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Some explorations of the life history ratios to describe length composition, spawning-per-recruit, and the spawning potential ratio

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Evaluating the status of data-poor fish stocks is often limited by incomplete knowledge of the basic life history parameters: the natural mortality rate (M), the von Bertalanffy growth parameters (L_∞ and k), and the length at maturity (L_m). A common approach to estimate these individual parameters has been to use the Beverton–Holt life history invariants, the ratios M/k and L_m/L_∞, especially for estimating M. In this study, we assumed no knowledge of the individual parameters, and explored how the information on life history strategy contained in these ratios can be applied to assessing data-poor stocks. We developed analytical models to develop a relationship between M/k and the von Bertalanffy growth curve, and demonstrate the link between the life history ratios and yield- and spawning-per-recruit. We further developed the previously recognized relationship between M/k and yield- and spawning-per-recruit by using information on L_m/L_∞, knife-edge selectivity (L_c/L_∞), and the ratio of fishing to natural mortality (F/M), to demonstrate the link between an exploited stock's expected length composition, and its spawning potential ratio (SPR), an internationally recognized measurement of stock status. Variation in length-at-age and logistic selectivity patterns were incorporated in the model to demonstrate how SPR can be calculated from the observed size composition of the catch; an advance which has potential as a cost-effective method for assessing data-poor stocks. A companion paper investigates the effects of deviations in the main assumptions of the model on the application of the analytical models developed in this study as a cost-effective method for stock assessment [Hordyk, A. R., Ono, K., Valencia, S., Loneragan, N. R., and Prince, J. D. this issue. A novel length based empirical estimation method of spawning potential ratio (SPR), and tests of its performance, for small-scale, data-poor fisheries. ICES Journal of Marine Science].

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Introduction

Studies of the life history information on the growth, mortality, and maturity schedules of fish stocks form the basis of fisheries science, and such information is essential for the effective management of exploited populations (Beverton and Holt, 1957; Hilborn and Walters, 1992). However, this information is only available for about 1200 of the 7000 or so exploited fish species, and it is not always available for all regions where the species are fished (Froese and Binohlan, 2000). Patterns of variation between life history parameters, particularly between natural mortality (M),

and the von Bertalanffy growth rate and asymptotic size (k and L_∞), have long been observed for many fish populations, and a large amount of work has been done to document and understand these relationships, often with the aim of providing cost-effective "short-cuts" to estimate the parameters, such as natural mortality, that are difficult or expensive to obtain (Beverton and Holt, 1959; Pauly, 1980; Roff, 1984; Beverton, 1992; Charnov, 1993). Typically, these studies have explored the relationships between single variables, such as M or k, that are commonly used in stock assessments.

The M/k ratio is one of the life history ratios that is known to be relatively consistent between closely related stocks (Beverton, 1992). The results of bio-energetic modelling by Jensen (1996) suggest that an optimal value for M/k is 1.5. Assuming von Bertalanffy growth, the relationship between the biomass and mean length of a cohort can be derived from the M/k ratio (Beverton, 1992; Jensen, 1996). Using this relationship, life history theory predicts that length at maturity (L_m) will be found at the length of maximum biomass in the population. This theoretical relationship provides the basis for the second life history ratio L_m/L_∞, with an optimal value of 0.66 (Jensen, 1996). Supported by the other empirical work (Pauly, 1980; Charnov, 1993), these values for the ratios of M/k and L_m/L_∞ have become known as the Beverton–Holt life history invariants (BH-LHI), and are often used as proxies for estimates of M/k (1.5) and L_m/L_∞ (0.66) in data-poor stocks. For example, it is not uncommon for studies to estimate the notoriously difficult parameter M by simply using the Beverton–Holt invariant $M = 1.5k$ (e.g. see many papers citing Jensen, 1996), or by estimating the fishing mortality rate F when the total mortality ($Z = F + M$) and k are known, by assuming that $M/k = 1.5$ (Beddington and Kirkwood, 2005).

Extending their earlier seminal work (Beverton and Holt, 1957), Beverton and Holt (1964) were the first to show that yield and biomass equations could be restated using the dimensionless ratios M/k and L_m/L_∞. Since then, others have built on their work to incorporate the dimensionless numbers into fisheries science (Jensen, 1996; Mangel, 1996; Williams and Shertzer, 2003; Beddington and Kirkwood, 2005). However, it has often been assumed that these ratios are invariant, which is evidently not the case. For example, a recent study of the Kyphosid *Scorpis aequipinnis*, in southwest Australia, has found that the M/k for the species is 0.33 (Coulson *et al.*, 2012) much lower than the BH-LHI of 1.5, and reminiscent of a life history more commonly associated with marine mammals (Prince *et al.*, this issue). Furthermore, a meta-analysis of 123 marine species of teleosts, chondrichthyes, invertebrates, and marine mammals found that the ratio of M/k ranged from 0.12 to 3.52, indicating that the life history ratios often vary considerably from the BH-LHI (Prince *et al.*, this issue). Others have also acknowledged this variability in M/k. For example, the widely used multivariate regression of Pauly (1980) implicitly correlated temperature and adult body size with M/k for each species, and Frisk *et al.* (2001) noted that M/k for elasmobranchs typically differs from that of bony fish. Although some studies have explicitly accounted for variability in the M/k ratio (e.g. Williams and Shertzer, 2003, 2005), the ratio is often assumed to be invariant, and the variability of the ratios of M/k and L_m/L_∞ in fish stocks has not been explored comprehensively.

This paper develops simple analytical models to explore the influence of changing the ratios of M/k, F/M, and L_m/L_∞ on the von Bertalanffy growth curve, the length composition of the stock, and as a consequence the yield and spawning-per-recruit, under the assumption of equilibrium. It uses the data collated in the meta-analysis of Prince *et al.* (this issue) to provide the basis for the range of values investigated in this study. The initial models are extended to include more complex assumptions about growth and selectivity, and investigate the relationship between the three ratios and the spawning potential ratio (SPR). By developing the link between the life history ratios, the expected equilibrium size composition, and SPR, this study provides the potential to develop a cost-effective technique to assess data-poor fisheries using length frequency data; an idea that is further developed in an accompanying paper (Hordyk *et al.,* this issue).

Analytical models
Redefining the von Bertalanffy equation in terms of M/k

The von Bertalanffy equation is commonly used to model fish growth, and is given as:

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right), \tag{1}$$

where L_t is the length at age t, L_∞ the theoretical length at infinite age, k the growth coefficient, and t_0 the theoretical age when length equals zero. The von Bertalanffy equation can be simplified by assuming $t_0 = 0$, and standardizing length to the asymptotic length:

$$\begin{aligned} \tilde{L}_t &= \frac{L_t}{L_\infty}, \\ &= 1 - e^{-kt}. \end{aligned} \tag{2}$$

The natural mortality rate (M) of fish is extremely difficult to estimate, especially for stocks that have been exploited for some time. A number of methods exist to estimate M from empirical data, including methods where M is assumed to be inversely correlated with longevity (Hoenig, 1983; Hewitt and Hoenig, 2005). A simple rule-of-thumb to estimate M involves the assumption that a certain proportion (P) of animals survive to some maximum age t_{max} (Quinn and Deriso, 1999):

$$M = \frac{-ln(P)}{t_{max}}. \tag{3}$$

Naturally, the accuracy of this rule-of-thumb depends on the appropriate value for the proportion P, and this has typically been assumed to be between 1 and 5% (Hewitt and Hoenig, 2005). The choice of $P = 5\%$ is somewhat arbitrary, and appears to overestimate M for a large range of species, with empirical work suggesting that $P = 1.5\%$ is more appropriate (Hoenig, 1983; Hewitt and Hoenig, 2005). The accuracy of this rule-of-thumb is also highly dependent on a good estimate of t_{max}, which is often taken as the maximum observed age, and depends on both the sampling method and how heavily the stock has been exploited before sampling. For simplicity, this study assumes that $P = 1\%$, and so t_{max} can be calculated from M as:

$$t_{max} = \frac{-ln\,0.01}{M}. \tag{4}$$

If age is standardized to t_{max} then x can be defined as t/t_{max}. From Equation (2), $\tilde{L}_t = 1 - e^{-kt}$ with $t = xt_{max} = -x\ln 0.01/M$, then:

$$\begin{aligned} \tilde{L}_x &= 1 - e^{(-k(-x ln\,0.01/M))}, \\ &= 1 - 0.01^{(x(k/M))}. \end{aligned} \tag{5}$$

This demonstrates that the shape of the standardized von Bertalanffy growth curve is solely determined by the ratio M/k, and does not depend on the absolute value of either the k or M parameters (Figure 1). The biological significance of L_∞ becomes increasingly vague as M/k increases (Figure 1). For a species that conforms to the Beverton–Holt invariant $M/k = 1.5$, the maximum size (L_{max}; i.e. the length at t_{max}) is $\sim 0.95 L_\infty$. However, a species with $M/k = 2.3$ would only be expected to reach about $0.8 L_\infty$ at t_{max} (bottom curve in Figure 1). In contrast, a species with $M/k = 0.3$, like *S. aequipinnis*,
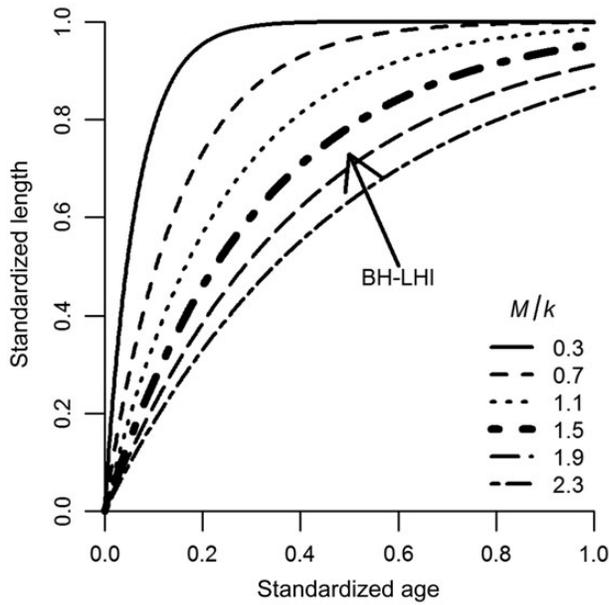
Figure 1. The standardized von Bertalanffy growth curves for fish at standardized length (L_t/L_∞) and standardized age (t/t_{max}) from Equation (5) for M/k ranging from 0.3 to 2.3. The BH-LHI of $M/k = 1.5$ is shown in bold.
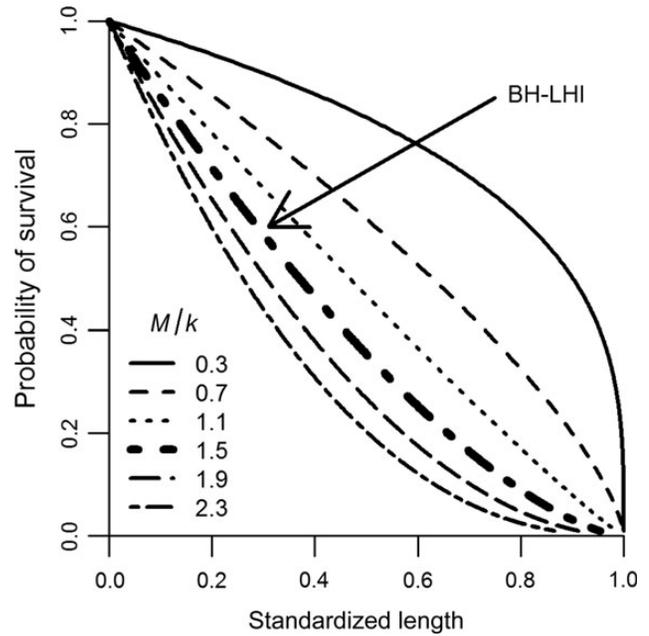

Figure 2. The probability of a fish in the unfished state surviving to standardized length from Equation (10) for a range of M/k (0.3–2.3). The BH-LHI of $M/k = 1.5$ is shown in bold.

would reach asymptotic size relatively early in life and then continue to live for a relatively long time without any further growth (top curve in Figure 1). The difference between L_{max} and L_∞ is more pronounced if P is larger. For example, if P was 0.05, L_{max} would be $0.86L_\infty$ and $0.73L_\infty$ for M/k values of 1.5 and 2.3, respectively. In reality, the length-at-age of fish is usually variable and the von Bertalanffy equation is used to describe the average growth curve of the stock, with the L_∞ parameter estimated as the average asymptotic size. This means that, in practice, some fish may have observed lengths greater than L_∞ (i.e. $L_{max} > L_\infty$), even for species with higher M/k. However, Figure 1 demonstrates that it must be emphasized to distinguish between the biological parameter L_{max} and the mathematical parameter L_∞, and any assumptions regarding the relationship between the two parameters must be carefully interpreted in the light of other knowledge of the species (i.e. the M/k ratio and the variability in length-at-age).

Number of animals at age in terms of M/k

Fish populations are often modelled with the assumption that the number of individuals in an unfished cohort decrease with constant natural mortality:

$$N_t = N_0 e^{-Mt}. \tag{6}$$

where N_t is the number of individuals at age t and N_0 the number of recruits (age 0). When working in terms of numbers per recruit, Equation (6) becomes the following:

$$\tilde{N}_t = e^{-Mt}, \tag{7}$$

where $\tilde{N}_t$ is the number per recruit. The number of animals alive at standardized age x can be expressed in terms of M/k by re-arranging

Equation (5) to find x at $\tilde{L}_x$,

$$x = \frac{M}{k} \frac{\ln(1 - \tilde{L}_x)}{\ln(0.01)} \tag{8}$$

Substituting $x t_{max}$ for t in Equation (7) gives:

$$\tilde{N}_x = e^{-M x t_{max}}. \tag{9}$$

Substituting $M = -(\ln 0.01/t_{max})$ and $x = (M/k)[\ln(1 - \tilde{L}_x)/\ln(0.01)]$ and simplifying (see Supplementary Appendix A) gives $\tilde{N}_x$ in terms of $\tilde{L}_x$ and M/k:

$$\tilde{N}_x = (1 - \tilde{L}_x)^{M/k}. \tag{10}$$

It is of note that the proportion P drops out of Equation (10), so that the result is independent of P which is typically unknown and difficult to estimate. Equation (10) is effectively a survival function, which shows that the probability of a fish in the unfished state surviving to greater than standardized length $\tilde{l}$ is determined by M/k:

$$\Pr\{\tilde{L} \geq \tilde{l}\} = (1 - \tilde{l})^{M/k}. \tag{11}$$

Figure 2 demonstrates Equation (11) for a range of M/k, and reiterates what is shown in Figure 1: a species with a high M/k has a low probability of reaching large size (lowest curve in Figure 2), with the probability of reaching larger size increasing as the M/k ratio decreases (upper curves in Figure 2). It follows from Equation (1) that the cumulative probability distribution is:

$$\begin{aligned} G(\tilde{l}) &= \Pr\{\tilde{L} \leq \tilde{l}\} \\ &= 1 - (1 - \tilde{l})^{M/k}, \end{aligned} \tag{12}$$

and, therefore, in the unfished state, the probability that an individual is in length class *i* can be calculated from:

$$P_{i_{\text{Unfished}}} = \begin{cases} 1 - (1 - \tilde{l}_{i+1}^{\text{lo}})^{M/k} & \text{if } i = 1 \\ (1 - \tilde{l}_i^{\text{lo}})^{M/k} - (1 - \tilde{l}_{i+1}^{\text{lo}})^{M/k} & \text{if } 1 < i < I , \\ (1 - \tilde{l}_i^{\text{lo}})^{M/k} & \text{if } i = I \end{cases} \quad (13)$$

where *I* is the number of length classes and $\tilde{l}_i^{\text{lo}}$ the lower bound of length class *i*. These equations can be used to simulate the expected unfished length composition for a given M/k, and Figure 3 shows that the equilibrium unfished length composition of species with low M/k (e.g. 0.6) would be expected to be dominated by large animals, with relatively few animals of smaller size. On the other hand, the equilibrium size structure of species with higher M/k (e.g. 3.0) would be expected to made up predominantly of small individuals, and large animals (i.e. near asymptotic size) would be rare, even in the unfished state.

Changing the scale of *M* and *k*

By convention, the rate parameters *M* and *k* are typically given as instantaneous annual rates, e.g. $M = 0.2 \text{ year}^{-1}$ or $k = 0.15 \text{ year}^{-1}$. Discrete age-structured population dynamics models implicitly assume that mortality and growth occurs once a year. Usually, this assumption is of little consequence in modelling the dynamics of fish populations. However, for short-lived species, the temporal resolution of annual parameters is too coarse to effectively model
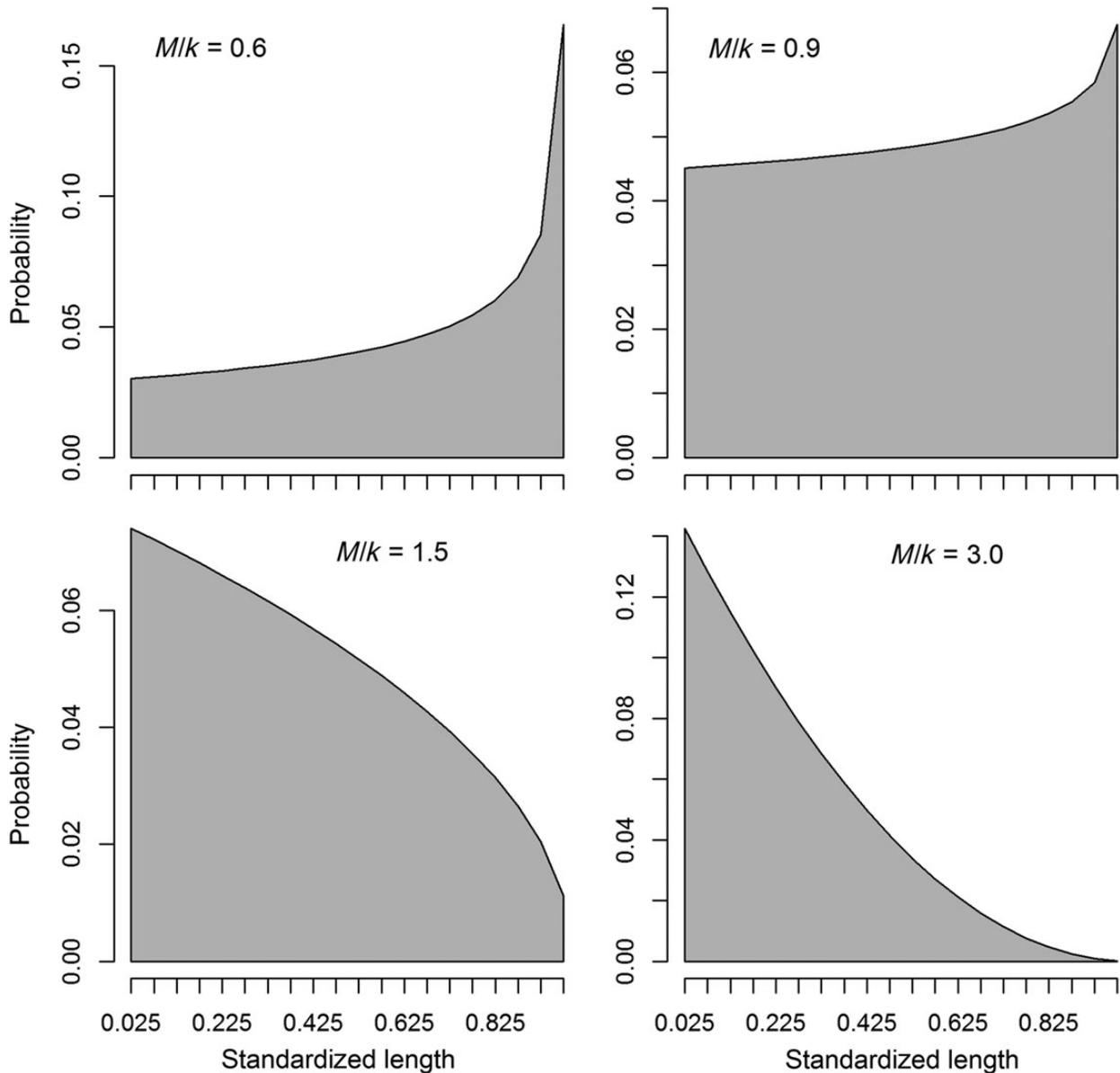

Figure 3. The probability distribution of length for an unfished stock for four values of the ratio M/k: 0.6, 0.9, 1.5 and 3.0. Low M/k means that large fish are most common in the population. As M/k increases the probability of large fish in the population decreases, while the probability of small fish increases.

population dynamics. For example, suppose a species had $t_{max} = 1$ year (e.g. some penaeid prawn species), then, from Equation (4), $M = 4.6$ year^{-1}. It is obvious that such a temporal resolution would be far too coarse to use in an age-structured model, as only two age classes would be represented: $t = 0, 1$. Clearly, an annual time-scale is too coarse and it makes sense to model growth at a higher temporal resolution. To ensure enough age classes, such short-lived species are usually modelled in a finer temporal resolution of months, weeks, or even days. Converting between time-scales is straightforward: $M = 4.6$ year^{-1} can be converted to a monthly rate $M = 4.6/12 = 0.38$ month^{-1}, where $t_{max} = 12$ months, or a weekly rate $M = 4.6/52 = 0.088$ week^{-1}, where $t_{max} = 52$ weeks. The k parameter can be scaled in the same way to ensure that it is in the same units as M. Obviously scaling to different units of time to adequate resolution in age-structured models does not change the underlying biology of the animal, and the expected age and length composition of the species remains unchanged regardless of the units of time used for the modelling. However, the true length composition of a stock is a continuous distribution, and any discretization is an approximation. In general, a finer resolution of the discrete model will result in better approximation, and, especially for short-lived species, the modelled age and length composition is expected to better approximate the "true" composition when modelled with increasingly finer time-scales, i.e. smaller units of time for M. For example, it is clear that the modelled length composition of the short-lived species mentioned above will better represent the "true" length composition when modelled in monthly or weekly units of time, rather than annual time-steps. Long-lived species can also be modelled in different units of time; however, there is a trade-off between increased temporal resolution and computational requirements, and annual units of time are usually sufficient for these species. Additionally, with real data, there is a trade-off between the resolution of the model and the variance of estimates caused by small sample sizes in each size or age class, and the resolution of the model is usually determined by the resolution of the observed data.

Relative biomass at age and length in terms of M/k

Holt (1958) was the first to identify that the M/k ratio determined the relationship between the size and the relative biomass of a cohort, and he used this information to determine the size of first capture that would result in the maximum yield-per-recruit. The relationship between relative age (and size) and the biomass of a cohort can be demonstrated by manipulating the previously derived equations. If the standardized weight at standardized age x is given as:

$$\tilde{W}_x = \tilde{L}_x^b, \tag{14}$$

where the exponent b is usually close to 3 for most species (Hilborn and Walters, 1992), then the relative biomass at standardized age x can be described by:

$$\begin{aligned} B_x &= \tilde{N}_x \tilde{W}_x \\ &= (1 - \tilde{L}_x)^{M/k} \tilde{L}_x^b. \end{aligned} \tag{15}$$

The shape of the relative biomass function is determined by a trade-off in growth and mortality (Figure 4). For example, species with a low M/k obtain maximum length (and weight) at a relatively young age, while the number of individuals in the cohort is still high (Figure 1), and hence biomass peaks at an early age and then rapidly declines as mortality reduces the number of fully grown individuals (Figure 4a). For example, the average female *S. aequipinnis* reaches asymptotic size around age 15, but then lives for another 50 years without further growth (Coulson *et al.*, 2012). As the average individual spends most of its lifetime at or near asymptotic size, most of the biomass is made up of large individuals (Figure 4b). The reverse pattern is observed for species with high M/k, where the continual, though relatively slower, growth means that older, and
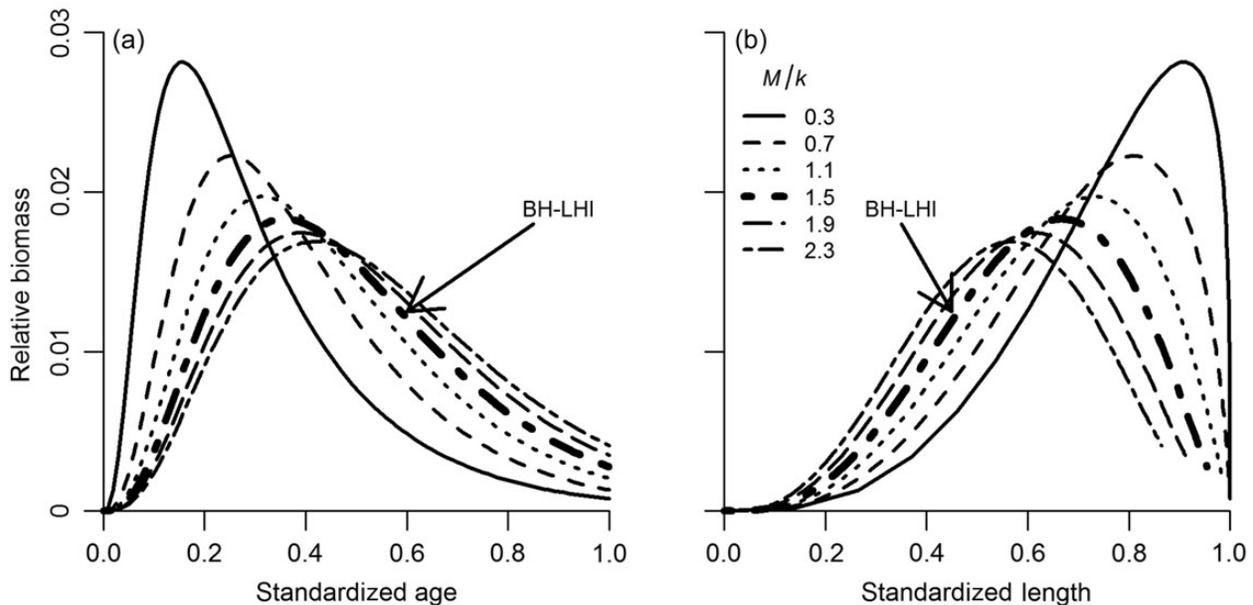

Figure 4. The relative biomass as a function of (a) standardized age and (b) standardized length for a range of M/k (0.3 – 2.3). The area under each curve sums to 1. It is clear that as M/k decreases, the unfished biomass is increasingly made up of a greater proportion of younger and larger individuals. The BH-LHI of $M/k = 1.5$ is shown in bold.

relatively smaller (Figure 1), individuals contribute more to the total unfished biomass (Figure 4a and b). For these species, the combination of relatively slower growth and higher natural mortality reduces the number of large individuals in the population, and smaller individuals contribute more to the total unfished biomass.

The influence of the M/k ratio on the relationship between the relative size and biomass of a cohort is recognized as an important extension of Beverton and Holt's work with the dimensionless numbers (Holt, 1958; Beverton and Holt, 1964; Beverton, 1992). For example, Jennings and Dulvy (2009) show the relationship between the relative weight and biomass of a cohort for three different M/k ratios. However, by standardizing age to t_{max}, this study further demonstrates that the relative age at which a cohort reaches maximum biomass will be the same for different species with the same M/k ratio (Figure 4a). Determining t_{max} is often difficult, and so in practice standardized age may be less useful than standardized length. However, Figure 4 shows that, when examined at the appropriate scale, species with vastly different lifespans (e.g. $M = 0.06$ and $M = 1.2$) but the same M/k ratio have similar life history.

An analytical solution to calculate the standardized length that maximizes the biomass ($\tilde{L}_{opt}$) can be found by differentiating Equation (15) with respect to $\tilde{L}$, and solving for $\tilde{L}$ (see Supplementary Appendix A for derivation):

$$\tilde{L}_{opt} = \frac{b}{(M/k) + b}, \tag{16}$$

and:

$$L_{opt} = L_\infty \frac{b}{(M/k) + b}, \tag{17}$$

which, although derived differently, is identical with Beverton's (1992) equation for L_{opt}. Many theoretical and empirical studies have suggested that evolutionary fitness is maximized if maturation coincides with L_{opt} (Fryer and Iles, 1972; Roff, 1984; Beverton, 1992), which suggests that, assuming knife-edge maturity, length at maturity (L_m) occurs at L_{opt}, and, assuming that egg production is proportional to biomass, a theoretical relationship can be derived between M/k and L_m/L_∞:

$$\frac{L_m}{L_\infty} = \frac{b}{(M/k) + b}, \tag{18}$$

$$\frac{M}{k} = \frac{b}{L_m/L_\infty} - b. \tag{19}$$

The L_m of a stock is often approximated at L_{50}, i.e. the length at which 50% of the individuals are mature, because of the variability in individual growth and maturity rates.

Estimating SPR from M/k, F/M, and L_m/L_∞ with simple assumptions

The SPR is defined as:

$$\text{SPR} = \frac{\text{Total Egg Production}_{\text{Fished}}}{\text{Total Egg Production}_{\text{Unfished}}}, \tag{20}$$

and is commonly used to set limit and target reference points for fisheries (Clark, 2002; Restrepo and Powers, 1999). Typically, the

calculation of SPR requires estimates of the current fishing mortality (F), as well as estimates of natural mortality (M) and fecundity- and selectivity-at-age (Walters and Martell, 2004). The estimation of these parameters is often data intensive and difficult to obtain, especially for data-poor fisheries. However, with several simplifying assumptions, SPR can be calculated from the ratios M/k, F/M, and L_m/L_∞, without knowledge of the individual parameters.

Assuming that maturity is knife-edge at L_m, then the relative length at maturity is $\tilde{L}_m = L_m/L_\infty$ and x_m is the standardized age that corresponds to $\tilde{L}_m$. Let f be the fecundity per unit of body weight for animals above x_m, then:

$$\begin{aligned}
\text{Total Egg Production}_{\text{Unfished}} &= f \sum B_x \\
&= f \sum \tilde{N}_x \tilde{W}_x \\
&= f \sum (1 - \tilde{L}_x)^{M/k} \tilde{L}_x^b \quad \text{for } x_m \leq x \leq 1.
\end{aligned} \tag{21}$$

If all size classes are fully selected by the fishery, then the number of individuals at each standardized age x and length $\tilde{L}_x$ in the fished state can be calculated by simply replacing M/k in Equation (21) with Z/k (where $Z = M + F$) and expressing in terms of M/k and F/M (see Supplementary Appendix A for full derivation), which gives:

$$\begin{aligned}
\text{Total Egg Production}_{\text{Fished}} &= f \sum (1 - \tilde{L}_x)^{(M/k[(F/M)+1])} \tilde{L}_x^b \\
&\text{for } x_m \leq x \leq 1.
\end{aligned}$$

SPR can then be calculated in terms of M/k and F/M as:

$$\text{SPR} = \frac{\sum (1-\tilde{L}_x)^{(M/k[(F/M)+1])} \tilde{L}_x^b}{\sum (1-\tilde{L}_x)^{M/k} \tilde{L}_x^b} \quad \text{for } x_m \leq x \leq 1. \tag{22}$$

This demonstrates that, with the simple assumptions of knife-edge maturation, full selectivity, and no variation of length-at-age, SPR is determined by the ratios M/k, F/M, and L_m/L_∞, and does not depend on the absolute values of the individual parameters. In other words, all species with the same ratios of M/k, F/M, and L_m/L_∞ will have the same SPR, regardless of their absolute values of M and k (Figure 5a).

Estimating SPR from M/k, F/M, and L_m/L_∞ with knife-edge selectivity

Usually, not all length/age classes of a stock are vulnerable to fishing, and only a part of the stock is selected by the fishing gear. The simplest assumption is that selectivity is knife-edge at some standardized length $\tilde{L}_c$, i.e. all fish smaller than $\tilde{L}_c$ are not vulnerable to fishing mortality and only experience natural mortality, while all fish larger than $\tilde{L}_c$ are fully vulnerable to fishing mortality F. Accounting for knife-edge selectivity adds some complexity to the calculation of numbers of individuals alive at age, and hence the calculation of SPR. Simply replacing M/k in Equation (21) with Z/k assumes that the animals have experienced total mortality Z for their entire lives. However, with knife-edge selectivity, this is not the case, and the equation must be modified to account for the
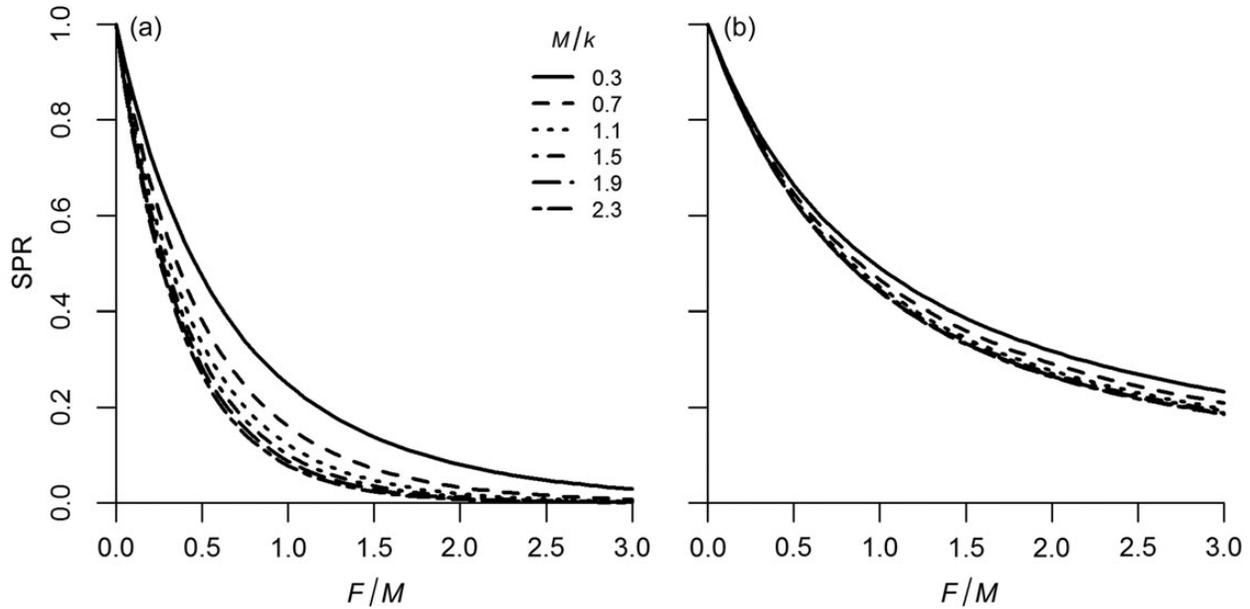
Figure 5. The SPR for a range of F/M ($0-3$) and M/k ($0.3-2.3$). Maturity is assumed to be knife-edge with L_m defined from Equation (18) and selectivity is assumed to be (a) full selectivity (all size classes fully selected) and (b) knife-edge selectivity at L_m (only mature fish are selected).

period when the fish were only experiencing natural mortality:

$$\tilde{N}_x = \begin{cases} (1-\tilde{L}_x)^{M/k} & \text{for } 0 \le x < x_c \\ (1-\tilde{L}_x)^{Z/k}(1-\tilde{L}_c)^{-(F/k)} & \text{for } x_c \le x \le 1 \end{cases}$$

$$= \begin{cases} (1-\tilde{L}_x)^{M/k} & \text{for } 0 \le x < x_c \\ (1-\tilde{L}_x)^{M/k+(M/k)(F/M)}(1-\tilde{L}_c)^{-(M/k)(F/M)} & \text{for } x_c \le x \le 1, \end{cases}$$

$$(23)$$

where x_c is the standardized age that corresponds to $\tilde{L}_c$. It must be emphasized that $\tilde{L}_x$ has the same meaning as defined in Equation (2), i.e. it refers to the expected (standardized) length at age x in the unfished state. In reality, the observed mean length-at-age in the fished state is likely to be less than $\tilde{L}_x$ due to size selective fishing mortality removing the larger individuals from the population. Total egg production in the fished state can then be given as:

Total egg production$_{\text{fished}}$

$$= f \sum_x \begin{cases} (1-\tilde{L}_x)^{M/k} \tilde{L}^3 & \text{for } 0 \le x < x_c, \\ (1-\tilde{L}_x)^{M/k+(M/k)F/M}(1-\tilde{L}_c)^{-(M/k)F/M} \tilde{L}^3 & \text{for } x_c \le x \le 1 \end{cases}$$

$$(24)$$

which can be substituted into Equation (22) to calculate SPR with knife-edge selectivity (Figure 5b). Figure 5 shows the significance of the size at selection in relation to the size at maturity (Walters and Martell, 2004). For example, SPR declines very quickly with increasing F/M when all size classes are selected by the fishery, with SPR = 0.4 occurring between $F/M \approx 0.3$ and 0.6 for the range of M/k shown in Figure 5a. On the other hand, when only mature fish are selected (i.e. $L_c = L_m$) SPR declines at a slower rate, and it takes a much higher F/M to decrease SPR to 0.4 (i.e. $F/M > 1$, Figure 5b). If L_c is considerably larger than L_m, it is possible to

maintain high levels of SPR even with effectively infinite F/M, although yield-per-recruit is likely to also decline with increasing L_c.

Fished length composition in terms of M/k and F/M

Similar to Equation (11), the probability of a fish in the fished state being greater than length $\tilde{l}$ can be determined from Equation (23) (see Supplementary Appendix A):

$$\Pr\{\tilde{L} \ge \tilde{l}\} = \frac{(1-\tilde{l})^{M/k+(F/M)(M/k)}(1-\tilde{L}_c)^{-(M/k)(F/M)}}{(1-\tilde{L}_c)^{M/k}}$$

$$\text{for } \tilde{L}_c \le \tilde{l} \le 1, \quad (25)$$

and so:

$$G(\tilde{l})_{\text{Fished}} = \Pr\{\tilde{L} \le \tilde{l}\}$$

$$= 1 - \left(\frac{(1-\tilde{l})^{M/k+(F/M)(M/k)}(1-\tilde{L}_c)^{-(M/k)(F/M)}}{(1-\tilde{L}_c)^{M/k}}\right) \quad (26)$$

$$\text{for } \tilde{L}_c \le \tilde{l} \le 1.$$

With the simplifying assumptions of knife-edge selectivity at $\tilde{L}_c$, no variation of length-at-age, and given knowledge of M/k from meta-analysis or some other source, the ratio F/M can be estimated from the length composition of the catch, by minimizing the following multinomial negative log-likelihood function (NLL):

$$\text{NLL} = \sum_i O_i \ln \frac{P_i}{O_i^p}, \quad (27)$$

where O_i is the observed number of the catch in length class i, O_i^p the observed proportion of the catch in length class i, and P_i the predicted proportion of individuals in length class i, calculated from Equation (26) (see Supplementary Appendix A).

Equation (26) can also be re-written in terms of Z/k:

$$G(\tilde{l})_{\text{Fished}} = 1 - \left(\frac{1-\tilde{l}}{1-\tilde{L}_c}\right)^{Z/k} \quad \text{for } \tilde{L}_c \leq \tilde{l} \leq 1, \qquad (28)$$

which is equivalent to Wetherall et al.'s (1987) Equation (3). Assuming knife-edge selectivity at $\tilde{L}_c$, and no variation in length-at-age, P_i can be calculated from Equation (28) and Equation (27) can be used to estimate the ratio Z/k from length composition data.

Incorporating variation in length-at-age

The assumption of no variability in length-at-age is not realistic and growth is almost always variable in fish stocks. If the growth of individual fish follows the von Bertalanffy function, variable length-at-age for the stock can arise from variability in the L_∞, k, or t_0 parameters for each individual (Pilling et al., 2002). The L_∞ and k parameters of the von Bertalanffy function are often found to be negatively correlated (Xiao, 1994; Pilling et al., 2002), probably caused by bioenergetic constraints (Jensen, 1997). However, it must be emphasized to distinguish between the correlation of the estimated parameters and the real biological correlation of the population parameters (Pilling et al., 2002). For simplicity, variability in length-at-age is commonly assumed to be due to variability in L_∞ alone, with k and t_0 constant across individuals, although some simulation models do account for the correlation between L_∞ and k of individuals (e.g. Williams and Shertzer, 2005). Furthermore, length-at-age is often assumed to be normally distributed with a constant coefficient of variation (CV), although in reality this is not always the case (Erzini, 1994; Bowker, 1995). Using the simplifying assumption that individual growth is described by the von Bertalanffy equation, and that the sole source of variability in length-at-age is caused by a normally distributed L_∞, then the length-at-age (L_x) can be standardized to the expected L_∞ (i.e. the value typically thought of as the L_∞ of the stock):

$$\tilde{L}_x^{'} = \frac{L_x}{E[L_\infty]}$$
$$= \frac{L_\infty(1 - e^{-kxT_{\max}})}{E[L_\infty]}. \qquad (29)$$

The expected value and the standard deviation of the standardized length-at-age x can then be given as [see Equation (2) and Supplementary Appendix A]:

$$E[\tilde{L}_x^{'}] = 1 - 0.01^{(x(k/M))}. \qquad (30)$$

$$\sigma_{\tilde{L}_x^{'}} = CV_{\tilde{L}_\infty}(1 - 0.01^{(x(k/M))}). \qquad (31)$$

Note that this derivation is true only if L_∞ is the only source of variability in length-at-age, and that k and t_0 are constant across all individuals. While this assumption is common in fisheries science, the implications of variability in the individual k and t_0 parameters for individuals should be investigated with simulation testing.

These derivations can be used to construct an age–length transition matrix to determine the expected length composition of an unfished stock in terms of M/k. For example, if there are X elements in the standardized age vector x, and I length classes, then $\mathbf{P}$ can be an $X \times I$ matrix which defines the probability of fish at age x being in length class i (see Supplementary Appendix A). The expected

number of individuals in each length class i for an unfished stock is then:

$$\tilde{N}_{i_{\text{Unfished}}} = \tilde{N}_{x_{\text{Unfished}}} \mathbf{P}$$
$$= (1 - E[\tilde{L}_x^{'}])^{M/k} \mathbf{P}. \qquad (32)$$

The expected length frequency distribution is demonstrated in Figure 6 for four different values of M/k, which is similar to Figure 3 but with the important addition of variable length-at-age. While the shape of the expected length composition for each M/k is still effectively the same, Figure 6 shows that some individuals may reach sizes greater than L_∞. This is especially the case for species with low M/k (e.g. 0.6) where a large proportion of the unfished population is distributed around L_∞. In contrast, for species with higher M/k (e.g. 3.0), individuals at lengths approaching L_∞ are expected to be rare, even with variable length-at-age.

Modelling the expected length composition of only the vulnerable portion of the population is slightly more complicated, as the selectivity at length needs to be accounted for, and the variability of length-at-age means that although selectivity is assumed to be knife-edge at L_c, it is no longer knife-edge with respect to age. Let $\tilde{L}_c^{'} = L_c/E[L_\infty]$, then this can addressed by modifying the matrix $\mathbf{P}$ to have 0 probability that a fish at standardized age x is $< \tilde{L}_c^{'}$:

$$\mathbf{C}_{x,i} = \begin{cases} 0 & \text{if } \tilde{l}_i < \tilde{L}_c^{'}, \\ \mathbf{P}_{x,i} & \text{if } \tilde{l}_i \geq \tilde{L}_c^{'} \end{cases} \qquad (33)$$

The matrix $\mathbf{C}$ must be standardized so that all probabilities sum to 1:

$$\ddot{\mathbf{C}}_{x,i} = \frac{\mathbf{C}_{x,i}}{\sum_x \mathbf{C}_{x,i}}, \qquad (34)$$

then the expected number of individuals in each length class $\tilde{l}$ for the vulnerable part of a fished stock with knife-edge selectivity at $\tilde{L}_c$ is:

$$\tilde{N}_{i_{\text{Vul}}} = \tilde{N}_{x_{\text{Fished}}} \ddot{\mathbf{C}}$$
$$= \begin{cases} (1 - E[\tilde{L}_x^{'}])^{M/k} \ddot{\mathbf{C}} & \text{if } \tilde{L}_x^{'} < \tilde{L}_c^{'} (12) \\ (1 - E[\tilde{L}_x^{'}])^{M/k+(F/M)(M/k)} (1 - \tilde{L}_c^{'})^{-(M/k)(F/M)} \ddot{\mathbf{C}} & \text{if } \tilde{L}_c^{'} \leq \tilde{L}_x^{'} \leq 1 \end{cases}. \qquad (35)$$

Assuming that the catch is a representative sample of the exploited population, the length structure of the catch is equivalent to that of the vulnerable part of the population (Figure 7). With knowledge of the M/k ratio, L_∞, CV_{L_∞}, and L_c, it is possible to estimate F/M from the observed length structure of the catch, which in turn can be used to calculate SPR and inform management decisions.

Resolving the issue of non-knife-edge selectivity

The simplifying assumption of knife-edge selectivity at $\tilde{L}_c^{'}$ is often violated and more complex selectivity patterns are common. When selectivity is not knife-edge, calculating the number of individuals alive at age x (or at $\tilde{L}_x^{'}$) in terms of M/k and F/M becomes more difficult as Equation (23) must be modified to incorporate the more complex selectivity pattern. Currently, no analytical solution exists which gives $\tilde{N}_{x_{\text{Fished}}}$ in terms of M/k and F/M when selectivity is not knife-edge. However, there is a numerical solution which enables the calculation of $\tilde{N}_{x_{\text{Fished}}}$ (and so the expected fished length
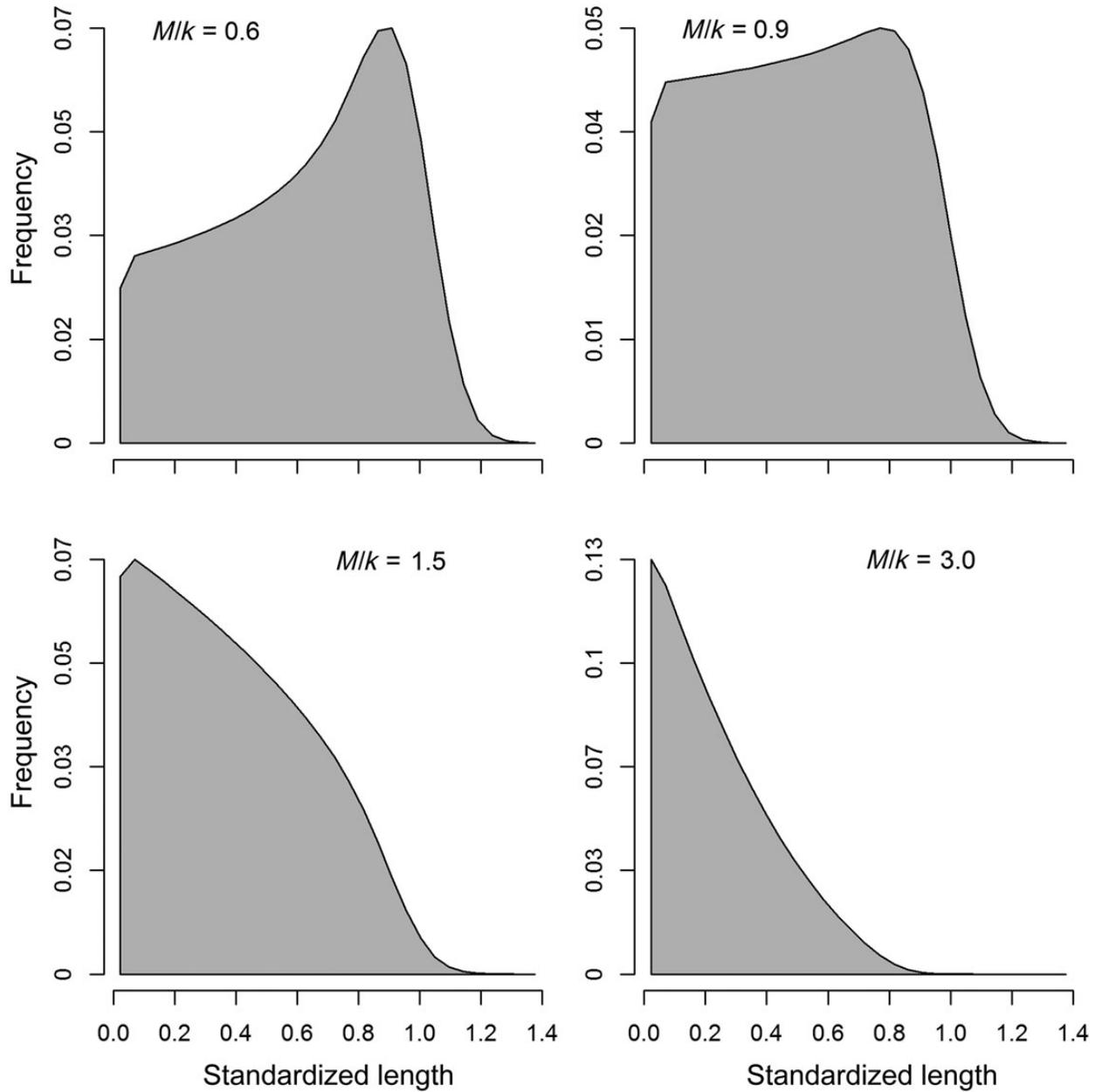
Figure 6. The expected standardized length composition for an unfished stock with variable length-at-age ($CV_{L_\infty} = 0.1$), and M/k values of 0.6, 0.9, 1.5, and 3.0.

composition) while maintaining that the true value of the M and k parameters are not known.

As in the previous sections, the growth curve and length composition of a stock can be modelled with any time-scale, but the discretely modelled length composition better approximates the continuous distribution with increasingly fine temporal resolution. That is, the modelling of the length composition does not depend on the actual units of time, rather it depends on a enough age classes in the age-structured model to construct a smooth length composition. If X is the minimum number of discrete age classes required to approximate a continuous length composition, then the discrete age classes (t) would be a vector of integers of length X, with values from 0 to t_{max}, and $t_{max} = X - 1$. The corresponding M can be calculated

from Equation (4): $M = -ln(0.01)/t_{max} = -ln(0.01)/X - 1$. The unit of time relating to t_{max} (and therefore M) is not known, so let this M be referred to as $\dot{M}$ to identify it as a generic parameter with unknown time-scale.

For example, suppose that a length composition was modelled with 100 discrete age classes, i.e. $X = 100$, then $t_{max} = 99$ and $\dot{M} = 0.0465$. If the true maximum age of a species was 99 years, then $\dot{M} = 0.0465$ year^{-1}. However, if the true maximum age of a species was 99 months, then $\dot{M} = 0.0465$ month^{-1}. Of course, if the true maximum age of the species was something quite different (i.e. not 99 years, months, weeks, or days), then $\dot{M} = 0.0465$ in some arbitrary unknown unit of time. However, the fact that the unit of time is unknown is of little consequence, as the age composition is only
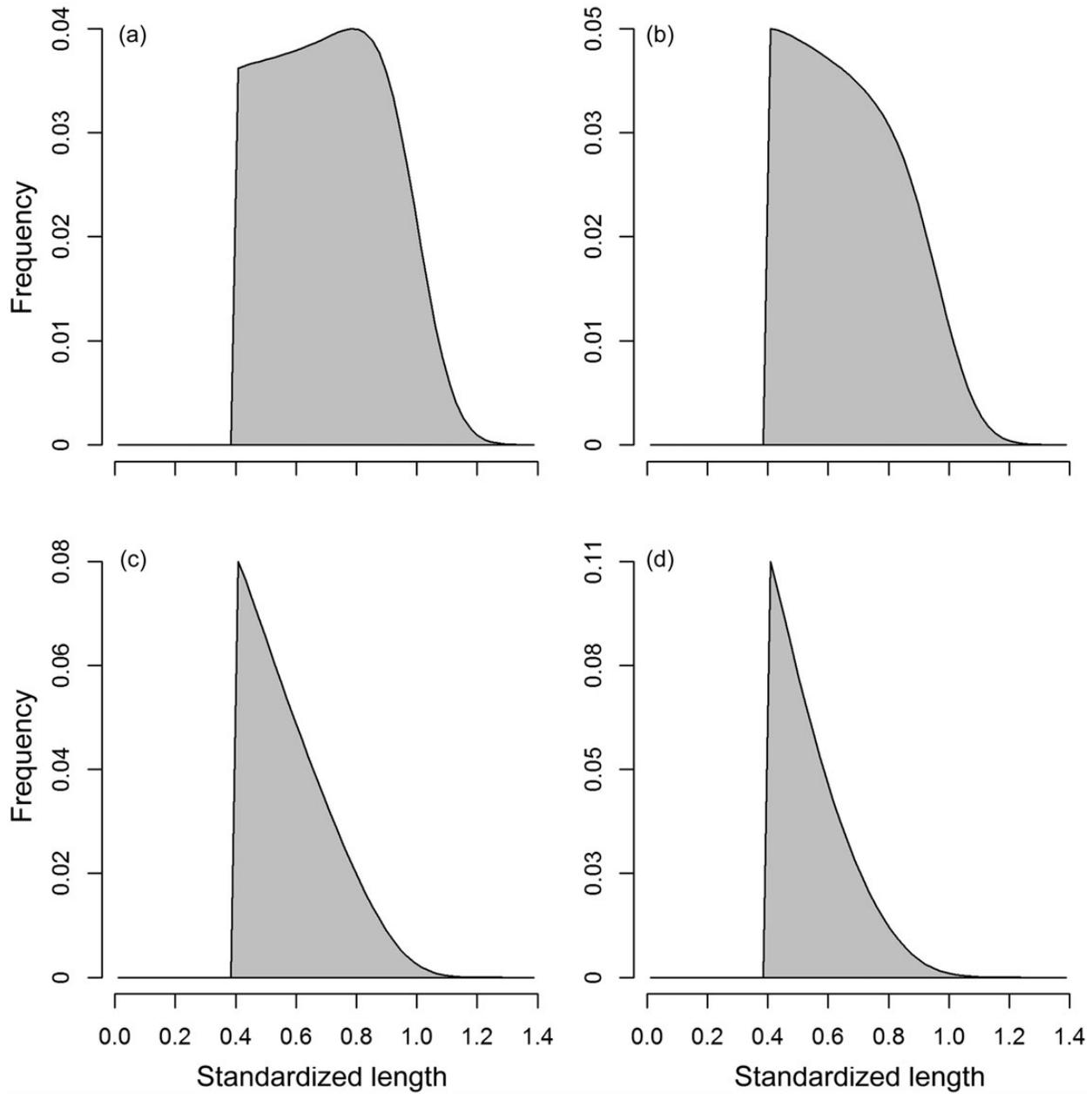
Figure 7. The expected standardized length composition for the catch for a fished stock with knife-edge selectivity at $Lc = 0.40$, and variable length-at-age ($CV_{L_{\infty}} = 0.1$) for (a) $M/k = 0.6$, $F/M = 0.5$; (b) $M/k = 0.6$, $F/M = 1.0$; (c) $M/k = 1.5$, $F/M = 0.5$; and (d) $M/k = 0.6$, $F/M = 1.0$.

being used to construct the length composition, and as demonstrated above, given the same M/k, the shape of the length composition will be equivalent for these species. It must be emphasized that for M/k to be dimensionless both M and k must be in the same units. Continuing the previous example, if $M/k = 1.5$ then $\dot{k}$ would be 0.031 in the same arbitrary unit of time [$\dot{k} = \dot{M}/(M/k)$].

Total mortality at age t is then:

$$\dot{Z}_t = \dot{M} + \dot{F}S_t, \tag{36}$$

where S_t is the selectivity at age t, and the time-scale of t is unknown (i.e. it could be years, months, days, or any other arbitrary scale of time). As previously, $x = t/t_{\max}$, and so x is also a vector of length

X, with values ranging from 0 to 1, and so a vector of total mortality at standardized age x can then be defined as:

$$\dot{Z}_x = \dot{M} + \dot{M}\frac{\dot{F}}{M}\tilde{S}_x$$
$$= \dot{M} + \dot{M}\frac{F}{M}\tilde{S}_x, \tag{37}$$

where $\tilde{S}_x$ is the selectivity at standardized age x. Assuming a logistic selectivity pattern, selectivity-at-length (S_l) can be described by:

$$S_l = \frac{1}{1 + e^{-ln(19)(l - L_{S50})/L_{S95} - L_{S50}}}, \tag{38}$$

where L_{S50} and L_{S95} are the lengths at 50 and 95% selectivity, respectively, and $\ln(19)$ is a constant for this particular parameterization of the logistic function. If $\tilde{L}'_{S50}$ and $\tilde{L}'_{S95}$ are defined as $L_{S50}/E[L_\infty]$ and $L_{S95}/E[L_\infty]$, respectively, then Equation (38) can be used to calculate the selectivity at standardized length ($\tilde{S}_l$). The selectivity at standardized age x ($\tilde{S}_x$) can be calculated from the selectivity at standardized length $\tilde{l}$ by multiplying the vector $\tilde{S}_l$ by the matrix **P**:

$$\tilde{S}_x = \tilde{S}_l \, \mathbf{P}. \tag{39}$$

The relative number of individuals alive at standardized age x can then be calculated using the traditional fisheries model:

$$\tilde{N}_{x_{\text{Fished}}} = \begin{cases} 1 & \text{if } x = 0 \\ \tilde{N}_{x_{\text{Fished}}-1}\, e^{-\dot{Z}_{x-1}} & \text{if } 0 < x \leq X \end{cases}. \tag{40}$$

As previously, the age–length transition matrix of the catch (**C**) can be constructed by modifying the matrix **P** to find the probability that an individual in the catch at standardized age x is in length class i:

$$\mathbf{C}_{x,i} = \mathbf{P}_{x,i}\, \tilde{S}_i, \tag{41}$$

where $\tilde{S}_i$ is the selectivity of length class i. The matrix **C** must be standardized so that all probabilities sum to one [Equation (34)]. The proportion of animals in the catch in length class i is then:

$$\tilde{P}_{i_{\text{Catch}}} = \frac{(\tilde{N}_{x_{\text{Fished}}}\, \tilde{S}_x)\ddot{\mathbf{C}}}{\sum_i [(\tilde{N}_{x_{\text{Fished}}}\, \tilde{S}_x)\ddot{\mathbf{C}}]}. \tag{42}$$

Equation (42) can be used to calculate the expected length composition of the catch for a fished stock in terms of M/k, F/M, $\tilde{L}'_{S50}$, and
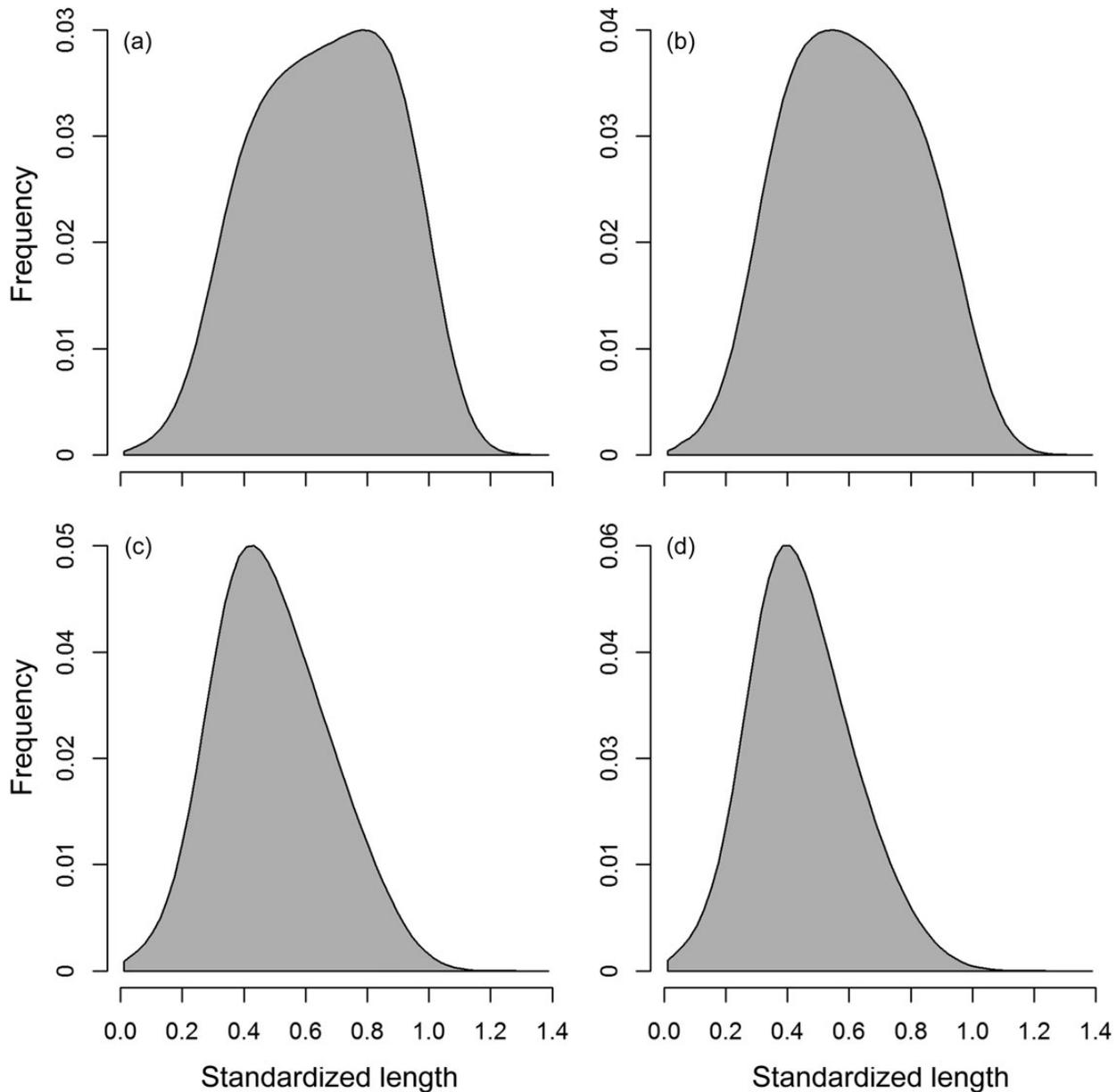

Figure 8. The expected standardized length composition for the catch for a fished stock with logistic selectivity ($\tilde{L}_{S50} = 0.3$, $\tilde{L}_{S95} = 0.5$), and variable length-at-age ($CV_L = 0.1$) for (a) $M/k = 0.6, F/M = 0.5$; (b) $M/k = 0.6, F/M = 1.0$; (c) $M/k = 1.5, F/M = 0.5$; and (d) $M/k = 0.6, F/M = 1.0$.

$\tilde{L}'_{S95}$ (Figure 8). By substituting Equation (42) into Equation (27), the maximum likelihood estimates of F/M, $\tilde{L}'_{S50}$, and $\tilde{L}'_{S95}$ can be obtained from the observed length structure of the catch, and, given an estimate of maturity-at-size, SPR can be calculated.

Although the selectivity-at-length pattern here is assumed to be logistic, other selectivity patterns are common (Sampson and Scott, 2012). For example, fishers may target areas with high catch rates of smaller individuals and the resulting length composition of the catch would underrepresent the proportion of adults in the population. Additionally, the physical characteristics of some fishing gears types, for example, gillnets or hooks, exclude larger individuals, resulting in a dome-shaped selectivity pattern. The assumption of asymptotic selectivity is crucial to apply the methodology presented in this study, and the method is likely to give biased estimates of F/M and SPR if the length data come from a fishery with dome-shaped selectivity. Often a dome-shaped selectivity pattern may be expected. For these situations, it may be possible to generalize Equation (23) to accommodate a knife-edge upper selectivity limit (e.g. a protective slot limit), although this form of selectivity is not common in fisheries. If there was *a priori* reason to expect a dome-shaped selectivity pattern, Equation (38) could be modified with an extra parameter to allow for doming on the right-hand side of the selectivity curve. However, without additional information, it is difficult to estimate the shape of the descending limb of the selectivity curve with only the length composition of the catch. In practice, it is likely that the utility of the methodology presented in this study will be limited to cases where asymptotic selectivity is a reasonable assumption, although the extent of the bias introduced by dome-shaped selectivity patterns is explored in a simulation study by Hordyk *et al.* (this issue).

Conclusion

The individual life history parameters, M, k, L_m, and L_∞, are recognized as prescribing the life history strategy of a species. Biological studies of exploited stocks often report estimates for these parameters, and systems for assessing the ecological risk of fishing commonly use them individually in assessing the risk of being impacted by fishing (Hobday *et al.*, 2011). When these parameters are not known for a stock, typically they are taken from other similar or closely related species and used in stock assessment to provide initial estimates of the status of the stock. Less detail is paid, however, to the ratios of the life history parameters M/k and L_m/L_∞, and how they vary across closely related species. This study has shown, however, that these dimensionless ratios give great insight into the life history strategy of a fish species.

By standardizing to asymptotic size, the models developed in this study allow for growth patterns and life history strategies to be recognized and compared across a range of theoretical values for M/k, based on the comprehensive meta-analysis of 123 species by Prince *et al.* (this issue). While the BH-LHI values of $M/k = 1.5$ and $L_m/L_\infty = 0.66$ are commonly used when data are not available for all parameters, the range of M/k reported in the literature for fish species is much more variable (Pauly, 1980; Beverton, 1992; Prince *et al.*, this issue). By examining a wide range of M/k (0.3–2.3), the results of this study show the important consequences of significant divergence from the BH-LHI, which have important consequences for management. Although the M/k ratio has long been recognized to influence the shape of the unfished length composition, this study has demonstrated that the shape of the von Bertalanffy curve is also determined by the M/k ratio. In addition, this study has shown that there is a direct relationship between the

four ratios, M/k, L_m/L_∞, F/M, L_c/L_∞, and SPR, which has allowed a new form of size-based assessment to be developed.

A number of important assumptions were made that underlie the methodology developed in this paper. Like many length-based methods, this is an equilibrium-based model, and assumes that the observed length composition does not deviate from the expected length structure because of variability in recruitment or mortality. The model also assumes that the fish growth is adequately described by the von Bertalanffy growth equation, with known L_∞, CV_{L_∞}, M/k, and $t_0 = 0$. Additionally, the model assumes that the observed length structure of the catch is representative of the population, i.e. the length composition is not affected by dome-shaped selectivity or a biased sample of the population. The utility of the methodology outlined in this paper as a cost-effective tool for assessing data-poor fisheries is examined in a companion paper (Hordyk *et al.*, this issue), where sensitivity tests are conducted to examine how the model behaves under various scenarios, including parameter misspecification, population disequilibria, and small sample size.

An important challenge for fisheries science is to develop cost-effective approaches for determining the stock status of the world's many data-poor and small-scale stocks (Worm and Branch, 2012). In data-poor situations, reliable estimates of the life history ratios (M/k and L_m/L_∞) may be easier to obtain than estimates of the individual parameters, and the methodology presented in this paper provides a tool for the rapid and cost-effective assessment of exploited fish stocks with only minimal data requirements. Additionally, the cross-species comparison of the life history ratios holds great potential for developing a rigorous framework for borrowing biological information from well-studied species for applying to poorly studied stocks as described in Prince *et al.* (this issue).

Supplementary material

Supplementary material is available at the *ICESJMS* online version of the manuscript.

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