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

4 Adrian Hordyk ^{*1}, Kotaro Ono², Keith Sainsbury³, Neil Loneragan¹ and Jeremy
5 Prince^{1,4}

6 ¹Centre for Fish, Fisheries and Aquatic Ecosystems Research, Murdoch University, 90
7 South Street, Murdoch, Western Australia, 6150

8 ²School of Aquatic and Fisheries Science, University of Washington, USA

9 ³University of Tasmania, Tasmania, Australia

10 ⁴Biospherics, P/L South Fremantle, Western Australia

11 **Abstract**

12 The estimation of the status of data-poor fish stocks is often severely limited by incomplete
13 knowledge of the basic life history parameters: the natural mortality rate (M), the von Bertalanffy
14 growth parameters (L_∞ and k), and the length at maturity (L_m). A common approach to estimate
15 these individual parameters has been to use the Beverton-Holt life history invariants (BH-LHI),
16 the ratios $\frac{M}{k}$ and $\frac{L_m}{L_\infty}$, especially for estimating M . In this study, we assumed no knowledge of the
17 individual parameters, and explored how the information on life history strategy contained in these
18 ratios can be applied to assessing data-poor stocks, with $\frac{M}{k}$ values ranging from 0.3 to 2.3, spanning
19 the BH-LHI value of 1.5. We developed simple analytical models to develop a relationship between
20 $\frac{M}{k}$ and the von Bertalanffy growth curve, and demonstrate the link between the life history ratios
21 and yield- and spawning-per-recruit. We further developed the previously recognised relationship

*Corresponding author; Ph: +61893606685 E: a.hordyk@murdoch.edu.au

22 between $\frac{M}{k}$ and yield- and spawning-per-recruit (Beverton and Holt, 1964) by using information on
23 $\frac{L_m}{L_\infty}$, knife-edge selectivity $\left(\frac{L_c}{L_\infty}\right)$ and the ratio of fishing to natural mortality $\left(\frac{F}{M}\right)$, to demonstrate
24 the link between an exploited stock's expected length composition, and its spawning potential ratio
25 (SPR); an internationally recognised measurement of stock status. Variation in length-at-age,
26 and logistic selectivity patterns were incorporated in the model to demonstrate how SPR can be
27 calculated from the observed size composition of the catch; an advance which has great potential
28 as a cost-effective method for assessing data-poor stocks. The application of the analytical models
29 developed in this study as a cost-effective stock assessment method is examined in a companion
30 paper that investigates deviations in the assumptions of equilibrium and imperfect knowledge of
31 the life history parameters (Hordyk *et al.*, this issue).

32 **Keywords.** life history, dimensionless numbers, Beverton-Holt invariants, fish growth, mortality

33 Introduction

34 Studies of the life history information on the growth, mortality and maturity schedules of fish stocks
35 form the basis of fisheries science, and such information is essential for the effective management of
36 exploited populations (Beverton and Holt, 1957; Hilborn and Walters, 2001). However, this information
37 is only available for about 1,200 of the 7,000 or so exploited fish species, and it is not always available
38 for all regions where the species are fished (Froese and Binohlan, 2000). Patterns of variation between
39 life history parameters, particularly between natural mortality (M), and the von Bertalanffy growth
40 rate and asymptotic size (k and L_∞), have long been observed for many fish populations, and a large
41 amount of work has been done to document and understand these relationships, often with the aim
42 of providing cost-effective “short-cuts” to estimate the parameters, such as natural mortality, that are
43 difficult or expensive to obtain (Beverton and Holt, 1959; Beverton, 1992; Charnov, 1993; Pauly, 1980;
44 Roff, 1984). Typically, these studies have explored the relationships between single variables, such as
45 M or k , and these are the variables that are used in stock assessments.

46 The $\frac{M}{k}$ ratio is one the life history ratios that is known to be relatively consistent between closely
47 related stocks (Beverton, 1992). The results of bio-energetic modelling by Jensen (1996) suggest that
48 an optimal value for $\frac{M}{k}$ is 1.5. Assuming von Bertalanffy growth, the relationship between the biomass
49 and mean length of a cohort can be derived from the $\frac{M}{k}$ ratio (Beverton, 1992; Jensen, 1996). Using
50 this relationship, life history theory predicts that length at maturity (L_m) will be found at the length

51 of maximum biomass in the population. This theoretical relationship provides the basis for the second
52 life history ratio $\frac{L_m}{L_\infty}$, with an optimal value of 0.66 (Jensen, 1996). Supported by other empirical
53 work (Charnov, 1993; Pauly, 1980), these value for the ratios of $\frac{M}{k}$ and $\frac{L_m}{L_\infty}$ have become known as the
54 Beverton-Holt life history invariants (BH-LHI), and are often used as proxies for estimates of $\frac{M}{k}$ and $\frac{L_m}{L_\infty}$
55 in data-poor stocks. For example, it is not uncommon for studies to estimate the notoriously difficult
56 parameter M by simply using the Beverton-Holt invariant $M = 1.5k$ (e.g., see many papers citing
57 Jensen, 1996), or by estimating the fishing mortality rate F when the total mortality ($Z = F + M$)
58 and k are known, by assuming that $\frac{M}{k} = 1.5$ (Beddington and Kirkwood, 2005).

59 Extending their earlier seminal work (Beverton and Holt, 1957), Beverton and Holt (1964) were
60 the first to show that yield and biomass equations could be restated using the dimensionless ratios $\frac{M}{k}$
61 and $\frac{L_m}{L_\infty}$. Since then, others have built on their work to incorporate the dimensionless numbers into
62 fisheries science (Beddington and Kirkwood, 2005; Jensen, 1996; Mangel, 1996; Williams and Shertzer,
63 2003). However, it has often been assumed that these ratios are invariant, and the variability of the
64 ratios of $\frac{M}{k}$ and $\frac{L_m}{L_\infty}$ in fish stocks has not been explored comprehensively. For example, a recent
65 study has found that the $\frac{M}{k}$ for *Scorpius aequipinnis* (Kyphosidae) is 0.33 (Coulson *et al.*, 2012), much
66 lower than the BH-LHI of 1.5, and reminiscent of a life history more commonly associated with marine
67 mammals (Prince *et al.*, this issue). Furthermore, a meta-analysis of 123 marine species of teleosts,
68 chondrichthyes, invertebrates and marine mammals, to investigate patterns in life history parameters
69 and the ratios of $\frac{M}{k}$ and $\frac{L_m}{L_\infty}$, found that $\frac{M}{k}$ ranged from 0.12-3.52, indicating that the life history
70 ratios are not as “invariant”, as previously thought (Prince *et al.*, this issue).

71 This paper develops simple analytical models to explore the influence of changing the ratios of
72 $\frac{M}{k}$, $\frac{F}{M}$ and $\frac{L_m}{L_\infty}$ on the von Bertalanffy growth curve, the length composition of the stock, and as a
73 consequence the yield and spawning-per-recruit, under the assumption of equilibrium. It uses the data
74 collated in the meta-analysis of Prince *et al.* (this issue) to provide the basis for the range of values
75 investigated in this study. The models are extended to include more complex assumptions about growth
76 and selectivity, and investigate the relationship between the three ratios and the spawning potential
77 ratio (SPR). By developing the link between the life history ratios, the expected equilibrium size
78 composition, and SPR, this study provides the potential to develop a cost-effective technique to assess
79 data-poor fisheries using length frequency data; an idea that is further developed in an accompanying
80 paper (Hordyk *et al.*, this issue).

81 Analytical Models

82 Redefining the von Bertalanffy equation in terms of $\frac{M}{k}$

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

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

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

$$\begin{aligned} \tilde{L}_t &= \frac{L_t}{L_\infty} \\ &= 1 - e^{-kt} \end{aligned} \quad (2)$$

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

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

92 Naturally, the accuracy of this rule-of-thumb is dependent on the appropriate value for the proportion
93 P , and this has typically been assumed to be 1% or 5% (Hewitt and Hoenig, 2005). The choice
94 of $P=5\%$ is somewhat arbitrary, and appears to over-estimate M for a large range of species, with
95 empirical work suggesting that $P=1.5\%$ is more appropriate (Hoenig, 1983; Hewitt and Hoenig, 2005).
96 For simplicity, this study assumes that $P = 1\%$, and so t_{\max} can be calculated from M as:

$$t_{\max} = \frac{-\ln 0.01}{M} \quad (4)$$

97 If age is standardised to t_{\max} then x can be defined as $\frac{t}{t_{\max}}$. From Equation 2, $\tilde{L}_t = 1 - e^{-kt}$ with

98 $t = xt_{\max} = -\frac{x \ln 0.01}{M}$, then:

$$\begin{aligned}\tilde{L}_x &= 1 - e\left(-k \frac{-x \ln 0.01}{M}\right) \\ &= 1 - 0.01\left(x \frac{k}{M}\right)\end{aligned}\tag{5}$$

99 This demonstrates that the shape of the standardised von Bertalanffy growth curve is solely determined
 100 by the ratio $\frac{M}{k}$, and does not depend on the absolute value of either the k or M parameters (Figure
 101 1). As $\frac{M}{k}$ increases, the biological significance of L_∞ becomes increasingly vague (Figure 1). For a
 102 species that conforms to the Beverton–Holt invariant $\frac{M}{k} = 1.5$, the maximum size (L_{\max} ; i.e., the
 103 length at t_{\max}) is approximately $0.95L_\infty$. However, a species with $\frac{M}{k} = 2.3$ would only be expected
 104 to reach about $0.8L_\infty$ at t_{\max} (bottom curve on Figure 1). In contrast, a species with $\frac{M}{k} = 0.3$, like *S.*
 105 *aequipinnis*, would reach asymptotic size relatively quickly and then continuing to live for a relatively
 106 long time without any further growth (top curve on Figure 1).

107 **Number of animals at age in terms of $\frac{M}{k}$**

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

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

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

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

112 where \tilde{N}_t is number per recruit. The number of animals alive at standardised age x can be expressed
 113 in terms of $\frac{M}{k}$ by re-arranging Equation 5 to find x at \tilde{L}_x ,

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

114 Substituting xt_{\max} for t in Equation 7 gives:

$$\tilde{N}_x = e^{-Mxt_{\max}} \quad (9)$$

115 Substituting $M = -\frac{\ln 0.01}{t_{\max}}$ from Equation 4 and $x = \frac{M}{k} \frac{\ln(1-\tilde{L}_x)}{\ln(0.01)}$ from Equation 8 gives:

$$\begin{aligned} \tilde{N}_x &= e\left(-\frac{\ln(0.01)}{t_{\max}} \frac{M}{k} \frac{\ln(1-\tilde{L}_x)}{\ln(0.01)} t_{\max}\right) \\ &= e^{\left(\ln(1-\tilde{L}_x) \frac{M}{k}\right)} \\ &= \left(1 - \tilde{L}_x\right)^{\frac{M}{k}} \end{aligned} \quad (10)$$

116 This equation (Equation 10) has been used to simulate the number of individuals alive at each length
117 for a range of $\frac{M}{k}$ (Figure 2), which shows that the probability of a fish in the unfished state surviving
118 to greater than length \tilde{l} is determined by $\frac{M}{k}$:

$$\Pr\{\tilde{L} \geq \tilde{l}\} = \left(1 - \tilde{l}\right)^{\frac{M}{k}} \quad (11)$$

119 which implies that the cumulative probability distribution is:

$$\begin{aligned} G(\tilde{l}) &= \Pr\{\tilde{L} \leq \tilde{l}\} \\ &= 1 - \left(1 - \tilde{l}\right)^{\frac{M}{k}} \end{aligned} \quad (12)$$

120 It follows from Equation 12 that, in the unfished state, the probability that an individual is in
121 length class i can be calculated from:

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

122 where I is the number of length classes, and \tilde{l}_i° is the lower bound of length class i (Figure 3).

123 Changing the scale of M and k

124 By convention that the rate parameters M and k are typically given as instantaneous annual rates, e.g.
125 $M = 0.2 \text{ year}^{-1}$ or $k = 0.15 \text{ year}^{-1}$. When used in typical population models, these rates assume im-
126 plicitly that mortality and growth occurs once a year. Usually, this assumption is of little consequence
127 in modelling the dynamics of fish populations. However, for short-lived species the temporal resolution
128 of annual parameters is too coarse to effectively model population dynamics. For example, suppose a
129 species had $t_{\max} = 1$ year (e.g. some penaeid prawn species), then, from Equation 4, $M = 4.6 \text{ year}^{-1}$.
130 It is obvious that such a temporal resolution would be far too coarse to use in an age-structured model,
131 as only 2 age classes would be represented: $t = 0, 1$. Clearly, such a temporal scale is too coarse, and
132 it makes sense to model growth at a high temporal resolution. To ensure a sufficient number of age
133 classes, such short-lived species are usually modelled in a finer temporal resolution of months, weeks
134 or even days. Converting between time scales is straightforward: $M = 4.6 \text{ year}^{-1}$ can be converted to
135 a monthly rate $M = \frac{4.6}{12} = 0.38 \text{ month}^{-1}$ where $t_{\max} = 12$ months, or a weekly rate $M = \frac{4.6}{52} = 0.088$
136 week^{-1} where $t_{\max} = 52$ weeks. The k parameter can be scaled the same way to ensure it is in the
137 same units as M . Obviously scaling to different units of time for the purpose of adequate resolution
138 in age structured models does not change the underlying biology of the animal, and the expected
139 age and length composition of the species remains unchanged regardless of the units of time used for
140 the modelling. However, especially for short-lived species, the modelled age and length composition
141 is expected to converge to the “true” composition when modelled with increasingly finer time scales,
142 i.e., smaller units of time for M . For example, it is clear that the modelled length composition of the
143 short-lived species mentioned above will more closely represent the “true” length composition when
144 modelled in monthly or weekly units of time, rather than annual time-steps. Long-lived species can
145 also be modelled in different units of time, however there is a trade-off between increased temporal
146 resolution and computational requirements, and annual units of time are usually sufficient for these
147 species.

148 **Relative biomass at age and length in terms of $\frac{M}{k}$**

149 The relationship between fish length and weight (W) is often well described by:

$$W_t = aL_t^b \quad (14)$$

150 where a is a scaling coefficient which varies between species and the exponent b is usually close to 3
 151 for most species (Hilborn and Walters, 2001). Standardised weight is then given as:

$$\begin{aligned} \tilde{W}_t &= \frac{W_t}{W_\infty} \\ &= \frac{aL_t^b}{aL_\infty^b} \\ &= \tilde{L}_t^b \end{aligned} \quad (15)$$

152 and weight at standardised age x is:

$$\tilde{W}_x = \tilde{L}_x^b \quad (16)$$

153 The relative biomass at standardised age x can be described by:

$$\begin{aligned} B_x &= \tilde{N}_x \tilde{W}_x \\ &= \left(1 - \tilde{L}_x\right)^{\frac{M}{k}} \tilde{L}_x^b \end{aligned} \quad (17)$$

154 The shape of the relative biomass function is determined by a trade-off in growth and mortality (Figure
 155 4). For example, species with a low $\frac{M}{k}$ obtain maximum length (and weight) early in life (Figure 1),
 156 and hence biomass peaks at an early age and then rapidly declines as mortality reduces the number of
 157 fully grown individuals (Figure 4a). For these same species, the majority of the biomass is comprised
 158 of large individuals (Figure 4b). The reverse pattern is observed for species with high $\frac{M}{k}$, where
 159 the continual, albeit relatively slower, growth means that older, and relatively smaller (Figure 1),
 160 individuals contribute more to the total unfished biomass (Figure 4a & b).

An analytical solution to calculate the standardised length at which biomass is at a maximum

(\tilde{L}_{opt}) can be found by differentiating Equation 17 with respect to \tilde{L} and setting equal to zero:

$$\begin{aligned} \frac{dB}{dL} &= 0 \\ (1 - \tilde{L})^{\frac{M}{k}} \frac{d}{d\tilde{L}} \tilde{L}^b + \tilde{L}^b \frac{d}{dL} (1 - \tilde{L})^{\frac{M}{k}} &= 0 \\ (1 - \tilde{L})^{\frac{M}{k}} b \tilde{L}^{b-1} - \tilde{L}^b \frac{M}{k} (1 - \tilde{L})^{\frac{M}{k}-1} &= 0 \\ [\tilde{L}^{b-1}] \left[b - L \left(b + \frac{M}{k} \right) \right] \left[(1 - \tilde{L})^{\frac{M}{k}-1} \right] &= 0 \end{aligned} \quad (18)$$

161 which solved for \tilde{L} gives two solutions: 0 and $\frac{b}{\frac{M}{k}+b}$ when b & $\frac{M}{k} > 0$. Calculating the second derivative
 162 confirms that $\frac{b}{\frac{M}{k}+b}$ is the maximum of the function, so:

$$\tilde{L}_{\text{opt}} = \frac{b}{\frac{M}{k} + b} \quad (19)$$

163 and:

$$L_{\text{opt}} = L_{\infty} \frac{b}{\frac{M}{k} + b} \quad (20)$$

164 which, although derived differently, is identical to Beverton's (1992) equation for L_{opt} . Numerous the-
 165 oretical and empirical studies have demonstrated that evolutionary fitness is maximised if maturation
 166 coincides with L_{opt} (Fryer and Iles, 1972; Roff, 1984; Beverton, 1992), which suggests that, assuming
 167 knife-edge maturity, length at maturity (L_m) occurs at L_{opt} , and, assuming that egg production is
 168 proportional to biomass, provides a theoretical relationship between $\frac{M}{k}$ and $\frac{L_m}{L_{\infty}}$:

$$\frac{L_m}{L_{\infty}} = \frac{b}{\frac{M}{k} + b} \quad (21)$$

$$\frac{M}{k} = \frac{b}{\frac{L_m}{L_{\infty}} - b} \quad (22)$$

169 Given the variability in growth and maturity rates that is often observed between individuals in a
 170 stock, L_m is often approximated as L_{50} , i.e., the length at which 50% of the individuals are mature.

171 **Estimating SPR from $\frac{M}{k}$, $\frac{F}{M}$ & $\frac{L_m}{L_{\infty}}$ with simple assumptions**

172 The spawning potential ratio (SPR) is defined as:

$$\text{SPR} = \frac{\text{Total Egg Production}_{\text{Fished}}}{\text{Total Egg Production}_{\text{Unfished}}} \quad (23)$$

173 Assuming that maturity is knife-edge at L_m :

$$\tilde{L}_m = \frac{L_m}{L_\infty} \quad (24)$$

174 and x_m is the standardised age that corresponds to \tilde{L}_m . Let f be fecundity per unit of body weight
175 for animals above x_m , then:

$$\begin{aligned} \text{Total Egg Production}_{\text{Unfished}} &= f \sum B_x \\ &= f \sum \tilde{N}_x \tilde{W}_x \\ &= f \sum \left(1 - \tilde{L}_x\right)^{\frac{M}{k}} \tilde{L}_x^b \quad \text{for } x_m \leq x \leq 1 \end{aligned} \quad (25)$$

176 If all size classes are fully selected by the fishery, then the number of individuals at each standardised
177 age x and length \tilde{L}_x in the fished state can be calculated by simply replacing $\frac{M}{k}$ in Equation 25 with
178 $\frac{Z}{k}$, which gives:

$$\begin{aligned} \text{Total Egg Production}_{\text{Fished}} &= f \sum B_x^{\text{Fished}} \\ &= f \sum \tilde{N}_x^{\text{Fished}} \tilde{W}_x \\ &= f \sum \left(1 - \tilde{L}_x\right)^{\frac{Z}{k}} \tilde{W}_x \\ &= f \sum \left(1 - \tilde{L}_x\right)^{\frac{F+M}{k}} \tilde{L}_x^b \\ &= f \sum \left(1 - \tilde{L}_x\right)^{\left(\frac{M}{k} \left[\frac{F}{M} + 1\right]\right)} \tilde{L}_x^b \quad \text{for } x_m \leq x \leq 1 \end{aligned} \quad (26)$$

179 SPR can then be calculated in terms of $\frac{M}{k}$ and $\frac{F}{M}$ as:

$$\text{SPR} = \frac{\sum \left(1 - \tilde{L}_x\right)^{\left(\frac{M}{k} \left[\frac{F}{M} + 1\right]\right)} \tilde{L}_x^b}{\sum \left(1 - \tilde{L}_x\right)^{\frac{M}{k}} \tilde{L}_x^b} \quad \text{for } x_m \leq x \leq 1 \quad (27)$$

180 This demonstrates that, with the simple assumptions of knife-edge maturation, full selectivity, and no
 181 variation of length-at-age, SPR is determined by the ratios $\frac{M}{k}$, $\frac{F}{M}$ and $\frac{L_m}{L_\infty}$, and does not depend on
 182 the absolute values of the individual parameters. In other words, all species with the same ratios of
 183 $\frac{M}{k}$, $\frac{F}{M}$ and $\frac{L_m}{L_\infty}$ will have the same SPR, regardless of their absolute values of M and k (Figure 5a).

184 **Estimating SPR from $\frac{M}{k}$, $\frac{F}{M}$ & $\frac{L_m}{L_\infty}$ 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 standardised 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 $\frac{M}{k}$ in Equation 25 with $\frac{Z}{k}$ 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 period of time when the fish were only experiencing natural mortality:

$$\begin{aligned} \tilde{N}_x &= \begin{cases} \left(1 - \tilde{L}_x\right)^{\frac{M}{k}} & \text{for } 0 \leq x < x_c \\ \left(1 - \tilde{L}_x\right)^{\frac{Z}{k}} \left(1 - \tilde{L}_c\right)^{-\frac{F}{k}} & \text{for } x_c \leq x \leq 1 \end{cases} \\ &= \begin{cases} \left(1 - \tilde{L}_x\right)^{\frac{M}{k}} & \text{for } 0 \leq x < x_c \\ \left(1 - \tilde{L}_x\right)^{\frac{M}{k} + \frac{M}{k} \frac{F}{M}} \left(1 - \tilde{L}_c\right)^{-\frac{M}{k} \frac{F}{M}} & \text{for } x_c \leq x \leq 1 \end{cases} \end{aligned} \quad (28)$$

185 where x_c is the standardised age that corresponds to \tilde{L}_c . Total egg production in the fished state can
 186 then be given as:

$$\text{Total Egg Production}_{\text{Fished}} = f \sum_x \begin{cases} \left(1 - \tilde{L}_x\right)^{\frac{M}{k}} \tilde{L}^3 & \text{for } 0 \leq x < x_c \\ \left(1 - \tilde{L}_x\right)^{\frac{M}{k} + \frac{M}{k} \frac{F}{M}} \left(1 - \tilde{L}_c\right)^{-\frac{M}{k} \frac{F}{M}} \tilde{L}^3 & \text{for } x_c \leq x \leq 1 \end{cases} \quad (29)$$

187 which can be substituted into Equation 27 to calculate SPR with knife-edge selectivity (Figure 5b).

188 **Fished length composition in terms of $\frac{M}{k}$ & $\frac{F}{M}$**

Similarly to Equation 11, the probability of a fish in the fished state being greater than length \tilde{L} is given by Equation 28:

$$\begin{aligned}
 \Pr\{\tilde{L} \geq \tilde{l}\} &= \frac{N_x}{N_c} \\
 &= \frac{(1 - \tilde{l})^{\frac{M}{k} + \frac{F}{M} \frac{M}{k}} (1 - \tilde{L}_c)^{-\frac{M}{k} \frac{F}{M}}}{(1 - \tilde{L}_c)^{\frac{M}{k} + \frac{F}{M} \frac{M}{k}} (1 - \tilde{L}_c)^{-\frac{M}{k} \frac{F}{M}}} \\
 &= \frac{(1 - \tilde{l})^{\frac{M}{k} + \frac{F}{M} \frac{M}{k}} (1 - \tilde{L}_c)^{-\frac{M}{k} \frac{F}{M}}}{(1 - \tilde{L}_c)^{\frac{M}{k}}} \quad \text{for } \tilde{L}_c \leq \tilde{l} \leq 1
 \end{aligned} \tag{30}$$

189 and so:

$$\begin{aligned}
 G(\tilde{l})_{\text{Fished}} &= \Pr\{\tilde{L} \leq \tilde{l}\} \\
 &= 1 - \left(\frac{(1 - \tilde{l})^{\frac{M}{k} + \frac{F}{M} \frac{M}{k}} (1 - \tilde{L}_c)^{-\frac{M}{k} \frac{F}{M}}}{(1 - \tilde{L}_c)^{\frac{M}{k}}} \right) \quad \text{for } \tilde{L}_c \leq \tilde{l} \leq 1
 \end{aligned} \tag{31}$$

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

$$\text{NLL} = \sum_i O_i \ln \frac{P_i}{O_i^P} \tag{32}$$

194 where O_i is the observed number of the catch in length class i , O_i^P is the observed proportion of the
 195 catch in length class i , and P_i is the predicted proportion of individuals in length class i , calculated

196 from Equation 31:

$$P_{i_{\text{Fished}}} = \begin{cases} 1 - \left(\frac{(1-\tilde{l}_{i+1}^o)^{\frac{M}{k} + \frac{F}{M} \frac{M}{k}} (1-\tilde{L}_c)^{-\frac{M}{k} \frac{F}{M}}}{(1-\tilde{L}_c)^{\frac{M}{k}}} \right) & \text{if } i = 1 \\ \left(\frac{(1-\tilde{l}_i^o)^{\frac{M}{k} + \frac{F}{M} \frac{M}{k}} (1-\tilde{L}_c)^{-\frac{M}{k} \frac{F}{M}}}{(1-\tilde{L}_c)^{\frac{M}{k}}} \right) - \left(\frac{(1-\tilde{l}_{i+1}^o)^{\frac{M}{k} + \frac{F}{M} \frac{M}{k}} (1-\tilde{L}_c)^{-\frac{M}{k} \frac{F}{M}}}{(1-\tilde{L}_c)^{\frac{M}{k}}} \right) & \text{if } 1 < i < I \\ \left(\frac{(1-\tilde{l}_i^o)^{\frac{M}{k} + \frac{F}{M} \frac{M}{k}} (1-\tilde{L}_c)^{-\frac{M}{k} \frac{F}{M}}}{(1-\tilde{L}_c)^{\frac{M}{k}}} \right) & \text{if } i = I \end{cases} \quad (33)$$

197 Equation 31 can also be re-written in terms of $\frac{Z}{k}$:

$$\begin{aligned} G(\tilde{l})_{\text{Fished}} &= 1 - \left(\frac{(1-\tilde{l})^{\frac{M}{k} + \frac{F}{M} \frac{M}{k}} (1-\tilde{L}_c)^{-\frac{M}{k} \frac{F}{M}}}{(1-\tilde{L}_c)^{\frac{M}{k}}} \right) \\ &= 1 - (1-\tilde{l})^{\frac{Z}{k}} (1-\tilde{L}_c)^{-\frac{Z}{k}} \\ &= 1 - \left(\frac{1-\tilde{l}}{1-\tilde{L}_c} \right)^{\frac{Z}{k}} \quad \text{for } \tilde{L}_c \leq \tilde{l} \leq 1 \end{aligned} \quad (34)$$

198 which is equivalent to Wetherall et al.'s (1987) Equation 3:

$$G(l)_{\text{Fished}} = 1 - \left(\frac{L_\infty - l}{L_\infty - L_c} \right)^{\frac{Z}{k}} \quad \text{for } L_c \leq l \leq L_\infty \quad (35)$$

199 Assuming knife-edge selectivity at \tilde{L}_c , and no variation in length-at-age, Equation 34 can be substituted
 200 into Equation 33 to give the probability of an individual in the catch being in one of the I length classes,
 201 which can then be used to estimate the ratio $\frac{Z}{k}$ from Equation 32.

202 Incorporating variation in length-at-age

203 The assumption of no variability in length-at-age is not realistic and growth is almost always variable in
 204 fish stocks. If the growth of individual fish follows the von Bertalanffy function, variable length-at-age
 205 for the stock can arise from variability in the L_∞ , k or t_0 parameters for each individual. Variability
 206 in length-at-age is commonly assumed to be due to variability in L_∞ alone, with k and t_0 constant
 207 across individuals, and is often modelled by assuming that length-at-age is normally distributed with
 208 a constant coefficient of variability (CV), although in reality this is not always the case (Erzini, 1994;

209 Bowker, 1995). Using the simplifying assumption that individual growth is described by the von
 210 Bertalanffy equation, and that the sole source of variability in length-at-age is caused by a normally
 211 distributed L_∞ , then the length-at-age (L_x) can be standardised to the expected L_∞ (i.e., the value
 212 typically thought of as the L_∞ of the stock):

$$\begin{aligned}\tilde{L}'_x &= \frac{L_x}{\mathbb{E}[L_\infty]} \\ &= \frac{L_\infty (1 - e^{-kxT_{\max}})}{\mathbb{E}[L_\infty]}\end{aligned}\tag{36}$$

213 The expected standardised length-at-age x is then:

$$\begin{aligned}\mathbb{E}[\tilde{L}'_x] &= \frac{\mathbb{E}[L_\infty] (1 - e^{-kxT_{\max}})}{\mathbb{E}[L_\infty]} \\ &= 1 - e^{-kxT_{\max}} \\ &= 1 - 0.01^{(x \frac{k}{M})}\end{aligned}\tag{37}$$

214 and the variance of length-at-age x is:

$$\sigma_{\tilde{L}'_x}^2 = \frac{\sigma_{L_\infty}^2 \mathbb{E}[\tilde{L}'_x]^2}{\mathbb{E}[L_\infty]^2}\tag{38}$$

215 from which the standard deviation is:

$$\begin{aligned}\sigma_{\tilde{L}'_x} &= \text{CV}_{\tilde{L}'_x} \left(\mathbb{E}[\tilde{L}'_x] \right) \\ &= \text{CV}_{\tilde{L}'_x} \left(1 - 0.01^{(x \frac{k}{M})} \right)\end{aligned}\tag{39}$$

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

220 The probability distribution of length at standardised age x is then:

$$p(\tilde{l}) = \frac{1}{\sigma_{\tilde{L}'_x} \sqrt{2\pi}} e^{-\frac{(\tilde{l} - \text{E}[\tilde{L}'_x])^2}{2\sigma_{\tilde{L}'_x}^2}} \quad (40)$$

221 If there are I length classes and \tilde{l}_i is the mid-point of length class i , then the probability of a fish at
 222 standardised age x being in length class i can be given by:

$$P_{i,x} = \begin{cases} \phi\left(\frac{\tilde{l}_{i+1}^{\circ} - \text{E}[\tilde{L}'_x]}{\sigma_{\tilde{L}'_x}}\right) & \text{if } i = 1 \\ \phi\left(\frac{\tilde{l}_{i+1}^{\circ} - \text{E}[\tilde{L}'_x]}{\sigma_{\tilde{L}'_x}}\right) - \phi\left(\frac{\tilde{l}_i^{\circ} - \text{E}[\tilde{L}'_x]}{\sigma_{\tilde{L}'_x}}\right) & \text{if } 1 < i < I \\ 1 - \phi\left(\frac{\tilde{l}_i^{\circ} - \text{E}[\tilde{L}'_x]}{\sigma_{\tilde{L}'_x}}\right) & \text{if } i = I \end{cases} \quad (41)$$

223 where ϕ is the standard normal cumulative density function. Equation 41 can be used to construct the
 224 expected length composition of an unfished stock, by constructing a age-length transition matrix. For
 225 example, if there are X elements in the standardised age vector x , and I length classes, then \mathbf{P} can
 226 be a $I \times X$ matrix which defines the probability of fish at age x being in length class i . The expected
 227 number of individuals in each length class i for an unfished stock is then:

$$\begin{aligned} \tilde{N}_{i_{\text{Unfished}}} &= \tilde{N}_{x_{\text{Unfished}}} \mathbf{P}^T \\ &= \left(1 - \text{E}[\tilde{L}'_x]\right)^{\frac{M}{k}} \mathbf{P}^T \end{aligned} \quad (42)$$

228 This is demonstrated in Figure 6 for four different values of $\frac{M}{k}$.

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

$$\mathbf{C}_{i,x} = \begin{cases} 0 & \text{if } \tilde{l}_i < \tilde{L}'_c \\ \mathbf{P}_{i,x} & \text{if } \tilde{l}_i \geq \tilde{L}'_c \end{cases} \quad (43)$$

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

$$\begin{aligned} \tilde{N}_{i_{\text{Vul}}} &= \tilde{N}_{x_{\text{Fished}}} \mathbf{C}^T \\ &= \begin{cases} (1 - \mathbb{E}[\tilde{L}'_x])^{\frac{M}{k}} \mathbf{C}^T & \text{if } \tilde{L}'_x < \tilde{L}'_c \\ (1 - \mathbb{E}[\tilde{L}'_x])^{\frac{M}{k} + \frac{F}{M} \frac{M}{k}} (1 - \tilde{L}'_c)^{-\frac{M}{k} \frac{F}{M}} \mathbf{C}^T & \text{if } \tilde{L}'_c \leq \tilde{L}'_x \leq 1 \end{cases} \end{aligned} \quad (44)$$

236 Assuming that the catch is a representative sample of the exploited population, the length structure
 237 of the catch is equivalent to the length structure of the vulnerable part of the population (Figure 7).

238 Resolving the issue of non knife-edge selectivity

239 The simplifying assumption of knife-edge selectivity at \tilde{L}'_c is often violated and more complex selectivity
 240 patterns are common. When selectivity is not knife-edge, calculating the number of individuals alive
 241 at age x (or at \tilde{L}'_x) in terms of $\frac{M}{k}$ and $\frac{F}{M}$ becomes more difficult as Equation 28 must be modified
 242 to incorporate the more complex selectivity pattern. Currently, no analytical solution exists which
 243 gives $\tilde{N}_{x_{\text{Fished}}}$ in terms of $\frac{M}{k}$ and $\frac{F}{M}$ when selectivity is not knife-edge. However, there is a numerical
 244 solution which enables the calculation of $\tilde{N}_{x_{\text{Fished}}}$ (and so the expected fished length composition) while
 245 maintaining that the true value of the M and k parameters are not known.

246 As in the previous sections, the growth curve and length composition of a stock can be modelled
 247 with any time-scale, but the modelled length composition converges to the “true” composition with
 248 increasingly fine temporal resolution. That is, the modelling of the length composition does not depend
 249 on the actual units of time, rather it depends on a sufficient number of age classes in the age-structured
 250 model to construct a smooth length composition. If X is the minimum number of discrete age classes
 251 required to model a sufficiently smooth length composition, then the discrete age classes (t) would be
 252 a vector of integers of length X , with values from 0 to t_{max} , and $t_{\text{max}} = X - 1$. The corresponding M
 253 can be calculated from Equation 4: $M = \frac{-\ln(0.01)}{t_{\text{max}}} = \frac{-\ln(0.01)}{X-1}$. The unit of time relating to t_{max} (and
 254 therefore M) is not known, so let this M be referred to as $\overset{\text{gen}}{M}$ to identify it as a generic parameter
 255 with unknown time scale.

256 For example, suppose that the minimum number of age classes needed to adequately construct a
 257 representative length composition was 100, i.e., $X = 100$, then $t_{\text{max}} = 99$ and $\overset{\text{gen}}{M} = 0.0465$. If the true

258 maximum age of a species was 99 years, then $\overset{\text{gen}}{M} = 0.0465 \text{ year}^{-1}$. However, if the true maximum age
 259 of a species was 99 months, then $\overset{\text{gen}}{M} = 0.0465 \text{ month}^{-1}$. Of course, if the true maximum age of the
 260 species was something quite different (i.e., not 99 years, months, weeks or days), then $\overset{\text{gen}}{M} = 0.0465$
 261 in some arbitrary unknown unit of time. However, the fact that unit of time is unknown is of little
 262 consequence, as the age composition is only being used to construct the length composition, and as
 263 demonstrated above, given the same $\frac{M}{k}$, the shape of the length composition will be equivalent for
 264 these species.

265 Total mortality at age t is then:

$$\overset{\text{gen}}{Z}_t = \overset{\text{gen}}{M} + \overset{\text{gen}}{F} \overset{\text{gen}}{S}_t \quad (45)$$

where S_t is 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, $x = \frac{t}{t_{\text{max}}}$, 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 standardised age x can then be defined as:

$$\begin{aligned} \overset{\text{gen}}{Z}_x &= \overset{\text{gen}}{M} + \overset{\text{gen}}{M} \frac{\overset{\text{gen}}{F}}{\overset{\text{gen}}{M}} \tilde{S}_x \\ &= \overset{\text{gen}}{M} + \overset{\text{gen}}{M} \frac{\overset{\text{gen}}{F}}{M} \tilde{S}_x \end{aligned} \quad (46)$$

266 where \tilde{S}_x is selectivity at standardised age x .

267 Assuming a logistic selectivity pattern, selectivity-at-length (S_l) can be described by:

$$S_l = \frac{1}{1 + e^{\frac{-\ln(19)(l - L_{S50})}{L_{S95} - L_{S50}}}} \quad (47)$$

268 where L_{S50} and L_{S95} are the lengths at 50% and 95% selectivity respectively. If \tilde{L}'_{S50} and \tilde{L}'_{S95} are
 269 defined as $\frac{L_{S50}}{E[L_{\infty}]}$ and $\frac{L_{S95}}{E[L_{\infty}]}$ respectively then:

$$\tilde{S}_l = \frac{1}{1 + e^{\frac{-\ln(19)(\tilde{l} - \tilde{L}'_{S50})}{\tilde{L}'_{S95} - \tilde{L}'_{S50}}}} \quad (48)$$

270 Selectivity at standardised age x (\tilde{S}_x) can be calculated from selectivity at standardised length \tilde{l} by

271 multiplying the vector \tilde{S}_l by the matrix \mathbf{P} :

$$\tilde{S}_x = \tilde{S}_l \mathbf{P} \quad (49)$$

272 The relative number of individuals alive at standardised age x can then be calculated using the tradi-
273 tional fisheries model:

$$\tilde{N}_{x_{\text{Fished}}} = \begin{cases} 1 & \text{if } x = 0 \\ \tilde{N}_{x_{\text{Fished}}-1} e^{-Z_{x-1}^{\text{gen}}} & \text{if } 0 < x \leq X \end{cases} \quad (50)$$

274 The length composition of the catch (i.e or the vulnerable part of the stock) can be constructed by
275 modifying the matrix \mathbf{P} to find the probability that an individual in the catch at standardised age x
276 is in length class i :

$$\mathbf{C}_{i,x} = \mathbf{P}_{i,x} \tilde{S}_i \quad (51)$$

277 where \tilde{S}_i is the selectivity of length class i . The matrix \mathbf{C} must be standardised so that all probabilities
278 sum to 1:

$$\mathbf{C}_{i,x}^{\text{norm}} = \frac{\mathbf{C}_{i,x}}{\sum_x \mathbf{C}_{i,x}} \quad (52)$$

279 The proportion of animals in the catch in length class i is then:

$$\tilde{P}_{i_{\text{Catch}}} = \frac{\left(\tilde{N}_{x_{\text{Fished}}} \tilde{S}_x \right) \mathbf{C}^{\text{norm}T}}{\sum_i \left[\left(\tilde{N}_{x_{\text{Fished}}} \tilde{S}_x \right) \mathbf{C}^{\text{norm}T} \right]} \quad (53)$$

280 Equation 53 can be used to calculate the expected length composition of the catch for a fished stock in
281 terms of $\frac{M}{k}$, $\frac{F}{M}$, \tilde{L}'_{S50} and \tilde{L}'_{S95} (Figure 8). By substituting Equation 53 into Equation 32 the maximum
282 likelihood estimates of $\frac{F}{M}$, \tilde{L}'_{S50} and \tilde{L}'_{S95} can be obtained from the observed length structure of the
283 catch, and, given an estimate of maturity-at-size, SPR can be calculated.

284 Although the selectivity-at-length pattern here is assumed to be logistic, other selectivity patterns
285 do exist. For example, dome-shaped selectivity is known to occur for a number of gear types. However,
286 with only length data of the catch it is difficult to detect the presence of dome-shaped selectivity.

287 Conclusion

288 The individual life history parameters, M , k , L_m and L_∞ , are recognised as prescribing a species' life
289 history strategy. Biological studies of exploited stocks often report estimates for these parameters, and
290 systems for assessing the ecological risk of fishing commonly use them individually in assessing the risk
291 of being impacted by fishing (Hobday *et al.*, 2011). When these parameters are not known for a stock,
292 typically they are taken from other similar or closely related species for initial estimates to be used in
293 stock assessment. Less detail is paid, however, to the ratios of the life history parameters $\frac{M}{k}$ and $\frac{L_m}{L_\infty}$,
294 and how they vary across closely related species. This is unfortunate, as this study has shown that
295 the dimensionless ratios give great insight into the life history strategy of a fish species.

296 By standardising to asymptotic size, the models developed in this study allow for growth patterns
297 and life history strategies to be recognised and compared across a range of theoretical values for $\frac{M}{k}$,
298 based on the comprehensive meta-analysis of 123 species by Prince *et al.* (this issue). While the BH-LHI
299 values of $\frac{M}{k} = 1.5$ and $\frac{L_m}{L_\infty} = 0.66$ are commonly used, the range of $\frac{M}{k}$ reported in the literature for fish
300 species is much more variable (Prince *et al.*, this issue). By examining a wide range $\frac{M}{k}$ (0.3 – 2.3) the
301 results of this study emphasise the important consequences of deviations from the BH-LHI. Although
302 the $\frac{M}{k}$ ratio has long been recognised to influence the shape of the unfished length composition, this
303 study has demonstrated that the shape of the von Bertalanffy curve is also determined by the $\frac{M}{k}$
304 ratio. In addition, this study has shown that there is a direct relationship between the four ratios,
305 $\frac{M}{k}$, $\frac{L_m}{L_\infty}$, $\frac{F}{M}$, $\frac{L_c}{L_\infty}$, and SPR, which allows the development of a new form of size based assessment.
306 This idea is developed further in a companion paper (Hordyk *et al.*, this issue), where numerous
307 sensitivity tests are conducted to examine how the model behaves under various scenarios, including
308 parameter misspecification, population disequilibria, and small sample size. Furthermore, the cross-
309 species comparison of the life history ratios holds great potential for developing a rigorous framework
310 for borrowing biological information from well-studied species for applying to poorly studied stocks as
311 described in Prince *et al.* (this issue).

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371 Figure Captions

Figure 1: The standardised von Bertalanffy growth curves for fish at standardised length $\left(\frac{L_t}{L_\infty}\right)$ and standardised age $\left(\frac{t}{t_{\max}}\right)$ from Equation 5 for $\frac{M}{k}$ ranging from 0.3 to 2.3. The Beverton-Holt life history invariant (BH-LHI) of $\frac{M}{k} = 1.5$ is shown in bold.

Figure 2: The probability of a fish in the unfished state surviving to standardised length from Equation 10 for a range of $\frac{M}{k}$ (0.3–2.3). The Beverton-Holt life history invariant (BH-LHI) of $\frac{M}{k} = 1.5$ is shown in bold.

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

Figure 4: The relative biomass as a function of a) standardised age and, b) standardised length for a range of $\frac{M}{k}$ (0.3–2.3). The area under each curve sums to 1. It is clear that as $\frac{M}{k}$ decreases, the unfished biomass is increasingly comprised of a greater proportion of younger and larger individuals. The Beverton-Holt life history invariant (BH-LHI) of $\frac{M}{k} = 1.5$ is shown in bold.

Figure 5: The spawning potential ratio (SPR) for a range of $\frac{F}{M}$ (0–3) and $\frac{M}{k}$ (0.3–2.3). Maturity is assumed to be knife-edge with L_m defined from Equation 21 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).

Figure 6: The expected standardised length composition for an unfished stock with variable length-at-age ($CV_{L_\infty} = 0.1$), and $\frac{M}{k}$ values of 0.6, 0.9, 1.5 & 3.0.

Figure 7: The expected standardised length composition for the catch for a fished stock with knife-edge selectivity at $L_c = 0.40$, and variable length-at-age ($CV_{L_\infty} = 0.1$) for a) $\frac{M}{k} = 0.6$, $\frac{F}{M} = 0.5$; b) $\frac{M}{k} = 0.6$, $\frac{F}{M} = 1.0$; c) $\frac{M}{k} = 1.5$, $\frac{F}{M} = 0.5$; and d) $\frac{M}{k} = 0.6$, $\frac{F}{M} = 1.0$.

Figure 8: The expected standardised 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) $\frac{M}{k} = 0.6$, $\frac{F}{M} = 0.5$; b) $\frac{M}{k} = 0.6$, $\frac{F}{M} = 1.0$; c) $\frac{M}{k} = 1.5$, $\frac{F}{M} = 0.5$; and d) $\frac{M}{k} = 0.6$, $\frac{F}{M} = 1.0$.