maximum length in the sample. If an age range was given instead, then length was calculated using the von Bertalanffy growth function (von Bertalanffy 1938):

$$L_t = L_\infty - (L_\infty - L_0)e^{-kt} = L_\infty \times (1 - e^{-kt})$$

where $L_t$ is the length at age $t$, $L_0$ is the length at age 0, $L_\infty$ is the asymptotic length, $k$ is a curve parameter describing how fast $L_\infty$ is approached, and $t_0$ is the theoretical age at zero length. $L_0$ can be obtained from $t_0$, as:

$$L_0 = L_\infty \times (1 - e^{-k \times t_0})$$

2.1.3. Life history data

Life history information on observed $t_{\text{max}}$ von Bertalanffy growth parameters, and $t_m$ were extracted from the same original study that estimated $M$ values, if possible, or obtained from a literature search. Only information from the same population was considered, and similar time periods and locations were preferred. If $t_m$ was not available, but length at maturity ($L_m$) and growth information were available, then $t_m$ was calculated using a rearranged von Bertalanffy growth function:

$$t = \frac{\log_e\left(\frac{L_\infty - L_0}{L_m - L_0}\right)}{k} = \frac{\log_e\left(1 - \frac{L_m}{L_\infty}\right)}{k}$$

where $t = t_m$ and $L_m = L_m$. Likewise, if $L_m$ was not available but $t_m$ and growth were available, then $L_m$ was estimated using the von Bertalanffy growth function (Eq. 3). For some bony fish where larvae are exceedingly small at birth, length at birth was assumed to be 0 if $t_0$ was not provided. The mean environmental temperature inhabited by the species, $T$ (°C), was mainly taken from Then et al. (2015) or FishBase (Froese & Pauly 2019), if not indicated otherwise in Table S1. Weight ($W$; in g) was calculated from the corresponding length class ($L$) using length-weight relationships (Froese 2006). If the direct $M$ estimate was only available for combined sexes, certain areas, or time periods, then the average of the life history parameters was taken across the corresponding sexes, areas, or time periods, if possible.

2.2. Adult $M$ estimator

In total, 4 updated indirect adult $M$ estimators were developed:

1. Given the log-linear relationship between $t_{\text{max}}$ and $M$ (Eq. 2), a linear regression analysis of direct $M$ estimates versus observed $t_{\text{max}}$ from the adult $M$ database was developed to estimate the parameters $\beta_0$ and $\beta_1$. This estimator is hereafter referred to as Estimator $T_{\text{max}}$. The response variable, $M$, and the covariate, $t_{\text{max}}$, were log-transformed.

2. Estimator $T_{\text{max}}$ requires an input of observed $t_{\text{max}}$. In the absence of an observed value, $t_{\text{max}}$ might be estimated from the von Bertalanffy growth function:

$$t_{\text{max}} = \frac{1}{k} \times \log_e\left(\frac{L_m - L_0}{(1 - X) \times L_0}\right)$$

where $X$ is the proportion of $L_m$ reached at $t_{\text{max}}$. Commonly, $X$ is assumed to be 0.95 (Taylor 1958, Ricker 1979), and the estimator with an estimated $t_{\text{max}}$ using $X = 0.95$ is hereafter referred to as Estimator $L_{\text{inf}}$95.

3. The proportion of $L_m$ reached at $t_{\text{max}}$ was also calculated using all available information on growth and observed $t_{\text{max}}$ in the adult $M$ database via:

$$X = \frac{L_m - (L_m - L_0) \times e^{(k \times t_{\text{max}})}}{L_m}$$

The estimated $t_{\text{max}}$ with $X$ as the median across all species was then used as input in the Estimator $T_{\text{max}}$. This estimator is hereafter referred to as Estimator $L_{\text{inf}}$.

4. The adult $M$ can also be estimated from the proportion of the cohort, $P$, that remains alive at $t_{\text{max}}$:

$$M = \frac{-\log_e(P)}{t_{\text{max}}}$$

$P$ has often been assigned an arbitrary value of 0.01 or 0.05, while empirical data suggest a value of 0.015 (Hewitt & Hoenig 2005). Here, the $P$ value was empirically updated. First, each single $P$ value was calculated from the corresponding directly estimated $M$ rate and the observed $t_{\text{max}}$ in the adult $M$ database, $P = e^{(-M \times t_{\text{max}})}$. Then, the median across all individual $P$ values was utilized in Eq. (8). This estimator is referred to as Estimator $P$.

2.3. Juvenile $M$ estimator

An updated indirect juvenile $M$ estimator was developed based on Lorenzen (2000), who suggested that $M$ scales inversely proportional with body length:

$$M_L = M \times \frac{L_j}{L}$$

This estimator needs a constant $M$ rate ($M_t$) at a specific reference length ($L_r$) as input, along with $L_m$ (Beyer et al. 1999) and $L_m$ (Brodziak et al. 2011), both proposed as reference lengths in the past. Here, this estimator was updated using the predicted constant adult $M$ rate from the Estimator $T_{max}$ as input for $M_t$, and a newly defined reference length, the length at the age after which $M$ can be assumed constant: $L_{ta}$. This length was derived as follows: the adult constant $M$ rate is related to the average life expectancy, $E$, in the form:

$$M = \frac{1}{E}$$  \hspace{1cm} (10)

Now $E$ can be defined as the average life expectancy after the age at which $M$ is assumed constant, $t_a$:

$$E = \frac{t_{max} - t_a}{2}$$  \hspace{1cm} (11)

It can be further defined that $x$ is the proportion of $t_{max}$ at which $M$ is assumed constant:

$$E = \frac{t_{max} - (x \times t_{max})}{2}$$  \hspace{1cm} (12)

and therefore:

$$M = \frac{2}{t_{max} - (x \times t_{max})} = \frac{2}{t_{max} \times (1-x)} = \frac{2}{t_{max} \times \left(1 - \frac{t_{max} - t_a}{t_{max}}\right)}$$  \hspace{1cm} (13)

This implies that $M$ can be estimated from a constant divided by $t_{max}$, which is equivalent to the definition in Eq. (8):

$$M = \frac{2}{t_{max} \times t_{max}} = -\log_e(P)$$  \hspace{1cm} (14)

From this, it follows that:

$$\frac{2}{(1-x)} = -\log_e(P)$$  \hspace{1cm} (15)

which can be solved for $x$:

$$x = \frac{2}{\log_e(P)} + 1$$  \hspace{1cm} (16)

and hence:

$$t_a = \left(\frac{2}{\log_e(P)} + 1\right) \times t_{max}$$  \hspace{1cm} (17)

The same empirically derived $P$ as in Estimator $P$ was used here, i.e. the median across all calculated proportions based on the information in the adult $M$ database. Finally, $L_{ta}$ was obtained from $t_a$ via the von Bertalanffy growth function. This estimator, with $L_{ta}$ as a reference length, is referred to as Estimator $L_{ta}$.

### 2.4. Evaluation of estimators

The linear regression assumptions underlying the indirect adult $M$ estimator (Estimator $T_{max}$) were evaluated using several well-established methods. Fitted values were plotted against the residuals to check for homogeneity of variances. Then et al. (2015) implied that the independence of observations assumption of linear regression might be violated when $M$ is estimated for the same species with information from different locations or sexes. Therefore, the residuals were tested on auto-correlation graphically via the auto-correlation-function (acf) plot in R version 3.5.2 (R Core Team 2018). For this purpose, the data for all investigated populations were ordered for taxonomy, species, sex, and location. In addition, a sensitivity analysis was performed. First, it was determined if a combined taxa (elasmobranch and teleost) estimator is valid by applying 3 approaches: (1) testing if taxon (elasmobranch or teleost) as an additional covariate is significant and if the model improves in terms of having a lower Akaike information criterion (AIC) value; (2) comparing the Estimator $T_{max}$ parameters for combined taxa with the parameters from linear regression models for each taxon; and (3) comparing the Estimator $T_{max}$ parameters with the parameters from a linear regression model that only utilized information from species where $t_{max} \geq 3$ yr, because elasmobranchs attain higher maximum ages than teleosts (Nielsen et al. 2016). A $t_{max}$ of 3 yr was selected because 3 yr is among the lowest reported values of $t_{max}$ in elasmobranchs (Cailliet & Goldman 2004). Second, it was determined if the use of (ordinary least squares) linear regression is valid by comparing the Estimator $T_{max}$ parameters with the parameters obtained from other linear regression techniques: (1) robust linear regression to investigate if a few observations have a high influence through the assessment of robustness weights computed in the fitting process, using the command ‘rim’ in the R package ‘MASS’ (Venables & Ripley 2002); (2) major axis regression (a special case of orthogonal regression or errors-in-variables regression), which minimizes a different loss function than the sum of squared residuals to take into account that the covariate $t_{max}$ is technically also measured with error (i.e. also random), using the R package ‘moodel2’ (Legende 2018). Furthermore, to evaluate indirect $M$ estimates obtained from Estimator $T_{max}$ against $M$ estimates obtained from direct methods, 10-fold cross validation was used to obtain an out-of-sample prediction error (Then et al. 2015, Hoenig et al. 2016) via the ‘DAAG’ package (Maindonald & Braun 2015). Here, the data were split into 10 random subsets; each subset was then excluded at a time so the remaining data points were used to re-fit the model to predict the excluded observations.
Hoenig et al. (2016) and Then et al. (2015) also suggest that the hierarchical nature of the data has to be taken into consideration, as this can violate assumptions of independence. We considered mixed-effect models with taxonomic order as a random intercept/slope to check for possible within-order dependence. The results were similar and not significantly different from ordinary regression, yet the small number of observations for many orders (7 out of 15 orders with only 1 observation) does not allow fitting such models with confidence. We therefore excluded random effect models from this analysis.

All updated indirect $M$ estimators (Estimator $T_{\text{max}}$, Estimator $P$, Estimator $L_{\text{inf}}95$ Estimator $L_{\text{inf}}$, and Estimator $L_{\text{ta}}$) were compared in their performance against previously published indirect $M$ estimators. This comparison was done by evaluating the accuracy and precision of the indirect estimators in predicting the direct $M$ estimates in the adult or juvenile $M$ database, respectively. For adult $M$, 10 more commonly applied indirect adult $M$ estimators were used for comparison (Table 1). For juvenile $M$, comparisons were done using 7 more commonly applied age-, size-, or weight-dependent indirect $M$ estimators (Table 2). For estimators using weight instead of length, the mean weight (in g) was calculated from mean length using length–weight relationships (Froese 2006). For estimators using age instead of length, mean age was obtained from mean length using the von Bertalanffy growth function (Eq. 5). To evaluate the performance of the different estimators, recommendations of Walther & Moore (2005) were followed, and scaled measures were used. First, the relative error (in %) was calculated:

$$\text{Relative error} = \frac{\hat{M}_i - M}{M} \times 100 \quad (18)$$

where $M$ is the reference parameter, i.e. the $M$ value obtained from the direct methods in the $M$ databases, and $\hat{M}_i$ is the corresponding $i$th estimate from each of the investigated estimators. Boxplots were used to show the median and variation in the relative error for each estimator. Then, to evaluate the performance based on accuracy and precision, 2 additional measures were calculated, the scaled mean absolute error, SMAE:

$$\text{SMAE} = \text{median}\left(\frac{\hat{M}_i - M}{M}\right) \quad (19)$$

and the scaled median absolute deviation, SMAD, to also evaluate a measure more robust against outliers:

$$\text{SMAD} = \text{median}\left(\frac{\hat{M}_i - M}{M}\right) \quad (20)$$

Smaller values for the relative error, SMAE, and SMAD indicated better performance. Note that SMAE and SMAD are strictly positive values, and only the relative error can be utilized to evaluate the potential direction of bias (overestimation or underestimation) of an estimator.

| Name                        | Formula                                                                 | Reference                  |
|-----------------------------|-------------------------------------------------------------------------|----------------------------|
| **Estimator $T_{\text{max}}$** | $M = e^{[1.44 - 0.982 \times \log_{10}(t_{\text{max}})]}$              | This study                 |
| **HoenigAll**               | $M = e^{[0.941 - 0.873 \times \log_{10}(t_{\text{max}})]}$              | Hoenig (1983)              |
| **HoenigCetacean**          | $M = e^{[0.461 - 1.01 \times \log_{10}(t_{\text{max}})]}$              | Hoenig (1983)              |
| **HoenigFish**              | $M = e^{[1.46 - 0.654 \times \log_{10}(L_\infty)]}$                     | Hoenig (1983)              |
| **Then$T_{\text{max}}$**    | $M = 4.899 t_{\text{max}}^{0.916}$                                      | Then et al. (2015)         |
| **Estimator $P$**           | $M = \frac{-\log_{10}(P)}{t_{\text{max}}}$                             | This study                 |
| **HewittHoenig$P$**         | $M = \frac{-\log_{10}(0.015)}{t_{\text{max}}}$                         | Hewitt & Hoenig (2005)     |
| **P0.05**                   | $M = \frac{-\log_{10}(0.05)}{t_{\text{max}}}$                         | Cadima (2003)              |
| **Jensen$T_{\text{m}}$**   | $M = 1.65 t_{\text{m}}$                                                 | Jensen (1996)              |
| **Jensen$Growth$**          | $M = 1.5 k$                                                             | Jensen (1996)              |
| **Then$Growth$**            | $M = 4.118 L_\infty^{-0.33}$                                            | Then et al. (2015)         |
| **Pauly$Growth$**           | $M = 10^{0.007 - 0.279 \times \log_{10}(L_\infty) - 0.015 \times \log_{10}(k) + 0.046 \times \log_{10}(T)}$ | Pauly (1980)              |
| **Estimator $L_{\text{inf}}95$** | $M = e^{[1.65 - 0.916 \times \log_{10}(L_\infty)]}$                      | This study                 |
| **Estimator $L_{\text{inf}}$** | $M = e^{[4.899 t_{\text{max}}^{0.916}] - 0.916}$                        | This study                 |
Table 2. Indirect estimators of juvenile natural mortality (Mr yr⁻¹), at length, age, or weight estimators based on von Bertalanffy growth parameters k (yr⁻¹) and L∞ (cm), weight (W; g), length (L; cm), age (t; years), and age at which senescence (the increase of mortality at old ages) commences (t₀ years). The method of Lorenzen (2000), LorL, requires a constant reference M rate (M₀) at a reference length. Here, adult M estimated from Estimator Tmax was utilized as M₀, and 3 reference lengths were tested: the length after which M is assumed constant (Lₒₒ), the length at maturity (Lₒₒ) (Brodziak et al. 2011) and L∞ (Beyer et al. 1999). The method of Peterson & Wroblewski (1984), PW, was derived from dry weights (in g); dry weight was assumed to be 20% of wet weight (Cortés 2002).

| Name     | Formula                                                                 | Reference                             |
|----------|-------------------------------------------------------------------------|---------------------------------------|
| Lta      |                         |                                       |
| LorLm    | Mₛ = Lₒₒ × Lₒₒ            | Lorenzen (2000), Brodziak et al. (2011) |
| LorLmax  | Mₛ = Lₒₒ × Lₒₒ            | Lorenzen (2000), Beyer et al. (1999)  |
| LorW     | M_w = 3W⁻²·²²           | Lorenzen (1996)                      |
| PW       | M_w = 1.92[W − (0.2 × W)]⁻⁰·₂₅ | Peterson & Wroblewski (1984), Cortés (2002) |
| CW       | Mₜ = \[ \frac{k}{1 - e^{-\frac{L}{L_{∞}}}} \] t ≤ tₛ  \[ \frac{a_0 + a_1(t - l_{∞}) + a_2(t - l_{∞})}{k} \] t ≥ tₛ  | Chen & Watanabe (1989)               |
| Cha      | Mₛ = \left( \frac{L}{L_{∞}} \right) × k | Charnov et al. (2013)                |
| Gis      | Mₛ = e^{[0.55−1.61×\log₉(Lₜ−1.44×\log₉(L_{∞})+\log₉(lₜ))]} | Gislason et al. (2010)               |

Each estimator was tested on the maximum number of observations, whether all life history information was complete for a particular observation or not. This process can introduce bias and prevent a fair comparison in which outlier species (or populations) or non-randomness would not affect all estimators the same (Hoenig et al. 2016). Therefore, all estimators were additionally tested on a common database, where only direct M estimates were included for which all other life history information that are required by any of the estimators were available. Furthermore, the residuals (direct M from databases minus predicted M from estimator) were plotted against the predicted M from the indirect estimators to identify estimators with better behaving error structure (Then et al. 2015).

3. RESULTS

3.1. Adult M

In total, 120 direct adult M estimates for marine fish from 70 different sources were utilized for the adult M database. Direct M estimates came from 105 teleosts and 15 elasmobranches from 15 taxonomic orders within 39 families, comprising 77 and 12 different teleost and elasmbranch species, respectively. The direct M estimates came primarily from catch curves, i.e. applying a linear regression to the logₑ-transformed Eq. (1) in unexploited or lightly exploited populations, so that M approximates Z. Direct M estimates ranged from 7.92 to 0.014 yr⁻¹; tmax range was 0.73–131.5 yr in teleosts and 5.7–73 yr in elasmobranchs. Lₒₒ range was 4.72–280 cm and k range was 2.555–0.034 yr⁻¹. Of the 120 direct M and tmax estimates, 118 estimates also had corresponding von Bertalanffy growth parameters available, and 86 estimates also had tₚ data available.

Based on the updated adult M database, the Estimator Tmax is given by:

\[
M = e^{[0.551−1.066×\log₉(t_{max})]} \quad (21)
\]

This estimator had a 10-fold cross validation prediction error of 0.13. The linear relationship between M (logₑ yr⁻¹) and tmax (logₑ yr) was highly significant (R² = 0.92, p < 0.0001; Table 3). The predictions from the Estimator Tmax showed a good fit to both elasmobranch and teleost data and when compared to existing tmax-based indirect estimators (Fig. 1). There was no significant difference when ‘taxa’ were added as an additional covariate (p = 0.74) nor did the model improve with the same coefficient of variation (R² = 0.92) and a slightly higher AIC (Table 3). Furthermore, the linear regression for each taxon individually and the linear regression based on comparable tmax only showed similar parameter estimates and overlapping confidence intervals when compared to Estimator Tmax (Table 4). Likewise, the parameter estimates were very similar across linear regression techniques and all were within the confidence intervals of the Estimator Tmax estimates (Table 4).
The variances of the Estimator $T_{max}$ predictions were homogeneous (Fig. S2), the residuals had an approximate normal distribution (Fig. S3; Shapiro-Wilk $p = 0.05$; Kolmogorov-Smirnov $p < 0.0001$), and there was no residual auto-correlation (Fig. S4). This suggests that the use of the ordinary linear regression model was appropriate.

In the absence of an observed value for $t_{max}$, it may be estimated using the von Bertalanffy growth function. The percentage of the $L_\infty$ reached at maximum age $X$ was set at 0.95 for the Estimator $T_{max}$ with only $t_{max}$ (loge yr) as a covariate ($\textbf{bold}$). The second model has an additional covariate, taxa (elasmobranch or teleost). Both models had a coefficient of variation, $R^2$, of 0.92. The model with only $t_{max}$ as a covariate had a slightly lower Akaike information criterion (AIC) of 100 compared to 102 for the model with $t_{max}$ and taxa as covariates.

Table 3. Relationship of natural mortality ($M$) and maximum age ($t_{max}$) between elasmobranchs and teleosts. Shown are the estimated coefficients from linear regression, 95\% CI and p-values for 2 models predicting adult $M$ (loge yr$^{-1}$). The first model is the Estimator $T_{max}$ with only $t_{max}$ (loge yr) as a covariate ($\textbf{bold}$). The second model has an additional covariate, taxa (elasmobranch or teleost). Both models had a coefficient of variation, $R^2$, of 0.92. The model with only $t_{max}$ as a covariate had a slightly lower Akaike information criterion (AIC) of 100 compared to 102 for the model with $t_{max}$ and taxa as covariates.

| Model                                      | $\beta$  | 95\% CI      | $p$    |
|--------------------------------------------|----------|---------------|--------|
| $\log_e(M) = \beta_0 + \beta_1 \times \log_e(t_{max})$ | Intercept | 1.551 | 1.39, 1.71 | <0.001 |
|                                            | $\log_e t_{max}$ | -1.066 | -1.12, -1.01 | <0.001 |
| $\log_e(M) = \beta_0 + \beta_1 \times \log_e(t_{max}) + \beta_2 \times \text{taxa}$ | Intercept | 1.519 | 1.27, 1.77 | <0.001 |
|                                            | $\log_e t_{max}$ | -1.065 | -1.12, -1.01 | <0.001 |
|                                            | Taxa     | 0.033 | -0.17, 0.23 | 0.74   |

Fig. 1. Relationships between natural mortality ($M$) and maximum age ($t_{max}$) in marine fish. (A) Black line: predicted relationship (Estimator $T_{max}$) of $M$ and $t_{max}$ for teleosts and elasmobranchs combined. Shaded area: 95\% CI. (B) Fit of predicted $M$ estimates from various $t_{max}$-based indirect estimators (colored lines) compared to the direct $M$ estimates from the adult $M$ database (grey dots) for elasmobranchs (left) and teleosts (right) independently. See Table 1 for details on the different indirect estimators.
Table 4. Sensitivity analysis showing results of different linear regression models used to evaluate if the relationship of natural mortality (M, log e yr⁻¹) and maximum age (tmax, log e yr) is (1) different for elasmobranchs and teleosts (linear regression for each taxon individually, linear regression based on comparable maximum ages [direct estimates with tmax ≥ 3]); (2) influenced by a few values (robust regression); or (3) influenced by errors in maximum age (model II major axis regression); tmax was significant (p < 0.0001) for each model. The Estimator Tmax (base case) with elasmobranchs and teleosts combined is shown in bold.

| Method                  | Model                                                                 | Intercept | Slope       |
|-------------------------|------------------------------------------------------------------------|-----------|-------------|
| Teleosts                | \( \log_e(M) = 1.550 - 1.064 \times \log_e(t_{\text{max}}) \)          | 1.38, 1.72 | -1.12, -1.00|
| Elasmobranch            | \( \log_e(M) = 1.583 - 1.087 \times \log_e(t_{\text{max}}) \)          | 0.99, 2.18 | -1.28, -0.89|
| Comparable tmax         | \( \log_e(M) = 1.565 - 1.071 \times \log_e(t_{\text{max}}) \)          | 1.30, 1.83 | -1.16, -0.98|
| Robust regression       | \( \log_e(M) = 1.557 - 1.063 \times \log_e(t_{\text{max}}) \)          | 1.40, 1.71 | -1.12, -1.01|
| Major axis regression   | \( \log_e(M) = 1.681 - 1.115 \times \log_e(t_{\text{max}}) \)          | 1.51, 1.85 | -1.18, -1.06|
| Estimator Tmax          | \( \log_e(M) = 1.551 - 1.066 \times \log_e(t_{\text{max}}) \)          | 1.39, 1.71 | -1.12, -1.01|

Estimator Linf95 estimator and estimated from the life history information in the adult M database for the Estimator Linf. For the latter, the estimated median X was 0.988, and X did not differ significantly between elasmobranchs and teleosts (Fig. 2A; Wilcoxon p = 0.54). Hence, the Estimator Linf is given by:

\[
M = e^{\left(1.551 - 1.066 \times \log_e\left(\frac{1}{1-0.98} x_{\text{max}}\right)\right)}
\]  

(22)

The proportion of individuals in a cohort surviving from birth to tmax (i.e., P) was also not significantly different between elasmobranchs and teleosts (Fig. 2B; Wilcoxon p = 0.36) and the median percentage of individuals remaining alive at tmax was 1.779%. Therefore, Estimator P is given by:

\[
M = \frac{-\log_e(0.0178)}{t_{\text{max}}}
\]  

(23)

Estimator Tmax performed best compared to all other tested indirect methods, across elasmobranchs and teleosts (Fig. 3A, Table 5) and among each taxon separately (Fig. S5, Table S4). The previously established indirect adult M estimators tend to overestimate M, with average relative errors of up to 100%. From the published indirect adult M estimators, the Hoenig-Fish estimator performed best (Fig. 3A, Table 5). Furthermore, the new Estimator Tmax, Estimator P, and Estimator Linf as well as all estimators from Hoenig (1983) and all estimators based on P had relative errors that were generally smaller than 50% across all taxonomic orders (Fig. S6), with Estimator Tmax performing generally well (Figs. S6–S8, Table S5).

To test all estimators on a common database, 34 data points were excluded because they were lacking at least one parameter required by any of the adult M estimators. Based on the remaining 86 direct estimates, Estimator Tmax also performed well (Fig. S9, Table S6). A similar pattern emerged when selecting 10 points randomly from these 86 direct estimates, applying all estimators, calculating the relative error, SMAE, and SMAD, and repeating these steps 1000 times (Fig. S10). The Estimator Tmax predictions also showed the best residual behavior (Fig. S11).

All estimators based on tmax performed better than estimators based on growth except for the Estimator Linf, which also performed better than any other estimator applicable in the absence of observed tmax.

3.2. Juvenile M

In total, 18 directly estimated juvenile M rates were obtained from 16 teleost and 2 elasmobranch populations. Direct estimates included 5 taxonomic orders of 7 families, comprising 8 different teleost and 2 different elasmobranch species. The juvenile direct M rates were estimated primarily from tagging data. Directly estimated M ranged from 3.285 to 0.13 yr⁻¹. The mean TL corresponding to the direct juvenile M estimate ranged from 2.8 to 129.1 cm, Lr ranged from 18.5 to 398.5 cm, and Lmax ranged from 11.5 to 232.5 cm, while k ranged from 0.43 to 0.057 yr⁻¹. Observed tmax of species in the juvenile M database ranged from 4.5 to 30 yr. For all 18 direct estimates, all life history parameters required by any of the indirect juvenile M estimators were available.

Based on the juvenile M database, the overall best performing estimator was Estimator Lt, \( M_t = \frac{L_t}{L} \), with \( M_t \) derived from Estimator Tmax and L as the reference length (Fig. 3B, Table 5). The Lorenzen (2000) method LorLm — with M, derived from Estimator Tmax but Lm as reference length — also performed well (Figs. 3B & S12, Tables 5 & S7). The residual pat-
terns of Estimators $L_{ta}$ and $L_{or}$ showed roughly constant variability throughout the range of the predicted $M$. However, the Estimator $L_{ta}$ predictions had better residual behavior (Fig. S13). The weight-based estimators all tended to underestimate $M$, while the growth-based estimators tended to overestimate $M$ (Fig. 3B, Table 5). $L_{ta}$ was obtained from $t_a$ using the von Bertalanffy growth function. Assuming that $P = 0.018$, then it follows from Eq. (17) that $t_a = 0.5 \times t_{\text{max}}$.

4. DISCUSSION

This study investigated if the same indirect approaches to estimate $M$ can be utilized for elasmobranchs and teleosts, or if taxa-specific estimators are required. We found that combined taxa estimators are valid and perform well among and across these 2 taxa. The best-performing indirect adult $M$ estimator, Estimator $T_{\text{max}}$, was based on updated data and ordinary linear regression, with $t_{\text{max}}$ as the only covariate. Another updated estimator also performed well, Estimator $P$, where the life history data suggests that in unfished cohorts $P$ is between 1 and 2% (median: 1.8%). In addition, life history data suggest that in the absence of observed $t_{\text{max}}$, this value can be estimated using the von Bertalanffy growth function with the assumption that the length at $t_{\text{max}}$ is at 99% of $L_\infty$. Juvenile $M$ rates were best estimated from a constant adult $M$, by assuming that $M$ is inversely proportional to body length (Lorenzen 2000) and by utilizing a newly introduced reference length, $L_{fu}$.
Although the true rate of $M$ is unknown and indirect estimators can only be tested on how well they can reproduce direct $M$ estimates (Then et al. 2015, Hoenig et al. 2016), some approaches presented here appear promising with results highly comparable to direct methods. However, most direct $M$ estimates considered in this study were based on catch curves, and therefore the indirect $M$ estimates are most reflective of estimates from the catch curve method. Hence, the assumptions that apply to the catch curve method should be considered when applying such $M$ estimators; specifically, (1) the sample should be representative of the entire population, with (2) accurate age classes for which the linear function is fitted, and (3) equal vulnerability to the fishing gear, and (4) constant mortality across these age classes, as well as (5) constant mortality and recruitment across years if years were pooled (Simpfendorfer et al. 2005).
Indirect adult $M$ estimators based on $t_{\text{max}}$ achieved the best overall results in predicting the direct $M$ estimate in the database. This is in accordance with previous studies (Punt et al. 2005, Kenchington 2014, Then et al. 2015). It has also been shown that estimators including information in addition to $t_{\text{max}}$ are not better in predicting $M$ (Then et al. 2015) and, similarly, no improvement was observed here when ‘taxa’ (elasmobranchs and teleosts) was utilized as an additional covariate.

The exclusion of unreliable $M$ estimates likely explains much of the deviation between the presented estimators here and many previously published and empirically derived estimators (Figs. 3 & S14). However, this explanation cannot hold for theoretically derived estimators. Jensen’s (1996) estimators are based on the ecological theory that species are selected to maximize lifetime fecundity, using Beverton-Holt life history invariants with $M/k = 1.5$. However, the $M/k$ ratio has been found to vary considerably among different species (Prince et al. 2015, Thorson et al. 2017), possibly explaining why the 2 indirect $M$ estimators proposed by Jensen (1996) did not perform well across taxa. In addition, the $M/k$ ratio has been reported to differ between some teleost and elasmobranch species (Frisk et al. 2001), whereas no evidence was found here that the relationship between $M$ and $t_{\text{max}}$ differs between these 2 taxa.

The results presented here suggest that for marine fish, similar proportions of individuals are surviving to $t_{\text{max}}$. In the past, arbitrary values of 1 or 5% have been used for this proportion, while empirical data have suggested 1.5% (Hewitt & Hoening 2005). The empirical data analyzed here suggest a very similar result, with approximately 1–2% of the individuals surviving from birth to $t_{\text{max}}$. This finding is further supported when examining the survivors from the age at 25% of $L_m$ (which might be used as a proxy for the average length when offspring are born; Cortés 2000) to $t_{\text{max}}$ and from $t_m$ to $t_{\text{max}}$ (Fig. 4). Approximately 2% survive from the age at 0.25$L_m$ to $t_{\text{max}}$ and 5% from $t_m$ to $t_{\text{max}}$, indicating that $P$ is likely smaller than 5%.

In the absence of direct observations, $t_{\text{max}}$ may be estimated in order to predict the $M$ rate. Approaches that estimate $t_{\text{max}}$ solely from maximum length (e.g. Ohsumi 1979) are likely not universal, even within taxa. For example, the oldest known whale is the bowhead whale Balaena mysticetus, reaching ages of more than 200 yr (George et al. 1999); however, it is not the largest whale species. Likewise, the spotted spiny dogfish Squalus suckleyi, a small species of shark, can live for more than 80 yr (Vega et al. 2009).

On the other hand, the von Bertalanffy model utilizes information on growth and has been used previously to estimate $t_{\text{max}}$. This requires an estimate for the proportion of $L_m$ reached at $t_{\text{max}}$, which has been commonly suggested at 95% (Taylor 1958, Ricker 1979). The findings here indicate that this value is on average closer to 99% for marine fish. The estimation of $t_{\text{max}}$ with the von Bertalanffy model also required a value for the length at birth (i.e. $L_0$), as observed in the wild. However, $t_{\text{max}}$ can also be expressed by applying the concept of half-lives. Fabens (1965) defined $t_{\text{max}}$ as the age reached after 7.22 half-lives, which corresponds to $X = 0.9933$, whereas $X = 0.95$ (Ricker 1979) corresponds to 4.32 half-lives. In both examples, $L_0$ was assumed to be 0. The number of half-lives will vary according to the value of $L_0$ assumed; for example, Cailliet et al. (2006) assumed $L_0 = 0.2L_m$ and $X = 0.95$, which resulted in a $t_{\text{max}}$ estimate of 4 half-lives. When calculating the half-lives with half-life $= \frac{t_{\text{max}}}{\log_e(2)}$ for each of the 118 observations for which $t_{\text{max}}$ and $k$ were present, the median value across all observations is 5.83 half-lives. This value is between the previously suggested definitions of $t_{\text{max}}$ using the half-life concept, which would be expected given that Fabens (1965) assumed $L_0$ to be 0, which would result in a greater half-life value despite a similar value for $X$ at ~0.99.

Similar to the findings for adults, this study also suggests that juvenile $M$ can be indirectly estimated using the same estimator for elasmobranchs and teleosts. However, the results should be viewed with caution, given the small sample size and uncertainty associated with the data. For example, the mean TL at the direct $M$ estimate was only given for 3 data points, and for one of these 3 data points, only fork length was given so TL had to be approximated. In most cases, the mean TL was estimated from age using the von Bertalanffy growth function rather than being directly observed in the study. Nevertheless, the presented Estimator Lta performed generally well in predicting juvenile $M$, with more accurate predictions than any other previously published age-, size-, or weight-dependent indirect estimator. The Estimator Lta utilized a newly introduced reference length, $L_{\text{ref}}$. This length was generally larger than $L_m$, with the median ratio $L_{\text{ref}}/L_m = 1.25$ (range: 0.91–1.89), while the ratio with $L_{\text{ref}}/L_m = 0.72$ (range: 0.48–0.92), for all 18 direct estimates. This indicates that $L_{\text{ref}}$ is typically larger than $L_m$ (Fig. S15), and therefore $L_{\text{ref}}$ might be more closely associated with the length at which all individuals are mature, $L_{m100}$. The corresponding value of $t_{\text{ref}}$ was found to occur at
~0.5 $t_{\text{max}}$, whereas $t_{m}$ generally occurs at 0.16–0.5 $t_{\text{max}}$ (Beverton 1992, Cortés 2000, Frisk et al. 2001), indicating $t_{m} \leq t_{a}$.

In conclusion, taxon-specific indirect $M$ estimators are not required for teleosts and elasmobranchs when based on $t_{\text{max}}$. Such a universal $M$ estimator has been suggested by Hoenig (1983) for molluscs, fish, and cetaceans combined. Hoenig’s (1983) reasoning for a combined taxa estimator, instead of using one estimator for each of the taxa, was to use the model with the widest range of $t_{\text{max}}$ and the highest coefficient of determination. In addition, we found that a combined taxa estimator for teleosts and elasmobranchs can likely be explained by the similar value of $P$ in an unfished cohort (Fig. 2B), which then suggests the same relationship between $t_{\text{max}}$ and $M$ when the numbers in a cohort decay exponentially (Eqs. 1 & 8). Therefore, a relatively simple, reliable, and general approach can be utilized for elasmobranchs and teleosts in data-poor situations when estimating adult $M$ rates from $t_{\text{max}}$. Although there is strong evidence that $M$ declines with increased individual length (Peterson & Wroblewski 1984, Chen & Watanabe 1989, Lorenzen 1996, 2000, Gislason et al. 2010), a constant $M$ for mature individuals might still be appropriate (Brodziak et al. 2011, Deroba & Schueller 2013, Johnson et al. 2015). The stress of reproduction and other intrinsic factors, such as the accumulation of harmful mutations, may cause $M$ to increase at larger sizes or older ages (actuarial senescence); however, this phenomenon is currently not easily predictable (Brodziak et al. 2011), and actuarial senescence was not examined in this study. It has been previously suggested that $M$ follows the Lorenzen curve up to $L_{m}$ and is constant thereafter. This suggestion is based on the assump-

Fig. 4. Percentage of individual teleosts and elasmobranchs surviving from (A) the age at 25% of the asymptotic maximum length ($L_{\infty}$) to maximum age ($t_{\text{max}}$) and (B) age at maturity, $t_{m}$, to $t_{\text{max}}$. Dashed line: 1% of individuals surviving; dotted line: 5% survivors. The distribution shape of the data is shown for (A) and (B) around the boxplots (boxplot limits as in Fig. 2)
tion that an increase in mortality after reproduction is compensated by a decrease in mortality due to larger size (Brodziak et al. 2011). The results presented here suggest that size-dependent $M$ for juveniles can be approximated using the adult constant $M$ (Lorenzen 2000), albeit the small sample size warrants future validation. In its minimal form, the Estimator $Linf$ allows size-dependent $M$ to be estimated from growth information alone by using $t_{max} = \frac{1}{k} \log_e \left( \frac{L_\infty - L_0}{1 - 0.99} \times L_\infty \right)$ and assuming that $P$ is between 1 and 2%. The results of this study, combined with recent advances in estimating growth (Dureuil 2019), could thus allow for relatively wide applicability in data-poor situations. More generally, the estimators could be used to indirectly estimate an $M$ rate for stock assessment purposes or to obtain informative priors in Bayesian analyses. Also, $M$ can play an important role when estimating pre-disturbance generation length (a critical measure to assess population reduction), to evaluate extinction risk on the IUCN Red List of Threatened Species (IUCN 2019), and in rebuilding plans (Patrick & Cope 2014). The presented estimators may also be applicable for species other than marine fish if there is reason to believe that mortality curves and $P$ are similar across disparate taxa or species, such as in freshwater fish, cetaceans, and invertebrates (Hoenig 1983, Hewitt et al. 2007, McCoy 2008, Maceina & Sammons 2016). The application of indirect estimators should, however, also consider some form of sensitivity analysis, given the importance of an accurate and precise $M$ estimate and the difficulties in estimating $M$. For example, the von Bertalanffy growth function and information from similar species could be used to determine if the observed $t_{max}$ growth, and the estimated $M$ rate are biologically reasonable. Furthermore, it should be recognized that the $M$ estimate pertains to the time period for which life history parameters were derived, and that $M$ can change over time (Deroba & Schueller 2013) and with exploitation pressure (Jørgensen & Fiksen 2010). In addition, Estimator $P$ is also less biased than Estimator $T_{max}$ when $t_{max}$ is highly underestimated (Fig. S16), which can be of particular interest in elasmobranch species with age underestimation (Harry 2018). Such considerations are highly relevant, given the complex relationships of $M$ to life history data and various properties relevant to fisheries management (Fig. 5). It is hoped that the updated estimators presented here will enhance the estimation of $M$ and thus fisheries assessments in data-poor situations, allowing for more species to be assessed and managed based on minimal data.

**Data-rich**

- Tagging (tag-recovery or capture-recapture, tag-reporting rate, tagging mortality and tag loss)
- Telemetry (long-term monitoring, fate)
- Catch curves (age or growth, indices, fishing mortality)
- Changes in total mortality and fishing effort (total mortality & fishing effort series)

**Data-poor**

- Estimator $T_{max}$ (maximum age)
- Estimator $P$ (maximum age)
- Estimator $Linf$ (growth)

Fig. 5. Estimation of natural mortality ($M$) in data-poor and data-rich stocks. Different direct and indirect methods to estimate $M$ are indicated along with their main data requirements. Generally, information on the population structure or emigration rate is required across methods. The heavier-weighted line indicates that a direct approach should be preferred when required data is available. The lower 4 boxes give examples of properties relevant for assessment and fisheries management that require an estimate of $M$ (bold type for emphasis).
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