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Revisiting the concept of Beverton-Holt Life History Invariants with the aim of informing data-poor fisheries assessment.

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Manuscripts

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8 **1 Revisiting the concept of Beverton-Holt Life History Invariants with the aim of**
9 **2 informing data-poor fisheries assessment.**
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20 **Abstract**

21 The complexity and cost of existing fishery assessment techniques prohibits their
22 application to 90% of fisheries globally. Simple, cost-effective, generic
23 approaches are needed for small-scale and data-poor fisheries that support the
24 majority of the world's fishing communities but cannot currently be assessed
25 quantitatively. This meta-analysis of the relationship between spawning potential
26 and the normalized size and age of 123 marine species suggests that the so-called
27 Beverton-Holt Life History Invariants (BH-LHI; L_m/L_∞ , M/k , $M \times Age_m$) actually
28 vary together in relation to life history strategy, determining the relationship
29 between size, age and reproductive potential for each species. Although little
30 realized, the common assumption of unique values for the BH-LHI also implies
31 that all species share the same relationship between size, age and reproductive
32 potential. This implicit assumption of is not supported by this meta-analysis,
33 which instead suggests there is considerable but predictable natural variation in
34 the BH-LHI ratios and the relationships between size, age and reproductive
35 potential that they determine. We believe this reconceptualization of the BH-LHI
36 has potential to provide a theoretical framework for 'borrowing' knowledge from
37 well-studied species to apply to related, unstudied species and populations, and
38 when applied together with the assessment technique described by Hordyk *et al.*
39 (this issue b), could make simple forms of size based assessment possible for
40 many data-poor fish stocks that are currently considered unassessable.

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8 **42 Keywords**

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10 **43** Beverton-Holt Life History Invariant, Data-poor assessment, parameter estimation

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15 **45 Introduction**

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17 **46** A persistent challenge for sustainable fisheries is the scale, complexity and cost of fishery
18 **47** assessment (Walters and Pearse, 1996; Hilborn *et al.*, 2005; Beddington and Kirkwood,
19 **48** 2005; Mullon *et al.*, 2005). Current assessment techniques require technical expertise,
20 **49** detailed biological knowledge and time-series data on catch, effort and/or surveyed
21 **50** abundance (Walters and Martell, 2004) resulting in an annual cost of \$US50,000 to
22 **51** millions of dollars per stock (Pauly, 2013). This represents a substantial impediment to
23 **52** assessing small-scale, spatially complex and developing-world fisheries (Mahon, 1997).
24 **53** By some estimates, 90% of the world's fisheries, which directly support 14 - 40 million
25 **54** fishers and indirectly support approximately 200 million people, are un-assessable using
26 **55** current methods (Andrew *et al.*, 2007).

27
28 **56** Considerable uncertainty surrounds the status of unassessed stocks (Costello *et al.*, 2012;
29 **57** Hilborn and Branch, 2012; Pauly, 2013) so that overfishing may go unrecognized until
30 **58** stocks collapse. Even where fishing communities want to change fishing practices, the
31 **59** technical difficulty and expense of current assessment techniques can prevent science-
32 **60** based harvest strategies from being developed and implemented for these fisheries. A
33 **61** new methodology is needed for small-scale and data-poor fisheries (Andrew *et al.*, 2007;
34 **62** Pauly, 2013) along with theoretical frameworks for informing the assessment of
35 **63** unstudied species with biological knowledge about related species (Punt *et al.* 2011).

64

65 The correlation between biological parameters across species has been widely used to
66 provide generic parameter estimates necessary for assessment modeling (Charnov, 1993)
67 and were first described in fisheries by Beverton and Holt (1959) for the clupeid and
68 engraulid (herring and anchovy-like bony fishes) stocks of the North Sea (Beverton,
69 1963). They observed correlations between: 1) the instantaneous natural mortality rate
70 (M) and the von Bertalanffy (1938) growth rate constant (k), 2) length at maturity (L_m)
71 and asymptotic length (L_∞), and 3) M and the age of maturity (T_m). Beverton and Holt's
72 primary interest was in estimating M , a parameter that is notoriously difficult to measure,
73 from studies of k , L_m and T_m , which by comparison, are easily estimated. Although
74 neither Beverton, nor Holt used the term, these three life history ratios (M/k , L_m/L_∞ and M
75 \times Age_m) are now commonly referred to as the Beverton-Holt Life History Invariants (BH-
76 LHI). Widely considered to be environmentally influenced constants (Pauly, 1980) the
77 BH-LHI have been used extensively to parameterize fisheries models (Charnov, 2003;
78 Beddington and Kirkwood, 2005; Gislason *et al.*, 2010). In this study we use Jensen's
79 (1996) definition of the three BH-LHI: $M/k = 1.5$, $L_m/L_\infty = 0.66$ and $M \times T_m = 1.65$.

80 The Spawning Potential Ratio, or Spawning Per Recruit (SPR), is a commonly used index
81 of the relative rate of reproduction (Mace and Sissenwine, 1993; Walters and Martell,
82 2004) in an exploited stock. Brooks *et al.* (2010) recommend its utility for applying to
83 stocks in data limited fisheries. The SPR is defined as the proportion of the unfished
84 reproductive potential left by any given level of fishing pressure. It can be conceptualized
85 as the total reproductive potential of all the cohorts in a population at equilibrium, or the

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8 86 life-time reproductive potential of an average individual passing through a population at
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10 87 equilibrium. By definition, unfished stocks and individuals in an unfished stock, have an
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12 88 *SPR* of 100% ($SPR_{100\%}$) and fishing mortality reduces $SPR_{100\%}$ from the unfished level to
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14 89 $SPR_{X\%}$. Shepherd (1982) used the *SPR* concept to integrate the separate approaches to
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16 90 fisheries modeling that had developed on opposite sides of the North Atlantic during the
17
18 91 1970s. Generic *SPR*-based reference points have been developed theoretically and
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20 92 through the meta-analysis of quantitatively assessed fisheries, and have been recognized
21
22 93 in international fisheries law (Restrepo and Powers, 1999; Australian Government, 2007),
23
24 94 for example $\sim SPR_{40\%}$ is generally considered a conservative proxy for maximum
25
26 95 sustainable yield (Mace and Sissenwine, 1993; Clark, 2002; Walters and Martell, 2004).
27
28 96 Until recently, estimating *SPR* has required unique population models to be
29
30 97 parameterised for each stock using estimates of natural mortality, growth, reproduction,
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32 98 and time series of abundance, or age composition data (e.g. Ault *et al.*, 1998; Walters and
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34 99 Martell 2004).

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36 100 This study and the accompanying studies of Hordyk *et al.* (this issue a&b) arose from our
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38 101 interest in developing a simple method for using size composition data to evaluate the
39
40 102 *SPR* of exploited populations (Prince *et al.* 2008; 2011). Prince *et al.* (2008) observed
41
42 103 that the spatial variability of size of maturity in *Haliotid* populations could be gauged
43
44 104 from the shape and appearance of their shells, and that qualitative evaluations of a
45
46 105 population's spawning potential can be made on the basis of size composition relative to
47
48 106 the visually evaluated size of maturity. This current collection of studies was prompted
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50 107 by a journal editor asking, how the finding of Prince *et al.* (2008) applied to other
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52 108 species? And our research began by addressing the question do all species exhibit the

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9 109 same relationship between size of maturity, relative size composition and *SPR*? To this
10 110 end we began with the empirical and descriptive study described here, of how *SPR* relates
11 111 to size of maturity, relative body size and age in 123 species of teleosts, chondrichthyans,
12 112 invertebrates and marine mammals. The results presented here suggested to us that there
13 113 are predictable patterns in life history ratios M/k and L_m/L_∞ which are related to each
14 114 species' life history strategy, unfished size compositions, and the distribution of
15 115 spawning potential by size. Exploring these results more rigorously Hordyk *et al.* (this
16 116 issue a) demonstrates that it is the life history ratios of M/k and L_m/L_∞ together with F/M
17 117 that determine the shape of size compositions and the *SPR* of populations, rather than the
18 118 individual parameter values as generally assumed. On this basis Hordyk *et al.* (this issue
19 119 b) developed and tested a new approach to size-based assessment, which we believe may
20 120 have great application to data-poor assessment. Returning to the empirical observations
21 121 made in this study, we postulate that extending our meta-analysis of well studied species
22 122 could make it possible to predict characteristic life history ratios of most exploited
23 123 populations based on general knowledge about each species life history strategy, and so
24 124 make simple size based assessments possible for many stocks currently considered too
25 125 data-poor to assess.

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43 127 **Materials and methods**

44 128 Selection of Parameter Sets

45 129 For our meta-analysis we collected studies of marine and estuarine species for which we
46 130 could find robust estimates of growth, natural mortality, age/size of maturity or fecundity

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9 131 | at age/size, and length-weight relationships. In order to control the quality of the
10 132 | parameter sets we applied strict selection criteria. Rather than developing our own criteria
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12 133 | *de novo* we based our criteria on the six criteria developed by Gislason *et al.* (2010),
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14 134 | which they define as: “

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17 135 | 1. Estimates were rejected if they had been derived from empirical relationships
18 136 | (e.g. Beverton and Holt, 1959; Pauly, 1980) or ‘borrowed’ from studies of similar
19 137 | species.
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22 138 | 2. Estimates by size or age were rejected if they had been derived from multi-species
23 139 | modeling.
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26 140 | 3. Parameters were rejected if they were based on an insufficient amount of data, if
27 141 | the authors expressed concern that they could be biased or uncertain, or if the
28 142 | sampling gears and/or procedures for working up the samples were likely to have
29 143 | biased the estimates.
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32 144 | 4. Estimates of total mortality based on catch-at-length, or catch-at-age were
33 145 | accepted as estimates of M , only if the data had been collected from an
34 146 | unexploited or lightly exploited stock over a sufficiently long time period to
35 147 | ensure that they reflected mortality and not simply differences in year class
36 148 | strength, and if growth parameters or ageing methods were considered
37 149 | appropriate.
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40 150 | 5. Estimates derived from tagging data were included only if the following factors
41 151 | had been considered: mortality associated with the tagging operation, tag loss,
42 152 | differences in mortality experienced by tagged and untagged fish, migration out of
43 153 | the study area and uncertainty regarding tag recovery.

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9 154 6. Estimates derived from regressions of total mortality and effort were included,
10 155 only if it was credible that total fishing mortality would be proportional to the
11 156 measure of fishing effort considered, and if extrapolation did not result in
12 157 excessively large confidence intervals.”

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16 158 While Gislason *et al.*'s focus was solely on ensuring the quality of natural mortality
17 159 estimates, we found that where other aspects of biology had been studied, these criteria
18 160 also ensured the quality of estimates for the broader list of parameters of interest to this
19 161 study (i.e. growth, age/size of maturity or fecundity at age/size, and length-weight
20 162 relationships).

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26 163 To ensure that each species' parameter set described a single population and a similar
27 164 population density we also applied a seventh criterion, which we defined as:

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31 165 7. All parameter estimates for a species should be from the same geographic
32 166 population, and from the same time period.

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35 167 Species were only included if they met all seven criteria and all the necessary parameters
36 168 could be estimated, this limited the number of studies available to our meta-analysis. We
37 169 were able to gather data for a total of 123 species, including representatives from teleosts,
38 170 invertebrates, chondrichthyans, and marine mammals. A complete list of species,
39 171 parameter values and source references are provided in supporting on-line material.

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45 172 It should be noted that these criteria biased our selection process towards well-studied
46 173 populations prior to, or during the early phase of exploitation. Thus almost all the studies
47 174 included in our database are of lightly exploited populations. We do not believe our
48 175 sample is representative of all, or even groups of, marine species. For this reason we have

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8 176 not attempted to apply statistical techniques of analysis, as we have no expectation that
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10 177 our samples are distributed normally or are representative of any mean condition,
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12 178 parameter value or relationships. As discussed below we do not believe such statistical
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14 179 concepts are applicable to a study such as this. In this study our aim was entirely
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16 180 qualitative; to look for, and to describe patterns of variation that exist in nature. For the
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18 181 quantitative analysis of the patterns we observed, the reader is directed to the
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20 182 accompanying theoretical study of Hordyk *et al.* (this issue a)

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26 184 Spawning Potential Ratio (SPR) Model for Meta-analysis

27 185 We modeled the *SPR* achieved at any given age for the 123 species to examine patterns in
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29 186 the relationships between age, length, weight and reproductive output. The *SPR* is usually
30
31 187 calculated by summing the total reproductive output of all age classes and dividing by the
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33 188 number of recruits in order to obtain a general measure of current rate of reproductive
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35 189 output in relation to the maximum potential reproductive output, i.e. the unfished level.
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37 190 However, here we are interested in calculating the cumulative percentage of total lifetime
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39 191 reproductive output achieved when an individual reaches each age/size, and how that
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41 192 varies across the widest possible range of marine species. For this purpose we developed
42
43 193 an age-based equilibrium *SPR* model for each species with an initial cohort size of 1,000.

44 194 The number of survivors, average individual length and weight, and percentage of the
45
46 195 total index of reproductive output (expressed variously for the differing species as eggs,
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48 196 pups, calves or simply mature biomass) achieved for both individuals and cohorts at each
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50 197 successive time step was calculated. To enable comparisons across species with varying

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8 198 | life spans, sizes and forms of reproductive output, all were normalized with respect to
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10 199 | their maximum value. The maximum age class (t_{max}) was determined to be the first age
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12 200 | class with an abundance of $\leq 1\%$ of the initial cohort size (i.e. ≤ 10 individuals), and
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14 201 | maximum length (L_{max}), weight (W_{max}) and reproductive output (EP_{max}) was defined as
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16 202 | the value estimated for that age class. This is consistent with the results of empirical
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18 203 | studies of Hewitt and Hoenig (2005) who note that a range of 1-5% has generally been
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20 204 | used for the purpose of estimating M , and who conclude that 1.5% is most appropriate. In
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22 205 | this range we tested a number of values and found it had little effect on our results.

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24 206 | For each parameter set, the cohort declined with constant natural mortality:

$$N_{t+1} = N_t e^{-M} \quad (1)$$

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30 208 | where N_t is the number of age t individuals, M is natural mortality, and N_0 is 1,000.

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32 209 | Reproductive output (EP) was estimated at each age t as:

$$EP_t = (N_{t-1} e^{-M}) f_t \quad (2)$$

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38 211 | where f_t is mean fecundity at age t . The cumulative Spawning Potential Ratio (SPR) was

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41 212 | calculated for each age class t :

$$SPR_t = \frac{\sum_{t=0}^t EP_t}{\sum_{t=0}^{t_{max}} EP_t} \quad (3)$$

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214 where SPR_t is the proportion of potential lifetime reproductive output achieved at age t .

215 When no fecundity data were available, the reproductive output of a mature age class was
216 assumed proportional to biomass:

$$217 \quad EP_t = N_t W_t m_t \quad (4)$$

218 where W_t is mean weight at age t , and m_t is the probability of being mature at age t .

219 We used the simplifying assumption that M remains constant over all age and size classes
220 in a population. This is unlikely to be true in nature, as juvenile mortality rates are
221 generally observed to be greater than adult mortality rates, and mortality rates maybe size
222 related throughout a species' life cycle (Gislasson *et al.* 2010; Charnov *et al.* 2013).
223 However as noted by Charnov *et al.* (2013) juvenile mortality rates do not influence the
224 estimation of life-time reproductive output in a species, and adult mortality rates tend to
225 be more constant than juvenile rates, and so more likely to be compatible with this
226 simplifying assumption.

227 A broad range of formulations to describe growth, size of maturity, fecundity, mortality
228 and relationships between age, length and weight were found in the literature, and these
229 are described below. We adapted the formulation of the SPR model for each species to
230 the formulations and units used in the source literature. If < 15 age classes were present,
231 we converted the unit of time to the next lowest unit (i.e. years to months, or months to
232 weeks) to smooth the functions being modeled.

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233 Five growth models were used by the collected literature to describe the growth for the
 234 123 selected species. The three-parameter von Bertalanffy growth function (VBGF) was
 235 used to describe the growth of 117 species:

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right) \tag{5}$$

236
 237 where L_t is mean length at age t , L_∞ is asymptotic length, k the growth coefficient, and t_0
 238 is the theoretical age at zero length. The Schnute growth function was used for three
 239 species:

$$L_t = \left[(y_1^B + (y_2^B - y_1^B)) \left(\frac{(1 - e^{-A(t-T_1)})}{1 - e^{-A(T_2-T_1)}} \right) \right]^{\frac{1}{B}} \tag{6}$$

240
 241 where T_1 and T_2 are reference ages, y_1 and y_2 length at each reference age respectively,
 242 and A and B are constants $\neq 0$. The Gompertz growth function was used for one species:

$$L_t = \omega_0 e^{G(1-e^{-gt})} \tag{7}$$

243
 244 where G , ω_0 & g are constants. Two generic length models were used for two species:

$$L_t = L_\infty + \alpha \beta^t \tag{8}$$

$$L_t = L_{t-1} + \frac{\alpha}{1 + e^{\frac{L_{t-1} - \beta}{\phi}}} \tag{9}$$

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 246
 247 where α , β and ϕ are constants.

248 Length-weight relationships were described in the literature for all except two species by:

$$W_t = aL_t^b \quad (10)$$

249

250 where a and b are constants. Polynomial regressions were reported for the length-weight
251 relationships for two species:

$$W_t = a - bL_t + cL_t^2 \quad (11)$$

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253 where a , b and c are constants.

254 When fecundity at length, weight, or age was not available, reproductive output was
255 assumed proportional to the biomass of an individual or cohort, based on the reported
256 maturity ogive for each species (Equation 4). Thus, in these cases reproductive output
257 was assumed to be the same as the mature biomass of a cohort. When no maturity ogive
258 was available, whichever available estimate of length at maturity (e.g. L_0 , L_{50} , L_{100}) was
259 used to delineate between juvenile and adult size classes, and maturity was assumed to be
260 knife edge at that size. Size-fecundity relationships were available for 24 species. For the
261 remaining 99 species, reproductive output was assumed proportional to individual weight
262 for teleosts (75 species) and some crustaceans (4 species) and molluscs (7 species), and
263 size-independent for elasmobranchs (8 species) and mammals (5 species).

264 Where sexual dimorphism was recorded only female parameters were used in the *SPR*
265 model developed for the species. Our database includes several hermaphroditic species,
266 for these species the maturity ogive was defined as female maturation ogive, and if
267 occurring after the female stage (which is generally the case), the male stage was

268 considered to contribute to the reproductive potential of the population, and for the
 269 purpose of *SPR* modeling treated as a continuation of the female phase.

270

271 Simulation of Length-Composition

272 To assist with our understanding of the patterns we observed an age-based model was
 273 developed to simulate the length frequency composition of the theoretical unfished
 274 populations across the range of M/k observed in our meta-analysis. To achieve the desired
 275 ratios of M/k for each simulation we fixed M at 0.2 and solved for the appropriate value
 276 of k . Size compositions were simulated using nine values of M/k (4.0, 1.65, 1.0, 0.8, 0.6,
 277 0.4, 0.3, 0.2, & 0.1). We assumed von Bertalanffy growth (mean $L_\infty = 1$, $CV_{L_\infty} = 0.1$, $t_0 = 0$)
 278 in arbitrary units, with L_∞ distributed normally among individuals, and with the variance
 279 in mean length a function of mean cohort length (Sainsbury, 1980). Because of the
 280 variation associated with length-at-age, some individuals have lengths greater than mean
 281 L_∞ (1.0); thus the length composition was calculated for lengths between 0 and 1.4. We
 282 estimated the size of maturity for these simulated size compositions using the Beverton
 283 (1992) equation derived for teleosts:

$$\frac{L_m}{L_\infty} = \frac{3}{3 + \frac{M}{k}} \quad (12)$$

284

285 **Results**

286 Figure 1a-d shows the modeled *SPR* for every species in our meta-analysis as functions
 287 of (a) normalized weight (W/W_{max}), (b) normalized length (L/L_{max}) and (c) normalized age

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8 288 | (t/t_{max}). As described in the methods W_{max} , L_{max} and t_{max} are defined as the value attained
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10 289 | when modeled cohort abundance declines to $\leq 1\%$ of initial abundance. In Figure 1d we
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12 290 | standardise the *SPR*-at-weight trajectories (Figure 1a) with respect to both weight-at-
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14 291 | maturity and maximum weight ($(W-W_m)/(W_{max}-W_m)$) making it evident that much of the
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16 292 | crossing of trajectories observed in Figures 1a & b is due to variation in size of maturity.
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18 293 | The spectrum of curves observed in Figures 1a-d appears to be determined by the range
19
20 294 | of M/k ratios observed in our meta-analysis; species with the greatest ratio ($M/k = 3.5$)
21
22 295 | have trajectories in the upper left of Figures 1a, b, and, while those with the lowest ratios
23
24 296 | ($M/k = 0.1$) have trajectories in the bottom right, and this empirical observation is
25
26 297 | confirmed theoretically by Hordyk *et al.* (this issue a).

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28 298 | Also plotted in Figures 1a-d (black lines) are the relationships expected for species with
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30 299 | biological parameters conforming to Jensen's (1996) estimates of the three BH-LHI (M/k
31
32 300 | = 1.5, $L_m/L_\infty = 0.66$ and $M \times Age_m = 1.65$), and the assumption that reproductive output is
33
34 301 | proportional to mature weight, which in turn is a cubic function of length. From this we
35
36 302 | conclude that the three BH-LHI, proscribe a unique relationship between normalized size,
37
38 303 | age and *SPR*, however, the BH-LHI relationship is apparently some form of 'median'
39
40 304 | form of the relationship we observe across all 123 species in our meta-analysis rather
41
42 305 | than an invariant relationship that is applicable to many species as we expected originally
43
44 306 | might be the case.

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46 307 | As demonstrated by Hordyk *et al.* (this issue a) and illustrated by simulation in Figure 2
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48 308 | the M/k ratio determines the relative shape of a population's unfished size composition.
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50 309 | Here, we note again our use of the simplifying assumption that M remains constant over
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8 310 the all age and size classes in a population, and the influence that this assumption has on
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10 311 the shape of these simulated size compositions. However, using the rationale of Charnov
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12 312 *et al.* (2013) that adult mortality rates are more likely to tend towards a level of
13
14 313 consistency, and determine life-time reproductive output, we observe that unfished
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16 314 populations with $M/k > 1.0$ do not tend to exhibit an adult modal size (Figure 2). This is
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18 315 because adults grow and die too rapidly to accumulate around a species' asymptotic size
19
20 316 (Hordyk *et al.* this issue a). This contrasts with unfished populations of species with M/k
21
22 317 < 1.0 (Hordyk *et al.* this issue a) in which adults grow relatively slowly and persist long
23
24 318 enough to accumulate around an asymptotic size so that a modal adult size becomes
25
26 319 observable, and increasingly prominent as M/k declines (Figure 2).

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28 320 To assist in our description of the variation we observed around the BH-LHI relationship
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30 321 between normalized size, age and *SPR*, we categorised the species in our meta-analysis
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32 322 with respect to $M/k = 1.0$, and whether their growth is determinate or indeterminate.
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34 323 Species with indeterminate growth continue growing throughout adult life, although
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36 324 slowing to some extent with increasing size, while species with determinate growth do
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38 325 not grow as adults. These two criteria defined three broad groups or 'Types' of species in
39
40 326 our meta-analysis; Type I – $M/k > 1.0$ and indeterminate growth, Type II – $M/k < 1.0$ and
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42 327 indeterminate growth, Type III – $M/k < 1.0$ and determinate growth (Figure 1). No species
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44 328 with $M/k > 1.0$ and determinate growth were observed in our meta-analysis (see also
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46 329 Hordyk *et al.* this issue a).

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48 330 A total of 49 Type I species (green lines) were identified, including 34 teleosts, 10
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50 331 chondrichthyes, 3 crustaceans and 2 molluscs. Their trajectories occupy the upper left

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8 332 hand side of Figs 1a-c and the lower right of Figure 1d. Type I species conform to the
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10 333 general shape of the BH-LHI trajectories, and have a slightly higher average M/k (1.95,
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12 334 cf. 1.5; Table 1) but slightly lower average L_m/L_∞ (0.55, cf. 0.65; Table 1) than those for
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14 335 the BH-LHI. They begin reproduction at relatively small sizes (Figures 1a&b) but at a
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16 336 relatively later stage of their life cycle (Figure 1c) than Types II & III. Unfished Type I
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18 337 populations are numerically dominated by juvenile length classes and do not exhibit an
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20 338 adult modal size (Fig. 2; top panels). Most (60-80%) of the reproductive potential in these
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22 339 populations comes from smaller individuals that are <80% of their asymptotic size
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24 340 (Figure 1a, b).

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26 341 A diverse range of species comprise the Type I category, including coastal bivalves *Gari*
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28 342 *solida*, *Semele solida*, a crab *Callinectes sapidus*, two spiny lobsters *Panulirus argus*,
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30 343 *P. ornatus*, several carcharhinid *Carcharhinus obscurus*, *C. plumbeus* and triakid sharks ,
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32 344 *Mustelus antarcticus*, *Prionace glauca*, and teleosts ranging from low tropic level species
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34 345 such as *Scomber japonicus*, *Cololabis saira* and the clupeid *Brevoortia patronus* to
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36 346 higher trophic level species, such as the rockfish *Sebastes chlorostictus*,
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38 347 *S. melanostomus* and two apex piscivores, the scombrid tunas *Thunnus alalunga*, and
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40 348 *T. tonggol*.

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42 349 Type II species (blue curves on Figure 1) are shifted to the right of Type I species in
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44 350 Figures 1a&b, and to the left in Figure 1c. They share the indeterminate growth pattern of
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46 351 Type I species. Type III species (red) grow to a determinant asymptotic adult size, and
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48 352 reproduce without further growth. Their trajectories are shifted to the extreme right in
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50 353 Figures 1a&b, and the extreme left in Figure 1c. The 74 Type II and III species share

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8 354 lower M/k ratios than Type I species (mean = 0.62, cf. 1.95; Table 1). In contrast to Type
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10 355 I species, Type II & III species do not reproduce until growth is almost complete; Type II
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12 356 species produce approximately 70% of their SPR at sizes >80% of the asymptotic size,
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14 357 while Type III species produce 90% of SPR at sizes >80% of asymptotic size (Figure 1).
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16 358 Unfished populations of Type II and III species are dominated by adult size classes, and
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18 359 exhibit distinct adult modes that become more pronounced with lower M/k ratios (Figure
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20 360 2; mid & lower panels).

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22 361 The Type II species (blue) form a middle group of 59 species (45 teleosts, 1
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24 362 elasmobranch, 5 crustaceans, and 8 molluscs) with average L_m/L_∞ similar to the BH-LHI
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26 363 ratio (0.69, cf. 0.66; Table 2), but a lower average M/k than the BH-LHI ratio (0.62, cf.
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28 364 1.5; Table 2). Type II species include crustaceans, *Nephrops norvegicus*, and all of the
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30 365 prawns (=shrimp) in our analysis *Penaeus indicus*, *P. latisulcatus*, *P. merguensis*, all
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32 366 three haliotid gastropods *Haliotis rubra*, *H. laevigata*, *H. iris*, a carcharhinid shark
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34 367 *Rhizoprionodon taylori*, and a range of teleosts including flat-forms *Pleuronectes*
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36 368 *platessa*, *Psettichthys melanostictus*, tropical snappers *Lutjanus malabaricus*, *L.*
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38 369 *carponotatus* *L. argentimaculatus* and the long-lived orange roughy *Hoplostethus*
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40 370 *atlanticus*.

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42 371 The 15 Type III species (red) exhibit trajectories that balloon into the bottom right of
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44 372 Figures 1a&b. These species reach maturity (Figure 1c) and a determinant asymptotic
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46 373 size (Figs 1a&b) relatively early in life. Type III species have the largest average L_m/L_∞
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48 374 ratio (0.88; Table 2) and lowest average M/k ratio (0.57; Table 2). Besides the five
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50 375 marine mammals in our database, Type III species include two triakid sharks

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8 376 *Galeorhinus galeus*, *Furgaleus macki*, eight teleosts, including the long-lived *Scorpius*
9 377 *aequipinnis*, and two short-lived *Lethrinidae* species.

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12 378 In Figure 3a the L_m/L_∞ of each species in our analysis is plotted as a function of M/k . The
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14 379 solid black line ($L_m/L_\infty = 3/(3+ M/k)$) is derived from Beverton (1992) and Hordyk *et al.*
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16 380 (this issue a), but is originally from Holt (1958) who used this equation to demonstrate
17 381 that size at maximum biomass ($L_{opt.}$) can be estimated from the ratio of M/k . Numerous
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19 382 empirical studies observe that length at maturity (L_m) coincides with $L_{opt.}$ and various
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21 383 theoretical studies postulate that this is because the evolutionary fitness of a species is
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23 384 maximized by this coincidence (Fryer and Iles, 1972; Roff, 1984; Beverton, 1992). The
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25 385 factor of '3' used in this equation comes from the assumption that weight is proportional
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27 386 to L^3 . The dashed and dotted lines plotted in Figure 3 indicate alternative relationships
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29 387 obtained by substituting factors of 2.5 or 3.5 into this equation, which would be
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31 388 equivalent to assuming weight and fecundity are proportional to $L^{2.5}$ and $L^{3.5}$
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33 389 respectively. These alternative relationships are plotted to provide some scaling of
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35 390 variance around the relationship.

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39 391 Very few of the species in our meta-analysis fall above the Beverton (1992) curve for the
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41 392 relationship between M/k and L_m/L_∞ ; most of the outliers are below (Figure 3a). This is
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43 393 primarily because our meta-analysis encompasses all marine species, some of which have
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45 394 fixed rates of reproduction, while Beverton (1992) worked almost entirely with teleosts
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47 395 for which fecundity is normally more closely related to adult body size. In Figure 3b, the
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49 396 relationship between M/k and L_m/L_∞ is plotted for the 9 teleost families with three or more

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8 397 species in our database and these conform much more closely to the Beverton (1992)
9 398 relationship (Figure 3b).

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12 399 In Figure 3b there is the suggestion that species within families tend to group together on
13 400 the M/k and L_m/L_∞ spectrum, which in Figure 4 is shown with our 3 most numerous
14 401 families to result in their SPR at size and age trajectories grouping into distinctive family
15 402 bands. Comparison to the plotted BH-LHI trajectories (Figure 4 – broken black line)
16 403 shows that to some extent the BH-LHI relationship describes the weight and length
17 404 trajectories of the Gobiidae in our study, but not their SPR at age relationship. The BH-
18 405 LHI relationship over-estimates the productivity of the Lethrinidae and Acanthuridae, by
19 406 suggesting higher than observed SPR at lower sizes for those families, while describing a
20 407 relationship between SPR and relative age that is intermediate between the Lethrinidae
21 408 and Acanthuridae relationships in our analysis.

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24 409 We also examined the predictive power of Pauly's (1980) equation for estimating M
25 410 empirically by comparing the M/k and L_m/L_∞ ratios of species in our meta-analysis with
26 411 those derived from Pauly's (1980) equation for estimating M empirically (Figure 5). The
27 412 relationship between M/k and L_∞ is plotted for the 109 species in our database with $L_\infty \leq$
28 413 200cm, which excludes marine mammals and large sharks (Figure 5a). The solid lines
29 414 indicate the estimates of M/k that would be derived using the Pauly equation across the
30 415 range of k values we observed. The Pauly equation requires an assumption about ambient
31 416 temperature. For simplicity we assume 15°C but sensitivity analyses showed that
32 417 increasing the assumed temperature only raised the plotted lines minimally. The Pauly
33 418 equation generally produces estimates of $M/k > 1$, especially for species with $L_\infty < 50$ cm.

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8 419 Our database includes a considerable number of teleosts with $L_{\infty} < 50$ cm and $M/k < 1$,
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10 420 for which the Pauly equation over-estimates M . This pattern is maintained even when the
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12 421 analysis is restricted to the teleost families with three or more species (Figure 5b).
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17 423 **Discussion**

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20 424 In fisheries science, the three Beverton Holt-Life History Invariants (BH-LHI) are most
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22 425 commonly used separately to estimate individual parameters for population modeling;
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24 426 generally they are only linked within studies seeking to relate evolutionary fitness and
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26 427 metabolic parameters to the optimization of life histories (e.g., Jensen, 1997; Charnov *et*
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28 428 *al.*, 2013). We believe our combination of them to reveal that they imply a unique
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30 429 generalized relationship between normalized size, age and *SPR* is relatively novel. Our
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32 430 meta-analysis suggests that rather than approximating some unique relationship between
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34 431 size, age and reproductive potential that is broadly applicable across species, the BH-LHI
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36 432 estimate some form of ‘median’ relationship for the 123 species in our meta-analysis
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38 433 (Figure 1) that is not necessarily found in any species.

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40 434 The first formulations of BH-LHI (Beverton and Holt 1959; Beverton 1963) were based
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42 435 on North Sea teleosts (clupeids and engraulids) that our analysis has classed as Type I
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44 436 species. Since that time fisheries biology has tended to accept, seemingly by default, that
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46 437 the values derived from those initial studies are relatively constant across much broader
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48 438 suites of species, particularly the ratio of M/k of ~ 1.5 . This was, however, not an
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50 439 assumption ever made by Holt (1958) nor Beverton (1992), who both conceptualized

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8 440 species as displaying a range of M/k values co-varying with L_m/L_∞ (Figure 3), nor by
9 441 Pauly (1980), who correlated ambient temperature and adult body size with the M/k ratio
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11 442 for each species.

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14 443 | Apparently confirming [these](#) earlier studies the descriptive meta-analysis we present here
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16 444 illustrates the natural variability observed across marine species. We defined three broad
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18 445 types of marine species with characteristic relationship between size, age and
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20 446 reproductive potential, and ratios of M/k and L_m/L_∞ . Our intent in doing so is not to imply
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22 447 | fundamental differences or strong boundaries between [our rather arbitrary groupings](#), but
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24 448 to provide an initial indicative categorization to aid our discussion of the phenomena we
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26 449 observe. Our aim here is to 1) illustrate that predictable patterns in size, age and *SPR*
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28 450 appear to exist in nature, and 2) to postulate that these predictable patterns might provide
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30 451 an alternative theoretical framework for deriving knowledge about unstudied species
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32 452 from studies of related species.

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35 453 When we apply the classification of teleost life strategies developed King and
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37 454 McFarlane's (2003) or the more generalized 'r and K' theory of Pianka (1970), which
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39 455 characterizes life history strategies as either 1) 'r-strategists' with high population turn-
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41 456 over rates, a tendency for boom and bust dynamics, and invasive 'weed-like'
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43 457 characteristics, or 2) 'K-strategists' with relatively stable population dynamics, lower
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45 458 turnover and adults that reproduce over many breeding cycles. We conclude that our
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47 459 Type I species which mature at relatively small sizes, reproduce for a relatively short and
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49 460 late part of their life cycle, continue growing relatively rapidly as they reproduce, have
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51 461 unfished populations that are dominated by juvenile size classes, and do not exhibit a

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9 462 modal adult size, are Opportunist and Intermediate Strategists (King and McFarlane
10 463 2003), and tend towards being ‘*r*-strategists’ (Pianka 1970). While Type II and III species
11 464 which mature at relatively high sizes, reproduce for a relatively extended part of their life
12 465 cycle, while growing slowly, or not at all, and have unfished populations that exhibit a
13 466 modal adult size, are typically Periodic and Equilibrium Strategists (King and McFarlane
14 467 2003), and *K*-strategists (Pianka 1970). From this, we surmise that, in the case of an
15 468 unstudied stock, general knowledge of a species typical life-history strategy might be
16 469 used to estimate a likely set of life history ratios and the likely relationships between size,
17 470 age and *SPR* those ratios proscribe. We propose that the estimations developed in this
18 471 way for a relatively unstudied stock will be more accurate than existing standard methods
19 472 for applying the concept of BH-LHI to data-poor stock assessment.

20 473 Currently the BH-LHI are widely assumed to be ‘invariant’ and individual parameters are
21 474 commonly estimated for data-poor assessments on that basis, but as illustrated here
22 475 (Figure 1) and proved by derivation in Hordyk *et al.* (this issue a) this implies all species
23 476 share the same BH-LHI relationships between size, age and reproductive output. Rather,
24 477 the so-called ‘Invariants’ vary together, matching patterns of growth and reproduction to
25 478 different life history strategies, presumably ensuring that for each life-history strategy,
26 479 length at maturity (L_m) and a cohort’s maximum biomass ($L_{opt.}$) coincide, optimizing each
27 480 species’ evolutionary fitness (Fryer and Iles, 1972; Roff, 1984; Beverton, 1992). From
28 481 our study, and those that precede us, it appears that the BH-LHI only tend towards
29 482 relative invariance within groups of species sharing similar life-history strategies,
30 483 reflecting the stage at which each life-history strategy transfers energy from allometric
31 484 growth to reproduction (Charnov, 2008; Charnov *et al.* 2013). In this conceptualization,

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8 485 tuna can be considered as 'larger, slower' anchovies which rarely reach asymptotic sizes,
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10 486 while some prawns are 'smaller, faster' versions of the fish, lobsters and gastropods that
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12 487 breed multiple times close to asymptotic sizes.

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14 488 The obvious question at this point is; where do phenotypic plasticity, and density
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16 489 dependent responses to fishing pressure fit into this conceptualization? Do they invalidate
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18 490 this conceptualization of BH-LHI? The short answer is not at all, and although not
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20 491 studied enough at the present time, we believe these two phenomena are likely to provide
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22 492 the broader context, which will in time fully validate and extend this concept's
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24 493 application. Implicitly because of the selection criteria used this meta-analysis is basically
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26 494 a study of unfished, or lightly fished, populations and this limits what can be
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28 495 demonstrated here. In each of the cases we have used we would expect that the individual
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30 496 parameter estimates used will have changed as the stocks for which they were estimated
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32 497 have been fished down, just as we expect the individual parameters to vary between
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34 498 geographically isolated populations of each species. In the case of *Cheilodactylus*
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36 499 *spectabilis* we know this to have occurred as the population was fished down (Ziegler *et*
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38 500 *al.* 2007). We are not proposing a new alternative form of invariance within families,
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40 501 species or stocks. Rather we are returning to the spirit of the original formulation of this
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42 502 concept by Holt (1958) which was that the physiological constraints of species and
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44 503 families imply that the life history ratios will remain more stable across geographical
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46 504 distributions and density ranges, than the individual life history parameters, and so for the
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48 505 purpose of data-poor stock assessment the life history ratios are expected to be more
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50 506 informative and useful than the more variable individual parameters (S.J. Holt, Personal
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52 507 Communication). There is a growing body of literature to support this supposition, and in

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8 508 this context the body of work by Choat on coral reef fish deserves to be highlighted and
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10 509 should be referred to (e.g., Choat & Robertson 2001; Gust *et al.* 2002). While the
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12 510 precedence set by fisheries science, and our selection criteria place a strong emphasis on
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14 511 the quality of component estimates of natural mortality, and our sampling of the literature
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16 512 has been strongly biased towards using lightly fished populations for this analysis, we
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18 513 suspect that exploited marine species do not distinguish between whether a seal or a
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20 514 human eats them. Thus we expect we would reach similar conclusions if we were to
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22 515 broaden our study to use the ratio of Z/k rather than M/k . On this basis we postulate that
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24 516 for metabolic and evolutionary reasons species respond to changes in total mortality by
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26 517 minimizing changes in their life history ratios, rather than the parameters themselves, and
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28 518 that this conceptualization of BH-LHI maybe useful for predicting how stocks are likely
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30 519 respond to fishing pressure, and thus the likely form and magnitude of density
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32 520 dependence mechanisms for each species.

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34 521 The data in our meta-analysis are as yet too few to properly extend these aspects of our
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36 522 analysis, but with the addition of further species we expect that the sharing of similar life-
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38 523 history ratios and bands of *SPR* trajectories by closely related species will become more
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40 524 evident amongst both teleost and non-teleost families. We expect that it will be possible
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42 525 to define a typical band of *SPR* at size and age trajectories for many marine families.
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44 526 From Figure 4a & b it can be seen already that assuming an average or median family
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46 527 value for an unstudied species of Lethrinid or Acanthuridae would produce a more
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48 528 accurate assessment of size data than the standard BH-LHI assumption of $M/k \sim 1.5$.
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50 529 Precautionary life history ratios and *SPR* trajectories might also be estimated for an
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8 530 unstudied species by taking the extreme bottom right hand and least productive of the
9 531 *SPR* at size trajectories observed for a family (Figure 4a & b).

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12 532 Our observation that the commonly assumed values of the BH-LHIs define a unique
13 533 ‘median’ form of the *SPR*-at-size and age relationships observed in nature also has
14 534 significant implications. Firstly, the results of empirical studies to more accurately derive
15 535 single estimates of the BH-LHIs and to develop correlative techniques for estimating
16 536 individual life history parameters (e.g., Pauly, 1980; Gislason *et al.*, 2010), will be
17 537 strongly influenced by the sample of species included in those studies We suspect that
18 538 many of these studies are implicitly (and unintentionally) biased against the inclusion of
19 539 low *M/k* species. Noting the inherently lower productivity of low *M/k* species, these
20 540 species are expected to be more prone to early depletion in poorly managed systems, and
21 541 less likely to sustain large, valuable fisheries (and thus research programs) in well
22 542 managed systems. This could well have resulted in low *M/k* species being under-
23 543 represented in the literature and meta-analyses, especially if those studies have an
24 544 implicit (and perhaps unavoidable) focus on research from regions with long histories of
25 545 heavy exploitation, such as the North Sea, Atlantic and South-east Asia (Costello *et al.*,
26 546 2012). This might explain the apparent conflict between the Pauly (1980) technique and
27 547 our meta-analysis (Figure 5). Being mainly based in Australia which has a relatively
28 548 recent history of fishing and a strong history of research, we had ready access to recent
29 549 research conducted in lightly exploited regions of Australia, and found numerous studies
30 550 documenting small bodied low *M/k* teleost species, which were, apparently, not as well
31 551 represented in Pauly’s (1980) analysis. In this context, the quest to more accurately
32 552 estimate unique values for the BH-LHI looks somewhat misguided, unless narrowed

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9 553 carefully on taxonomic grounds, as were the original studies of Beverton and Holt
10 554 (1959), and Beverton (1963).

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12 555 Another significant implication of our observation that the BH-LHI define a unique
13 556 'median' form of the relationships between size, age and *SPR* observed in nature, is that
14 557 existing stock assessments, using some derivation of the assumption that $M/k \sim 1.5$, are
15 558 implicitly over-estimating the productivity of stocks with $M/k < 1.5$. This could amount
16 559 to a serious systematic bias for our field as such techniques are commonly used with
17 560 long-lived species where the depletion of the older age classes through fishing is thought
18 561 to have rendered the estimation of M with aging studies unreliable. Species with $M/k <$
19 562 1.0 are most prone to having the older adult classes depleted through fishing, and are
20 563 consequently, more likely to have had a technique based on $M/k \sim 1.5$ applied to them.
21 564 Even without extending this meta-analysis rigorously down to the level of families,
22 565 assessments that have used the assumption of $M/k \sim 1.5$ could be improved using the
23 566 three Types of species we defined here on the basis of life-history strategies and forms of
24 567 growth.
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569 **Conclusions**

570 This meta-analysis suggests that the so-called Beverton-Holt Life History Invariants are
571 actually co-variants, varying together in relation to life history strategies and defining a
572 range of relationships between size, age and reproductive output. From our study, and
573 those that precede us, it appears that the BH-LHI only tend towards relative invariance

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8 574 within groups of species sharing similar life-history strategies, reflecting the stage at
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10 575 which differing life-history strategy transfers energy from allometric growth to
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12 576 reproduction (Charnov 2008; Charnov *et al.* 2013). We believe this conceptualization of
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14 577 BH-LHI has potential to provide a theoretical framework for ‘borrowing’ knowledge
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16 578 from well-studied species for application to related unstudied stocks, and that together
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18 579 with Hordyk *et al.* (this issue a, b) this may make it possible to assess many otherwise
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20 580 data-poor species from simple size studies.
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24 25 582 **Acknowledgements**

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27
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29
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31
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35
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39 40 41 589 **References**

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25 697 **Figure & Table Legends**

26
27 698 Table 1. Synopsis of the taxa and species in this meta-analysis summarizing the range of
28 699 parameters used for each species group. M = natural mortality; k = von Bertalanffy
30 700 growth parameter; L_m = length at maturity; L_{∞} = asymptotic length; max. = maximum.
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36 702 Figure 1.

37 703 Observed relationships for 123 selected marine species between Spawning Potential

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39 704 Ratio (SPR) and (a) standardised weight ($weight_{max}=1.0$), (b) standardised length

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41 705 ($length_{max}=1.0$), (c) standardised age ($age_{max}=1.0$), and (d) weight standardized for size of

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43 706 maturity ($weight_m=0$) and maximum weight ($weight_{max} = 1.0$). Green lines denote species

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45 707 with indeterminate growth and $M/k > 1.0$; blue lines denote species with indeterminate

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47 708 growth and $M/k < 1.0$; red lines denote species with determinate growth & $M/k < 1.0$;

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49 709 black lines show the relationship for species conforming with BH-LHI; $M/k = 1.5$,

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51 710 $L_m/L_{\infty} = 0.66$ and $M \times Age_m = 1.65$.

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712 Figure 2

713 Simulated length frequency histograms illustrating how the size compositions of unfished
714 populations are determined by the M/k ratio for a species'. The range of M/k ratios (0.1 to
715 4.0) chosen for simulating these histograms was based on the range of ratios observed in
716 the meta-analysis of 123 species. Top row: $M/k = 4.0, 1.65, 1.0$. Middle row: $M/k = 0.8,$
717 $0.6, 0.4$. Bottom row: $M/k = 0.3, 0.2, 0.1$. Shading indicates the proportion of the mature,
718 adults in the population, assuming $L_m/L_\infty = 3/(3 + M/k)$, as derived from Beverton (1992).

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720 Figure 3

721 The relationship between relative length of maturity (L_m/L_∞) in (a) the 123 marine species
722 selected for this meta-analysis; and (b) nine teleost families with more than three species
723 plotted against the M/k for each species. In a), green points denote species with
724 indeterminate growth and $M/k > 1.0$; blue points indeterminate growth and $M/k < 1.0$; red
725 points determinate growth and $M/k < 1.0$. The solid black lines plot the Beverton (1992)
726 relationship; $L_m/L_\infty = 3/(3 + M/k)$. The dashed and dotted lines, respectively show the
727 relationships $L_m/L_\infty = 2.5/(2.5 + M/k)$ and $L_m/L_\infty = 3.5/(3.5 + M/k)$.

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729 Figure 4

730 Observed relationships between Spawning Potential Ratio (SPR) and (a) standardised
731 weight ($weight_{max}=1.0$), (b) standardised length ($length_{max}=1.0$), (c) standardised age
732 ($age_{max}=1.0$) for the three most numerous teleost families in our meta-analysis; Gobiidae,

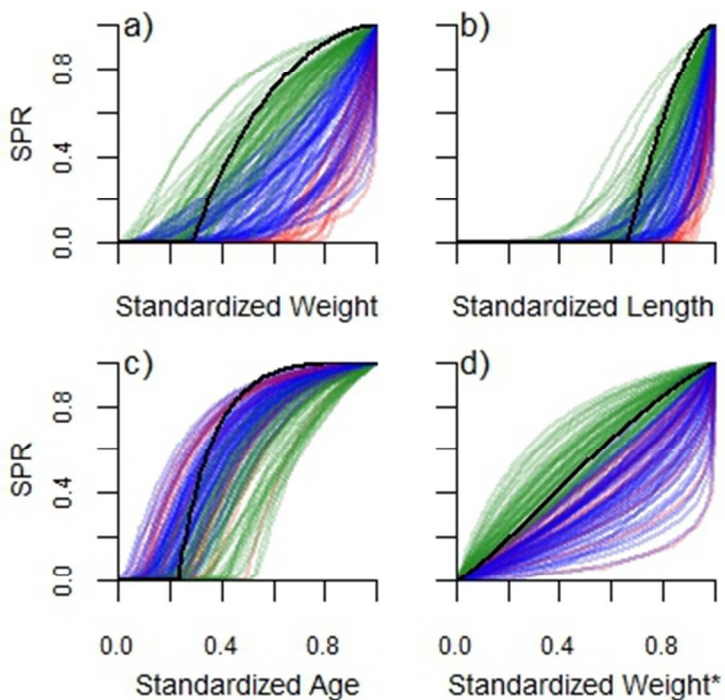
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8 733 n=5, green; Lethrinidae, n=10, red; Acanthuridae, n=7, blue. The broken black line show
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10 734 the BH-LHI relationships; $M/k = 1.5$, $L_m/L_\infty = 0.66$, and $M \times Age_m = 1.65$.

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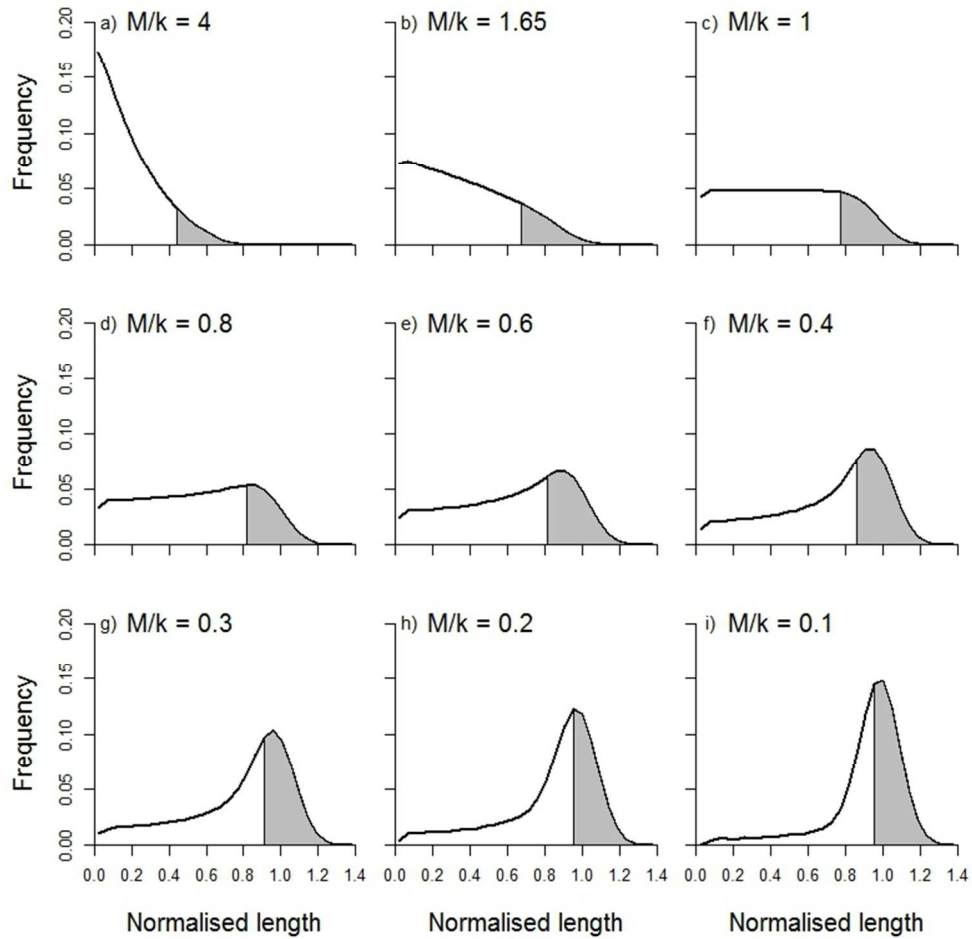
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14 736 Figure 5

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16 737 The relationship between asymptotic length (L_∞) and M/k for a) 109 marine species in our
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18 738 database with $L_\infty \leq 200$ cm and b) nine teleost families with more than three species, for
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20 739 those species with asymptotic size ≤ 200 cm. Coloured lines show the relationships
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22 740 estimated from Pauly's (1980) equation assuming the range of k observed in this meta-
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24 741 analysis (0.1 – 1.0) and an ambient temperature of 15°C.

Taxa	# Families	# Species	Max. age (yrs)	Max. length (m)	M/k mean (range)	L_m/L_{∞} mean (range)
Type I	34	49	<1-102	0.04-3.19	1.95 (1.00-3.52)	0.55 (0.32-0.79)
Chondrichthyes	8	10	10-49	0.57-3.19	2.07 (1.03-3.16)	0.64 (0.50-0.79)
Crustacean	2	3	<1-14	0.15-0.25	1.55 (1.20-1.90)	0.52 (0.46-0.56)
Mollusc	2	2	5	0.06-0.07	2.92 (2.74-3.10)	0.35 (0.32-0.39)
Teleost	22	34	<1-102	0.04-1.49	1.88 (1.00-3.52)	0.55 (0.32-0.71)
Type II	32	59	<1-154	0.03-1.83	0.62 (0.14-0.98)	0.69 (0.30-0.84)
Chondrichthyes	1	1	8	0.73	0.59	0.75
Crustacean	3	5	<1-15	0.03-0.08	0.74 (0.62-0.94)	0.55 (0.30-0.74)
Mollusc	5	8	3-154	0.07-0.14	0.53 (0.14-0.84)	0.55 (0.34-0.80)
Teleost	23	45	5-96	0.12-1.83	0.63 (0.21-0.98)	0.72 (0.32-0.84)
Type III	11	15	5-115	0.21-21.49	0.57 (0.12-0.83)	0.88 (0.85-0.93)
Chondrichthyes	2	2	17-46	1.21-1.62	0.68 (0.63-0.73)	0.92 (0.91-0.93)
Mammal	3	5	58-115	2.67-21.49	0.46 (0.20-0.75)	0.88 (0.87-0.91)
Teleost	6	8	5-77	0.21-0.69	0.61 (0.12-0.83)	0.87 (0.85-0.89)
Total	77	123	<1-154	0.03-21.49	1.17 (0.12-3.52)	0.66 (0.30-0.93)

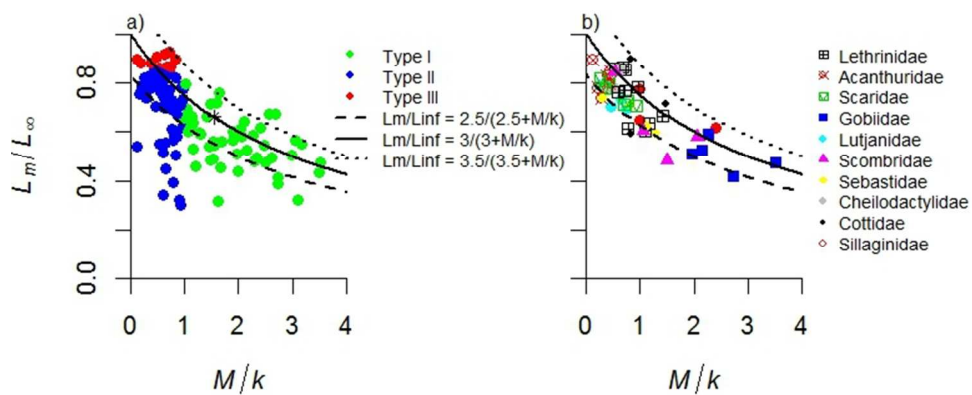


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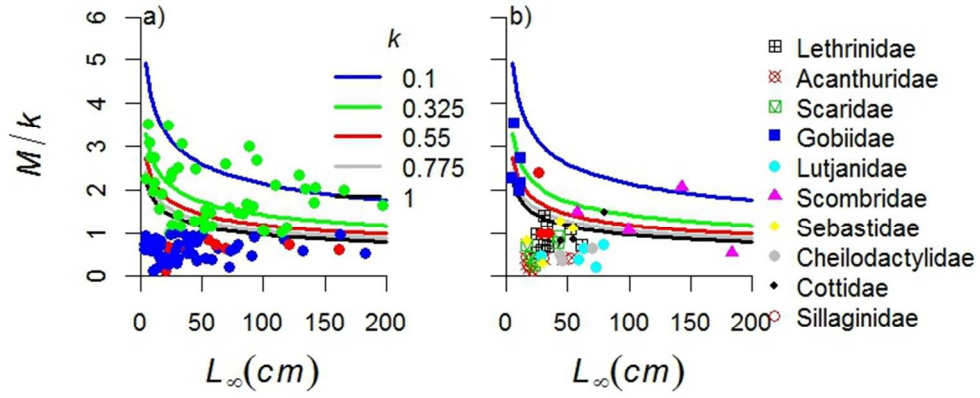


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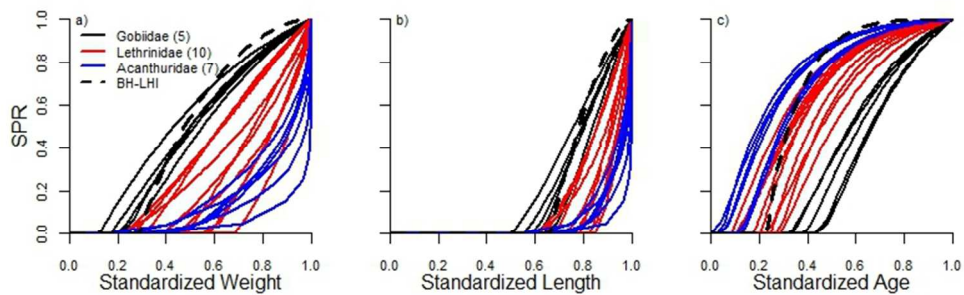


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1 Revisiting the concept of Beverton-Holt Life History Invariants with the aim of
2 informing data-poor fisheries assessment.

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20 **Abstract**

21 The complexity and cost of existing fishery assessment techniques prohibits their
22 application to 90% of fisheries globally. Simple, cost-effective, generic
23 approaches are needed for small-scale and data-poor fisheries that support the
24 majority of the world's fishing communities but cannot currently be assessed
25 quantitatively. This meta-analysis of the relationship between spawning potential
26 and the normalized size and age of 123 marine species suggests that the so-called
27 Beverton-Holt Life History Invariants (BH-LHI; L_m/L_∞ , M/k , $M \times Age_m$) actually
28 vary together in relation to life history strategy. determining the relationship
29 between size, age and reproductive potential for each species. Although little
30 realized, the common assumption of unique values for the BH-LHI also implies
31 that all species share the same relationship between size, age and reproductive
32 potential. This implicit assumption of is not supported by this meta-analysis,
33 which instead suggests there is considerable but predictable natural variation in
34 the BH-LHI ratios and the relationships between size, age and reproductive
35 potential that they determine. We believe this reconceptualization of the BH-LHI
36 has potential to provide a theoretical framework for 'borrowing' knowledge from
37 well-studied species to apply to related, unstudied species and populations, and
38 when applied together with the assessment technique described by Hordyk *et al.*
39 (this issue b), could make simple forms of size based assessment possible for
40 many data-poor fish stocks that are currently considered unassessable.

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8 **42 Keywords**

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11 **43** Beverton-Holt Life History Invariant, Data-poor assessment, parameter estimation
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15 **45 Introduction**

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17 **46** A persistent challenge for sustainable fisheries is the scale, complexity and cost of fishery
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19 **47** assessment (Walters and Pearse, 1996; Hilborn *et al.*, 2005; Beddington and Kirkwood,
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21 **48** 2005; Mullon *et al.*, 2005). Current assessment techniques require technical expertise,
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23 **49** detailed biological knowledge and time-series data on catch, effort and/or surveyed
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25 **50** abundance (Walters and Martell, 2004) resulting in an annual cost of \$US50,000 to
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27 **51** millions of dollars per stock (Pauly, 2013). This represents a substantial impediment to
28
29 **52** assessing small-scale, spatially complex and developing-world fisheries (Mahon, 1997).
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31 **53** By some estimates, 90% of the world's fisheries, which directly support 14 - 40 million
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33 **54** fishers and indirectly support approximately 200 million people, are un-assessable using
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35 **55** current methods (Andrew *et al.*, 2007).

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37 **56** Considerable uncertainty surrounds the status of unassessed stocks (Costello *et al.*, 2012;
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39 **57** Hilborn and Branch, 2012; Pauly, 2013) so that overfishing may go unrecognized until
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41 **58** stocks collapse. Even where fishing communities want to change fishing practices, the
42
43 **59** technical difficulty and expense of current assessment techniques can prevent science-
44
45 **60** based harvest strategies from being developed and implemented for these fisheries. A
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47 **61** new methodology is needed for small-scale and data-poor fisheries (Andrew *et al.*, 2007;
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49 **62** Pauly, 2013) along with theoretical frameworks for informing the assessment of
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51 **63** unstudied species with biological knowledge about related species (Punt *et al.* 2011).

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65 The correlation between biological parameters across species has been widely used to
66 provide generic parameter estimates necessary for assessment modeling (Charnov, 1993)
67 and were first described in fisheries by Beverton and Holt (1959) for the clupeid and
68 engraulid (herring and anchovy-like bony fishes) stocks of the North Sea (Beverton,
69 1963). They observed correlations between: 1) the instantaneous natural mortality rate
70 (M) and the von Bertalanffy (1938) growth rate constant (k), 2) length at maturity (L_m)
71 and asymptotic length (L_∞), and 3) M and the age of maturity (T_m). Beverton and Holt's
72 primary interest was in estimating M , a parameter that is notoriously difficult to measure,
73 from studies of k , L_m and T_m , which by comparison, are easily estimated. Although
74 neither Beverton, nor Holt used the term, these three life history ratios (M/k , L_m/L_∞ and M
75 \times Age_m) are now commonly referred to as the Beverton-Holt Life History Invariants (BH-
76 LHI). Widely considered to be environmentally influenced constants (Pauly, 1980) the
77 BH-LHI have been used extensively to parameterize fisheries models (Charnov, 2003;
78 Beddington and Kirkwood, 2005; Gislason *et al.*, 2010). In this study we use Jensen's
79 (1996) definition of the three BH-LHI; $M/k = 1.5$, $L_m/L_\infty = 0.66$ and $M \times T_m = 1.65$.

80 The Spawning Potential Ratio, or Spawning Per Recruit (SPR), is a commonly used index
81 of the relative rate of reproduction (Mace and Sissenwine, 1993; Walters and Martell,
82 2004) in an exploited stock. Brooks *et al.* (2010) recommend its utility for applying to
83 stocks in data limited fisheries. The SPR is defined as the proportion of the unfished
84 reproductive potential left by any given fishing pressure. It can be conceptualized as the
85 total reproductive potential of all the cohorts in a population at equilibrium, or the life-

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8 86 | time reproductive potential of an average individual passing through a population at
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10 87 | equilibrium. By definition, unfished stocks and individuals in an unfished stock, have an
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12 88 | *SPR* of 100% ($SPR_{100\%}$) and fishing mortality reduces $SPR_{100\%}$ from the unfished level to
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14 89 | $SPR_{x\%}$. Shepherd (1982) used the *SPR* concept to integrate the separate approaches to
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16 90 | fisheries modeling that had developed on opposite sides of the North Atlantic during the
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18 91 | 1970s. Generic *SPR*-based reference points have been developed theoretically and
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20 92 | through the meta-analysis of quantitatively assessed fisheries, and have been recognized
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22 93 | in international fisheries law (Restrepo and Powers, 1999; Australian Government, 2007),
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24 94 | for example $\sim SPR_{40\%}$ is generally considered a conservative proxy for maximum
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26 95 | sustainable yield (Mace and Sissenwine, 1993; Clark, 2002; Walters and Martell, 2004).
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28 96 | Until recently, estimating *SPR* has required unique population models to be
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30 97 | parameterised for each stock using estimates of natural mortality, growth, reproduction,
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32 98 | and time series of abundance, or age composition data (e.g. Ault *et al.*, 1998; Walters and
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34 99 | Martell 2004).

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36 100 | This study and the accompanying studies of Hordyk *et al.* (this issue a&b) arose from our
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38 101 | interest in developing a simple method for using size composition data to evaluate the
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40 102 | *SPR* of exploited populations (Prince *et al.* 2008; 2011). Prince *et al.* (2008) observed
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42 103 | that the spatial variability of size of maturity in *Haliotid* populations could be gauged
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44 104 | from the shape and appearance of their shells, and that qualitative evaluations of a
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46 105 | population's spawning potential can be made on the basis of size composition relative to
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48 106 | the visually evaluated size of maturity. This current collection of studies was prompted
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50 107 | by a journal editor asking, how the finding of Prince *et al.* (2008) applied to other
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52 108 | species? And our research began by addressing the question do all species exhibit the

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9 109 [same relationship between size of maturity, relative size composition and *SPR*? To this](#)
10 110 [end we began with the empirical and descriptive study described here, of how *SPR* relates](#)
11 111 [to size of maturity, relative body size and age in](#) 123 species of teleosts, chondrichthyans,
12 112 invertebrates and marine mammals. [The results presented here suggested to us that there](#)
13 113 [are predictable patterns in life history ratios \$M/k\$ and \$L_m/L_\infty\$ which are related to each](#)
14 114 [species' life history strategy, unfished size compositions, and the distribution of](#)
15 115 [spawning potential by size. Exploring these results more rigorously](#) Hordyk *et al.* (this
16 116 issue a) demonstrates that it is the life history ratios of M/k and L_m/L_∞ together with F/M
17 117 that determine the shape of size compositions and the *SPR* of populations, [rather than the](#)
18 118 [individual parameter values as generally assumed. On this basis Hordyk *et al.* \(this issue](#)
19 119 [b\) developed and tested a new approach to size-based assessment, which we believe may](#)
20 120 [have great application to data-poor assessment. Returning to the empirical observations](#)
21 121 [made in this study, we postulate that extending our meta-analysis of well studied species](#)
22 122 [could make it possible to predict characteristic life history ratios of most exploited](#)
23 123 [populations based on general knowledge about each species life history strategy, and so](#)
24 124 [make simple size based assessments possible for many stocks currently considered too](#)
25 125 [data-poor to assess.](#)

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127 **Materials and methods**

128 Selection of Parameter Sets

129 For our meta-analysis we collected [studies of marine and estuarine species for which we](#)
130 [could find robust](#) estimates of growth, natural mortality, reproduction, and length-weight

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8 131 relationships. In order to control the quality of the parameter sets we applied strict
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10 132 selection criteria. Rather than developing our own criteria *de novo* we based our criteria
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12 133 on the six criteria developed by Gislason *et al.* (2010), which they define as: “

- 134 1. Estimates were rejected if they had been derived from empirical relationships
135 (e.g. Beverton and Holt, 1959; Pauly, 1980) or ‘borrowed’ from studies of similar
136 species.
- 137 2. Estimates by size or age were rejected if they had been derived from multi-species
138 modeling.
- 139 3. Parameters were rejected if they were based on an insufficient amount of data, if
140 the authors expressed concern that they could be biased or uncertain, or if the
141 sampling gears and/or procedures for working up the samples were likely to have
142 biased the estimates.
- 143 4. Estimates of total mortality based on catch-at-length, or catch-at-age were
144 accepted as estimates of M , only if the data had been collected from an
145 unexploited or lightly exploited stock over a sufficiently long time period to
146 ensure that they reflected mortality and not simply differences in year class
147 strength, and if growth parameters or ageing methods were considered
148 appropriate.
- 149 5. Estimates derived from tagging data were included only if the following factors
150 had been considered: mortality associated with the tagging operation, tag loss,
151 differences in mortality experienced by tagged and untagged fish, migration out of
152 the study area and uncertainty regarding tag recovery.

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9 153 6. Estimates derived from regressions of total mortality and effort were included,
10 154 only if it was credible that total fishing mortality would be proportional to the
11 155 measure of fishing effort considered, and if extrapolation did not result in
12 156 excessively large confidence intervals.”

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16 157 While Gislason *et al.*'s focus was solely on ensuring the quality of natural mortality
17 158 estimates, we found that where other aspects of biology had been studied, these criteria
18 159 also ensured the quality of estimates for the broader list of parameters of interest to this
19 160 study (i.e. growth, reproduction, and length-weight relationships).

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24 161 To ensure that each species' parameter set described a single population and a similar
25 162 population density we also applied a seventh criterion, which we defined as:

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29 163 7. All parameter estimates for a species should be from the same geographic
30 164 population, and from the same time period.

31 165 Species were only included if they met all seven criteria and all the necessary parameters
32 166 could be estimated, this limited the number of studies available to our meta-analysis. We
33 167 were able to gather data for a total of 123 species, including representatives from teleosts,
34 168 invertebrates, chondrichthyans, and marine mammals. A complete list of species,
35 169 parameter values and source references are provided in supporting on-line material.

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43 170 It should be noted that these criteria biased our selection process towards well-studied
44 171 populations prior to, or during the early phase of exploitation. Thus almost all the studies
45 172 included in our database are of lightly exploited populations. We do not believe our
46 173 sample is representative of all, or even groups of, marine species. For this reason we have
47 174 not attempted to apply statistical techniques of analysis, as we have no expectation that

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9 175 our samples are distributed normally or are representative of any mean condition,
10 176 parameter value or relationships. As discussed below we do not believe such statistical
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12 177 concepts are applicable to a study such as this. In this study our aim was entirely
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14 178 qualitative: to look for, and to describe patterns of variation that exist in nature. For the
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16 179 quantitative analysis of the patterns we observed, the reader is directed to the
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18 180 accompanying theoretical study of Hordyk *et al.* (this issue a)
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22 23 182 Spawning Potential Ratio (SPR) Model for Meta-analysis

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25 183 We modeled the *SPR* achieved at any given age for the 123 species to examine patterns in
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27 184 the relationships between age, length, weight and reproductive output. The *SPR* is usually
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29 185 calculated by summing the total reproductive output of all age classes and dividing by the
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31 186 number of recruits in order to obtain a general measure of current rate of reproductive
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33 187 output in relation to the maximum potential output, i.e. the unfishes, level. However, here
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35 188 we are interested in calculating the cumulative percentage of total lifetime reproductive
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37 189 output achieved when an individual reaches each age/size, and how that varies across the
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39 190 widest possible range of marine species. For this purpose we developed an age-based
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41 191 equilibrium *SPR* model for each species, with an initial cohort size of 1,000. The number
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43 192 of survivors, average individual length and weight, and percentage of total reproductive
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45 193 output achieved for both individuals and cohorts at each successive time step was
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47 194 calculated. To enable comparisons across species age, length, weight and reproduction
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49 195 were normalized with respect to their maximum value. The maximum age class (t_{max}) was
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51 196 determined to be the first age class with an abundance of $\leq 1\%$ of the initial cohort size

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197 (i.e. ≤ 10 individuals). This is consistent with the results of empirical studies of Hewitt
198 and Hoenig (2005) who note that a range of 1-5% has generally been used for the purpose
199 of estimating M , and who conclude that 1.5% is most appropriate. In this range we tested
200 a number of values and found it had little effect on our results.

201 For each parameter set, the cohort declined with constant natural mortality:

$$N_{t+1} = N_t e^{-M} \quad (1)$$

202
203 where N_t is the number of age t individuals, M is natural mortality, and N_0 is 1,000.

204 Reproductive output (EP) was estimated at each age t as:

$$EP_t = (N_{t-1} e^{-M}) f_t \quad (2)$$

205
206 where f_t is mean fecundity at age t . The cumulative Spawning Potential Ratio (SPR) was
207 calculated for each age class t :

$$SPR_t = \frac{\sum_{t=0}^t EP_t}{\sum_{t=0}^{t_{\max}} EP_t} \quad (3)$$

208
209 where SPR_t is the proportion of potential lifetime reproductive output achieved at age t .

210 When no fecundity data were available, the reproductive output of a mature age class was
211 assumed proportional to biomass:

$$EP_t = N_t e^{-M} W_t m_t \quad (4)$$

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213 where W_t is mean weight at age t , and m_t is the probability of being mature at age t .

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9 214 We used the simplifying assumption that M remains constant over all age and size classes
10 215 in a population. This is unlikely to be true in nature, as juvenile mortality rates are
11 216 generally observed to be greater than adult mortality rates, and mortality rates maybe size
12 217 related throughout a species' life cycle (Gislasson *et al.* 2010; Charnov *et al.* 2013).
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14 218 However as noted by Charnov *et al.* (2013) juvenile mortality rates do not influence the
15 219 estimation of life-time reproductive output in a species, and adult mortality rates tend to
16 220 be more constant than juvenile rates, and so more likely to be compatible with this
17 221 simplifying assumption.

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24 222 A broad range of formulations to describe growth, fecundity, mortality and relationships
25 223 between age, length and weight were found in the literature, and these are described
26 224 below. We adapted the formulation of the *SPR* model for each species to the formulations
27 225 and units used in the source literature. If < 15 age classes were present, we converted the
28 226 unit of time to the next lowest unit (i.e. years to months, or months to weeks) to smooth
29 227 the functions being modelled.

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37 228 Five growth models were used by the collected literature to describe the growth for the
38 229 123 selected species. The three-parameter von Bertalanffy growth function (VBGF) was
39 230 used to describe the growth of 117 species:

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)}\right) \quad (5)$$

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46 232 where L_t is mean length at age t , L_∞ is asymptotic length, k the growth coefficient, and t_0
47 233 is the theoretical age at zero length. The Schnute growth function was used for three
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50 234 species:

$$L_t = \left[(y_1^B + (y_2^B - y_1^B)) \left(\frac{(1 - e^{-A(t-T_1)})}{1 - e^{-A(T_2-T_1)}} \right) \right]^{\frac{1}{B}} \quad (6)$$

235

236 where T_1 and T_2 are reference ages, y_1 and y_2 length at each reference age respectively,

237 and A and B are constants $\neq 0$. The Gompertz growth function was used for one species:

$$L_t = \omega_0 e^{G(1-e^{-gt})} \quad (7)$$

238

239 where G , ω_0 & g are constants. Two generic length models were used for two species:

$$L_t = L_\infty + \alpha \beta^t \quad (8)$$

240

$$L_t = L_{t-1} + \frac{\alpha}{1 + e^{\frac{L_{t-1} - \beta}{\phi}}} \quad (9)$$

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242 where α , β and ϕ are constants.

243 Length-weight relationships were described in the literature for all except two species by:

$$W_t = aL_t^b \quad (10)$$

244

245 where a and b are constants. Polynomial regressions were reported for the length-weight

246 relationships for two species:

$$W_t = a - bL_t + cL_t^2 \quad (11)$$

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248 where a , b and c are constants.

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9 249 When fecundity at length, weight, or age was not available, reproductive output was
10 250 assumed proportional to the biomass of an individual or cohort, based on the reported
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12 251 maturity ogive for each species (Equation 4). When no maturity ogive was available,
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14 252 whichever available estimate of length at maturity (e.g. L_0 , L_{50} , L_{100}) was used to
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16 253 delineate between juvenile and adult size classes, and maturity was assumed to be knife
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18 254 edge at that size. Size-fecundity relationships were available for 24 species. For the
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20 255 remaining 99 species, reproductive output was assumed proportional to individual weight
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22 256 for teleosts (75 species) and some crustaceans (4 species) and molluscs (7 species), and
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24 257 size-independent for elasmobranches (8 species) and mammals (5 species).

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26 258 Where sexual dimorphism was recorded only female parameters were used in the SPR
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28 259 model developed for the species. Our database includes several hermaphroditic species,
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30 260 for these species the maturity ogive was defined as female maturation ogive, and if
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32 261 occurring after the female stage (which is generally the case), the male stage was
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34 262 considered to contribute to the reproductive potential of the population, and for the
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36 263 purpose of SPR modeling treated as a continuation of the female phase.
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40 41 265 Simulation of Length-Composition

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43 266 To assist with our understanding of the patterns we observed an age-based model was
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45 267 developed to simulate the length frequency composition of the theoretical unfished
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47 268 populations across the range of M/k observed in our meta-analysis. To achieve the desired
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49 269 ratios of M/k for each simulation we fixed M at 0.2 and solved for the appropriate value
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51 270 of k . Size compositions were simulated using nine values of M/k (4.0, 1.65, 1.0, 0.8, 0.6,

271 0.4, 0.3, 0.2, & 0.1). We assumed von Bertalanffy growth (mean $L_\infty = 1$, $CV_{L_\infty} = 0.1$, $t_0 = 0$)
 272 in arbitrary units, with L_∞ distributed normally among individuals, and with the variance
 273 in mean length a function of mean cohort length (Sainsbury, 1980). Because of the
 274 variation associated with length-at-age, some individuals have lengths greater than mean
 275 L_∞ (1.0); thus the length composition was calculated for lengths between 0 and 1.4. We
 276 estimated the size of maturity for these simulated size compositions using the Beverton
 277 (1992) equation derived for teleosts:

$$\frac{L_m}{L_\infty} = \frac{3}{3 + \frac{M}{k}} \quad (12)$$

279 Results

280 Figure 1a-d shows the modeled *SPR* for every species in our meta-analysis as functions
 281 of (a) normalized weight (weight/weight_{max}), (b) normalized length (length/length_{max}) and
 282 (c) normalized age (age/age_{max}). As described in the methods Weight_{max}, length_{max} and
 283 age_{max} are defined as the value attained when modeled cohort abundance declines to
 284 < 1% of initial abundance. In Figure 1d we standardise the *SPR*-at-weight trajectories
 285 (Figure 1a) with respect to both weight-at-maturity and maximum weight ($(W_m -$
 286 $W_m)/(W_{max} - W_m)$) making it evident that much of the crossing of trajectories observed in
 287 Figures 1a & b is due to variation in size of maturity. The spectrum of curves observed in
 288 Figures 1a-d appears to be determined by the range of M/k ratios observed in our meta-
 289 analysis; species with the greatest ratio ($M/k = 3.5$) have trajectories in the upper left of
 290 Figures 1a, b, and, while those with the lowest ratios ($M/k = 0.1$) have trajectories in the

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9 291 bottom right, and this empirical observation is confirmed theoretically by Hordyk *et al.*
10 292 (this issue a).

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13 293 Also plotted in Figures 1a-d (black lines) are the relationships expected for species with
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15 294 biological parameters conforming to Jensen's (1996) estimates of the three BH-LHI (M/k
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17 295 = 1.5, $L_m/L_\infty = 0.66$ and $M \times Age_m = 1.65$), and the assumption that reproductive output is
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19 296 proportional to mature weight, which in turn is a cubic function of length. From this we
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21 297 conclude that the three BH-LHI, proscribe a unique relationship between normalized size,
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23 298 age and *SPR*, however, the BH-LHI relationship is apparently some form of 'median'
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25 299 form of the relationship we observe across all 123 species in our meta-analysis rather
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27 300 than an invariant relationship that is applicable to many species as we expected originally
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29 301 might be the case.

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31 302 As demonstrated by Hordyk *et al.* (this issue a) and illustrated by simulation in Figure 2
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33 303 the M/k ratio determines the relative shape of a population's unfished size composition.
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35 304 Here, we note again our use of the simplifying assumption that M remains constant over
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37 305 the all age and size classes in a population, and the influence that this assumption has on
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39 306 the shape of these simulated size compositions. However, using the rationale of Charnov
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41 307 *et al.* (2013) that adult mortality rates are more likely to tend towards a level of
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43 308 consistency, and determine life-time reproductive output, we observe that unfished
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45 309 populations with $M/k > 1.0$ do not tend to exhibit an adult modal size (Figure 2). This is
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47 310 because adults grow and die too rapidly to accumulate around a species asymptotic size
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49 311 (Hordyk *et al.* this issue a). This contrasts with unfished populations of species with M/k
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51 312 < 1.0 (Hordyk *et al.* this issue a) in which adults grow relatively slowly and persist long

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8 313 enough to accumulate around an asymptotic size so that a modal adult size becomes
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10 314 observable, and increasingly prominent as M/k declines (Figure 2).

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13 315 To assist in our description of the variation we observed around the BH-LHI relationship
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15 316 between normalized size, age and SPR , we categorised the species in our meta-analysis
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17 317 with respect to $M/k = 1.0$, and whether their growth is determinate or indeterminate.
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19 318 Species with indeterminate growth continue growing throughout adult life, although
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21 319 slowing to some extent with increasing size, while species with determinate growth do
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23 320 not grow as adults. These two criteria defined three broad groups or ‘Types’ of species in
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25 321 our meta-analysis; Type I – $M/k > 1.0$ and indeterminate growth, Type II – $M/k < 1.0$ and
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27 322 indeterminate growth, Type III – $M/k < 1.0$ and determinate growth (Figure 1). No species
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29 323 with $M/k > 1.0$ and determinate growth were observed in our meta-analysis (see also
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31 324 Hordyk et al. this issue a).

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33 325 A total of 49 Type I species (green lines) were identified, including 34 teleosts, 10
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35 326 chondrichthyes, 3 crustaceans and 2 molluscs. Their trajectories occupy the upper left
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37 327 hand side of Figs 1a-c and the lower right of Figure 1d. Type I species conform to the
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39 328 general shape of the BH-LHI trajectories, and have a slightly higher average M/k (1.95,
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41 329 cf. 1.5; Table 1) but slightly lower average L_m/L_∞ (0.55, cf. 0.65; Table 1) than those for
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43 330 the BH-LHI. They begin reproduction at relatively small sizes (Figures 1a&b) but at a
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45 331 relatively later stage of their life cycle (Figure 1c) than Types II & III. Unfished Type I
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47 332 populations are numerically dominated by juvenile length classes and do not exhibit an
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49 333 adult modal size (Fig. 2; top panels). Most (60-80%) of the reproductive potential in these

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8 334 populations comes from smaller individuals that are <80% of their asymptotic size
9 335 (Figure 1a, b).

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12 336 A diverse range of species comprise the Type I category, including coastal bivalves *Gari*
13 337 *solida*, *Semele solida*, a crab *Callinectes sapidus*, two spiny lobsters *Panulirus argus*,
14 338 *P. ornatus*, several carcharhinid *Carcharhinus obscurus*, *C. plumbeus* and triakid sharks ,
15 339 *Mustelus antarcticus*, *Prionace glauca*, and teleosts ranging from low tropic level species
16 340 such as *Scomber japonicus*, *Cololabis saira* and the clupeid *Brevoortia patronus* to
17 341 higher trophic level species, such as the rockfish *Sebastes chlorostictus*,
18 342 *S. melanostomus* and two apex piscivores, the scombrid tunas *Thunnus alalunga*, and
19 343 *T. tonggol*.

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22 344 Type II species (blue curves on Figure 1) are shifted to the right of Type I species in
23 345 Figures 1a&b, and to the left in Figure 1c. They share the indeterminate growth pattern of
24 346 Type I species. Type III species (red) grow to a determinant asymptotic adult size, and
25 347 reproduce without further growth. Their trajectories are shifted to the extreme right in
26 348 Figures 1a&b, and the extreme left in Figure 1c. The 74 Type II and III species share
27 349 lower M/k ratios than Type I species (mean = 0.62, cf. 1.95; Table 1). In contrast to Type
28 350 I species, Type II & III species do not reproduce until growth is almost complete; Type II
29 351 species produce approximately 70% of their SPR at sizes >80% of the asymptotic size,
30 352 while Type III species produce 90% of SPR at sizes >80% of asymptotic size (Figure 1).

31 353 Unfished populations of Type II and III species are dominated by adult size classes, and
32 354 exhibit distinct adult modes that become more pronounced with lower M/k ratios (Figure
33 355 2; mid & lower panels).

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8 356 The Type II species (blue) form a middle group of 59 species (45 teleosts, 1
9 357 elasmobranch, 5 crustaceans, and 8 molluscs) with average L_m/L_∞ similar to the BH-LHI
10 358 ratio (0.69, cf. 0.66; Table 2), but a lower average M/k than the BH-LHI ratio (0.62, cf.
11 359 1.5; Table 2). Type II species include crustaceans, *Nephrops norvegicus*, and all of the
12 360 prawns (=shrimp) in our analysis *Penaeus indicus*, *P. latisulcatus*, *P. merguensis*, all
13 361 three haliotid gastropods *Haliotis rubra*, *H. laevigata*, *H. iris*, a carcharhinid shark
14 362 *Rhizoprionodon taylori*, and a range of teleosts including flat-forms *Pleuronectes*
15 363 *platessa*, *Psettichthys melanostictus*, tropical snappers *Lutjanus malabaricus*, *L.*
16 364 *carponotatus* *L. argentimaculatus* and the long-lived orange roughy *Hoplostethus*
17 365 *atlanticus*.

18 366 The 15 Type III species (red) exhibit trajectories that balloon into the bottom right of
19 367 Figures 1a&b. These species reach maturity (Figure 1c) and a determinant asymptotic
20 368 size (Figs 1a&b) relatively early in life. Type III species have the largest average L_m/L_∞
21 369 ratio (0.88; Table 2) and lowest average M/k ratio (0.57; Table 2). Besides the five
22 370 marine mammals in our database, Type III species include two triakid sharks
23 371 *Galeorhinus galeus*, *Furgaleus macki*, eight teleosts, including the long-lived *Scorpius*
24 372 *aequipinnis*, and two short-lived *Lethrinidae* species.

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29 373 In Figure 3a the L_m/L_∞ of each species in our analysis is plotted as a function of M/k . The
30 374 solid black line ($L_m/L_\infty = 3/(3+ M/k)$) is derived from Beverton (1992) and Hordyk *et al.*
31 375 (this issue a), but is originally from Holt (1958) who used this equation to demonstrate
32 376 that size at maximum biomass ($L_{opt.}$) can be estimated from the ratio of M/k . Numerous
33 377 empirical studies observe that length at maturity (L_m) coincides with $L_{opt.}$ and various

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8 378 | theoretical studies postulate that this is because the evolutionary fitness of a species is
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10 379 | maximized by this coincidence (Fryer and Iles, 1972; Roff, 1984; Beverton, 1992). The
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12 380 | factor of '3' used in this equation comes from the assumption that weight is proportional
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14 381 | to L^3 . The dashed and dotted lines plotted in Figure 3 indicate alternative relationships
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16 382 | obtained by substituting factors of 2.5 or 3.5 into this equation, which would be
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18 383 | equivalent to assuming weight and fecundity are proportional to $L^{2.5}$ and $L^{3.5}$
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20 384 | respectively. These alternative relationships are plotted to provide some scaling of
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22 385 | variance around the relationship.

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24 386 | Very few of the species in our meta-analysis fall above the Beverton (1992) curve for the
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26 387 | relationship between M/k and L_m/L_∞ ; most of the outliers are below (Figure 3a). This is
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28 388 | primarily because our meta-analysis encompasses all marine species, some of which have
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30 389 | fixed rates of reproduction, while Beverton (1992) worked almost entirely with teleosts
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32 390 | for which fecundity is normally more closely related to adult body size. In Figure 3b, the
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34 391 | relationship between M/k and L_m/L_∞ is plotted for the 9 teleost families with three or more
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36 392 | species in our database and these conform much more closely to the Beverton (1992)
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38 393 | relationship (Figure 3b).

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41 394 | In Figure 3b there is the suggestion that species within families tend to group together on
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43 395 | the M/k and L_m/L_∞ spectrum, which in Figure 4 is shown with our 3 most numerous
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45 396 | families to result in their *SPR* at size and age trajectories grouping into distinctive family
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47 397 | bands. Comparison to the plotted BH-LHI trajectories (Figure 4 – broken black line)
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49 398 | shows that to some extent the BH-LHI relationship describes the weight and length
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51 399 | trajectories of the Gobiidae in our study, but not their SPR at age relationship. The BH-

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8 400 LHI relationship over-estimates the productivity of the Lethrinidae and Acanthuridae, by
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10 401 suggesting higher than observed *SPR* at lower sizes for those families, while describing a
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12 402 relationship between *SPR* and relative age that is intermediate between the Lethrinidae
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14 403 and Acanthuridae relationships in our analysis.
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17 404 We also examined the predictive power of Pauly's (1980) equation for estimating *M*
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19 405 empirically by comparing the *M/k* and L_m/L_∞ ratios of species in our meta-analysis with
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21 406 those derived from Pauly's (1980) equation for estimating *M* empirically (Figure 5). The
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23 407 relationship between *M/k* and L_∞ is plotted for the 109 species in our database with $L_\infty \leq$
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25 408 200cm, which excludes marine mammals and large sharks (Figure 5a). The solid lines
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27 409 indicate the estimates of *M/k* that would be derived using the Pauly equation across the
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29 410 range of *k* values we observed. The Pauly equation requires an assumption about ambient
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31 411 temperature. For simplicity we assume 15°C but sensitivity analyses showed that
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33 412 increasing the assumed temperature only raised the plotted lines minimally. The Pauly
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35 413 equation generally produces estimates of *M/k* >1, especially for species with $L_\infty < 50$ cm.
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37 414 Our database includes a considerable number of teleosts with $L_\infty < 50$ cm and *M/k* < 1,
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39 415 for which the Pauly equation over-estimates *M*. This pattern is maintained even when the
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41 416 analysis is restricted to the teleost families with three or more species (Figure 5b).
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418 **Discussion**

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48 419 In fisheries science, the three Beverton Holt-Life History Invariants (BH-LHI) are most
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50 420 commonly used separately to estimate individual parameters for population modeling;
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9 421 generally they are only linked within studies seeking to relate evolutionary fitness and
10 422 metabolic parameters to the optimization of life histories (e.g., Jensen, 1997; Charnov *et*
11 *al.*, 2013). We believe our combination of them to reveal that they imply a unique
12 423 generalized relationship between normalized size, age and *SPR* is relatively novel. Our
13 424 meta-analysis suggests that rather than approximating some unique relationship between
14 425 size, age and reproductive potential that is broadly applicable across species, the BH-LHI
15 426 estimate some form of ‘median’ relationship for the 123 species in our meta-analysis
16 427 (Figure 1) that is not necessarily found in any species.
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24 429 The first formulations of BH-LHI (Beverton and Holt 1959; Beverton 1963) were based
25 430 on North Sea teleosts (clupeids and engraulids) that our analysis has classed as Type I
26 431 species. Since that time fisheries biology has tended to accept, seemingly by default, that
27 432 the values derived from those initial studies are relatively constant across much broader
28 433 suites of species, particularly the ratio of M/k of ~ 1.5 . This was, however, not an
29 434 assumption ever made by Holt (Holt 1958) nor Beverton (1992), who both
30 435 conceptualized species as displaying a range of M/k values co-varying with L_m/L_∞ (Figure
31 436 3), nor by Pauly (1980), who correlated ambient temperature and adult body size with the
32 437 M/k ratio for each species.
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42 438 Apparently confirming earlier studies the descriptive meta-analysis we present here
43 439 illustrates the natural variability observed across marine species. We defined three broad
44 440 types of marine species with characteristic relationship between size, age and
45 441 reproductive potential, and ratios of M/k and L_m/L_∞ . Our intent in doing so is not to imply
46 442 fundamental differences or strong ‘significantly different’ boundaries between categories.
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8 443 but to provide an initial indicative categorization to aid our discussion of the phenomena
9 we observe. Our aim here is to 1) illustrate that predictable patterns in size, age and SPR
10 appear to exist in nature, and 2) to postulate that these predictable patterns might provide
11 an alternative theoretical framework for deriving knowledge about unstudied species
12 from studies of related species.
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18 When we apply the classification of teleost life strategies developed King and
19 McFarlane's (2003) or the more generalized 'r and K' theory of Pianka (1970), which
20 characterizes life history strategies as either 1) 'r-strategists' with high population turn-
21 over rates, a tendency for boom and bust dynamics, and invasive 'weed-like'
22 characteristics, or 2) 'K-strategists' with relatively stable population dynamics, lower
23 turnover and adults that reproduce over many breeding cycles. We conclude that our
24 Type I species which mature at relatively small sizes, reproduce for a relatively short and
25 late part of their life cycle, continue growing relatively rapidly as they reproduce, have
26 unfished populations that are dominated by juvenile size classes, and do not exhibit a
27 modal adult size, are Opportunist and Intermediate Strategists (King and McFarlane
28 2003), and tend towards being 'r-strategists' (Pianka 1970). While Type II and III species
29 which mature at relatively high sizes, reproduce for a relatively extended part of their life
30 cycle, growing slowly, or not at all, as they reproduce, and have unfished populations that
31 exhibit a modal adult size, are typically Periodic and Equilibrium Strategists (King and
32 McFarlane 2003), and K-strategists (Pianka 1970). From this, we surmise that, in the case
33 of an unstudied stock, general knowledge of a species typical life-history strategy might
34 be used to estimate a likely set of life history ratios and the likely relationships between
35 size, age and SPR those ratios proscribe. We propose that the estimations developed in
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8 466 this way for a relatively unstudied stock will be more accurate than existing standard
9 467 methods for applying the concept of BH-LHI to data-poor stock assessment.

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12 468 Currently the BH-LHI are widely assumed to be ‘invariant’ and individual parameters are
13 469 commonly estimated for data-poor assessments on that basis, but as illustrated here
14 470 (Figure 1) and proved by derivation in Hordyk *et al.* (this issue a) this implies all species
15 471 share the same BH-LHI relationships between size, age and reproductive output. Rather,
16 472 the so-called ‘Invariants’ vary together, matching patterns of growth and reproduction to
17 473 different life history strategies, presumably ensuring that for each life-history strategy,
18 474 length at maturity (L_m) and a cohort’s maximum biomass ($L_{opt.}$) coincide, optimizing each
19 475 species’ evolutionary fitness (Fryer and Iles, 1972; Roff, 1984; Beverton, 1992). From
20 476 our study, and those that precede us, it appears that the BH-LHI only tend towards
21 477 relative invariance within groups of species sharing similar life-history strategies,
22 478 reflecting the stage at which each life-history strategy transfers energy from allometric
23 479 growth to reproduction (Charnov, 2008; Charnov *et al.* 2013). In this conceptualization,
24 480 tuna can be considered as ‘larger, slower’ anchovies which rarely reach asymptotic sizes,
25 481 while some prawns are ‘smaller, faster’ versions of the fish, lobsters and gastropods that
26 482 breed multiple times close to asymptotic sizes.

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32 483 The obvious question at this point is; where do phenotypic plasticity, and density
33 484 dependent responses to fishing pressure fit into this conceptualization? Do they invalidate
34 485 this conceptualization of BH-LHI? The short answer is not at all, and although not
35 486 studied enough at the present time, we believe these two phenomena are likely to provide
36 487 the broader context, which will in time fully validate and extend this concept’s

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8 488 application. Implicitly because of the selection criteria used this meta-analysis is basically
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10 489 a study of unfished, or lightly fished, populations and this limits what can be
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12 490 demonstrated here. In each of the cases we have used we would expect that the individual
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14 491 parameter estimates used will have changed as the stocks for which they were estimated
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16 492 have been fished down, just as we expect the individual parameters to vary between
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18 493 geographically isolated populations of each species. In the case of *Cheilodactylus*
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20 494 *spectabilis* we know this to have occurred as the population was fished down (Ziegler *et*
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22 495 *al.* 2007). We are not proposing a new alternative form of invariance within families,
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24 496 species or stocks. Rather we are returning to the spirit of the original formulation of this
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26 497 concept by Holt (1958) which was that the physiological constraints of species and
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28 498 families imply that the life history ratios will remain more stable across geographical
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30 499 distributions and density ranges, than the individual life history parameters, and so for the
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32 500 purpose of data-poor stock assessment the life history ratios are expected to be more
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34 501 informative and useful than the more variable individual parameters (S.J. Holt, Personal
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36 502 Communication). There is a growing body of literature to support this supposition, and in
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38 503 this context the body of work by Choat on coral reef fish deserves to be highlighted and
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40 504 should be referred to (e.g., Choat & Robertson 2001; Gust *et al.* 2002). While the
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42 505 precedence set by fisheries science, and our selection criteria place a strong emphasis on
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44 506 the quality of component estimates of natural mortality, and our sampling of the literature
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46 507 has been strongly biased towards using lightly fished populations for this analysis, we
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48 508 suspect that exploited marine species do not distinguish between whether a seal or a
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50 509 human eats them. Thus we expect we would reach similar conclusions if we were to
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52 510 broaden our study to use the ratio of Z/k rather than M/k . On this basis we postulate that

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9 511 for metabolic and evolutionary reasons species respond to changes in total mortality by
10 512 minimizing changes in their life history ratios, rather than the parameters themselves, and
11 513 that this conceptualization of BH-LHI maybe useful for predicting how stocks are likely
12 514 respond to fishing pressure, and thus the likely form and magnitude of density
13 515 dependence mechanisms for each species.

14 516 The data in our meta-analysis are as yet too few to properly extend these aspects of our
15 517 analysis, but with the addition of further species we expect that the sharing of similar life-
16 518 history ratios and bands of *SPR* trajectories by closely related species will become more
17 519 evident amongst both teleost and non-teleost families. We expect that it will be possible
18 520 to define a typical band of *SPR* at size and age trajectories for many marine families.
19 521 From Figure 4a & b it can be seen already that assuming an average or median family
20 522 value for an unstudied species of Lethrinid or Acanthuridae would produce a more
21 523 accurate assessment of size data than the standard BH-LHI assumption of $M/k \sim 1.5$.
22 524 Precautionary life history ratios and *SPR* trajectories might also be estimated for an
23 525 unstudied species by taking the extreme bottom right hand and least productive of the
24 526 *SPR* at size trajectories observed for a family (Figure 4a & b).

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40 527 Our observation that the commonly assumed values of the BH-LHIs define a unique
41 528 ‘median’ form of the *SPR*-at-size and age relationships observed in nature also has
42 529 significant implications. Firstly, the results of empirical studies to more accurately derive
43 530 single estimates of the BH-LHIs and to develop correlative techniques for estimating
44 531 individual life history parameters (e.g. Pauly, 1980; Gislsson *et al.*, 2010), will be
45 532 strongly influenced by the sample of species included in those studies We suspect that

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8 533 many of these studies are implicitly (and unintentionally) biased against the inclusion of
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10 534 low M/k species. Noting the inherently lower productivity of low M/k species, these
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12 535 species are expected to be more prone to early depletion in poorly managed systems, and
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14 536 less likely to sustain large, valuable fisheries (and thus research programs) in well
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16 537 managed systems. This could well have resulted in low M/k species being under-
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18 538 represented in meta-analyses, especially if those studies have an implicit (and perhaps
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20 539 unavoidable) focus on research from regions with long histories of heavy exploitation,
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22 540 such as the North Sea, Atlantic and South-east Asia (Costello *et al.*, 2012). This might
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24 541 explain the apparent conflict between the Pauly (1980) technique and our meta-analysis
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26 542 (Figure 5). Being mainly based in Australia which has a relatively recent history of
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28 543 fishing and a strong history of research, we had ready access to recent research conducted
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30 544 in lightly exploited regions of Australia, and found numerous studies documenting small
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32 545 bodied low M/k teleost species, which were, apparently, not as well represented in
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34 546 Pauly's (1980) analysis. In this context, the quest to more accurately estimate unique
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36 547 values for the BH-LHI looks somewhat misguided, unless narrowed carefully on
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38 548 taxonomic grounds, as were the original studies of Beverton and Holt (1959), and
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40 549 Beverton (1963).

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42 550 Another significant implication of our observation that the BH-LHI define a unique
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44 551 'median' form of the relationships between size, age and SPR observed in nature, is that
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46 552 existing stock assessments, using some derivation of the assumption that $M/k \sim 1.5$, are
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48 553 implicitly over-estimating the productivity of stocks with $M/k < 1.5$. This could amount
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50 554 to a serious systematic bias for our field as such techniques are commonly used with
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52 555 long-lived species where the depletion of the older age classes through fishing is thought

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8 556 to have rendered the estimation of M with aging studies unreliable. Species with $M/k <$
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10 557 1.0 are most prone to having the older adult classes depleted through fishing, and are
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12 558 consequently, more likely to have had a technique based on $M/k \sim 1.5$ applied to them.
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14 559 Even without extending this meta-analysis rigorously down to the level of families,
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16 560 assessments that have used the assumption of $M/k \sim 1.5$ could be improved [using the](#)
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18 561 three Types of species [we defined here](#) on the basis of life-history strategies and forms of
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20 562 growth.

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564 Conclusions

565 This meta-analysis suggests that the so-called Beverton-Holt Life History Invariants are
566 actually co-variants, varying together in relation to life history strategies and [defining a](#)
567 [range of relationships between size, age and reproductive output](#). From our study, and
568 those that precede us, it appears that the BH-LHI only tend towards relative invariance
569 within groups of species sharing similar life-history strategies, reflecting the stage at
570 which [differing](#) life-history strategy transfers energy from allometric growth to
571 reproduction ([Charnov 2008; Charnov et al. 2013](#)). We believe this conceptualization of
572 BH-LHI has potential to provide a theoretical framework for ‘borrowing’ knowledge
573 from well-studied species for application to related unstudied stocks, and [that](#) together
574 with Hordyk *et al.* (this issue a, b) [this may](#) make it possible to assess many otherwise
575 data-poor species from simple size studies.

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9

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11
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13
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15
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17
18 582 part of AH's doctoral dissertation at Murdoch University.
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45 692 **Figure & Table Legends**

46
47 693 Table 1. Synopsis of the taxa and species in this meta-analysis summarizing the range of
48 parameters used for each species group. M = natural mortality; k = von Bertalanffy
49 growth parameter; L_m = length at maturity; L_∞ = asymptotic length; max. = maximum.
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10 697 Figure 1.
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12 698 Observed relationships for 123 selected marine species between Spawning Potential
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14 699 Ratio (*SPR*) and (a) standardised weight ($\text{weight}_{\text{max}}=1.0$), (b) standardised length
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16 700 ($\text{length}_{\text{max}}=1.0$), (c) standardised age ($\text{age}_{\text{max}}=1.0$), and (d) weight standardized for size of
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18 701 maturity ($\text{weight}_{\text{m}}=0$) and maximum weight ($\text{weight}_{\text{max}} = 1.0$). Green lines denote species
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20 702 with indeterminate growth and $M/k > 1.0$; blue lines denote species with indeterminate
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22 703 growth and $M/k < 1.0$; red lines denote species with determinate growth & $M/k < 1.0$;
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24 704 black lines show the relationship for species conforming with BH-LHI; $M/k = 1.5$,
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26 705 $L_m/L_\infty = 0.66$ and $M \times \text{Age}_m = 1.65$.

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31 707 Figure 2
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33 708 Simulated length frequency histograms illustrating how the size compositions of unfished
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35 709 populations are determined by the M/k ratio for a species'. The range of M/k ratios (0.1 to
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37 710 4.0) chosen for simulating these histograms was based on the range of ratios observed in
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39 711 the meta-analysis of 123 species. Top row: $M/k = 4.0, 1.65, 1.0$. Middle row: $M/k = 0.8,$
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41 712 $0.6, 0.4$. Bottom row: $M/k = 0.3, 0.2, 0.1$. Shading indicates the proportion of the mature,
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43 713 adults in the population, assuming $L_m/L_\infty = 3/(3 + M/k)$, as derived from Beverton (1992).

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47 715 Figure 3
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49 716 The relationship between relative length of maturity (L_m/L_∞) in (a) the 123 marine species
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51 717 selected for this meta-analysis; and (b) nine teleost families with more than three species

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8 718 plotted against the M/k for each species. In a), green points denote species with
9 719 indeterminate growth and $M/k > 1.0$; blue points indeterminate growth and $M/k < 1.0$; red
10 720 points determinate growth and $M/k < 1.0$. The solid black lines plot the Beverton (1992)
11 721 relationship; $L_m/L_\infty = 3/(3 + M/k)$. The dashed and dotted lines, respectively show the
12 722 relationships $L_m/L_\infty = 2.5/(2.5 + M/k)$ and $L_m/L_\infty = 3.5/(3.5 + M/k)$.
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20 724 Figure 4

21 725 Observed relationships between Spawning Potential Ratio (SPR) and (a) standardised
22 726 weight ($weight_{max}=1.0$), (b) standardised length ($length_{max}=1.0$), (c) standardised age
23 727 ($age_{max}=1.0$) for the three most numerous teleost families in our meta-analysis; Gobiidae,
24 728 $n=5$, green; Lethrinidae, $n=10$, red; Acanthuridae, $n=7$, blue. The broken black line show
25 729 the BH-LHI relationships; $M/k = 1.5$, $L_m/L_\infty = 0.66$, and $M \times Age_m = 1.65$.
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33 731 Figure 5

34 732 The relationship between asymptotic length (L_∞) and M/k for a) 109 marine species in our
35 733 database with $L_\infty \leq 200$ cm and b) nine teleost families with more than three species, for
36 734 those species with asymptotic size ≤ 200 cm. Coloured lines show the relationships
37 735 estimated from Pauly's (1980) equation assuming the range of k observed in this meta-
38 736 analysis (0.1 – 1.0) and an ambient temperature of 15°C.
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