ICES Journal of
Marine Science

Revisiting the concept of Beverton – Holt life-history invariants with the aim of informing data-poor fisheries assessment

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The complexity and cost of assessment techniques prohibits their application to 90% of fisheries. Simple generic approaches are needed for the world's small-scale and data-poor fisheries. This meta-analysis of the relationship between spawning potential and the normalized size and age of 123 marine species suggests that the so-called Beverton – Holt life-history invariants (BH-LHI; L_m/L_∞, M/k, $M \times Age_m$) actually vary together in relation to life-history strategy, determining the relationship between size, age, and reproductive potential for each species. Although little realized, the common assumption of unique values for the BH-LHI also implies that all species share the same relationship between size, age, and reproductive potential. This implicit assumption is not supported by this meta-analysis, which suggests that there is considerable but predictable natural variation in the BH-LHI ratios and the relationships between size, age, and reproductive potential that they determine. We believe that this reconceptualization of the BH-LHI has potential to provide a theoretical framework for "borrowing" knowledge from well-studied species to apply to related, unstudied species and populations, and when applied together with the assessment technique described by Hordyk et al. (this issue b), could make simple forms of size-based assessment possible for many currently unassessable fish stocks.

Keywords: Beverton – Holt life-history invariant, data-poor assessment, parameter estimation.

Introduction

A persistent challenge for sustainable fisheries is the scale, complexity, and cost of fishery assessment (Walters and Pearse, 1996; Beddington and Kirkwood, 2005; Hilborn et al., 2005; Mullon et al., 2005). Current assessment techniques require technical expertise, detailed biological knowledge, and time-series data on catch, effort, and/or surveyed abundance (Walters and Martell, 2004) resulting in an annual cost of $US50 000 to million of dollars per stock (Pauly, 2013). This represents a substantial impediment to assessing small-scale, spatially complex and developing-world fisheries (Mahon, 1997). By some estimates, 90% of the world's fisheries, which directly support 14 – 40 million fishers and indirectly support ~200 million people, are unassessable using current methods (Andrew et al., 2007).

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

The correlation between biological parameters across species has been widely used to provide generic parameter estimates necessary for assessment modelling (Charnov, 1993) and were first described in fisheries by Beverton and Holt (1959) for the clupeid and engraulid (herring and anchovy-like bony fish) stocks of the North Sea (Beverton, 1963). They observed correlations between: (i) the instantaneous natural mortality rate (M) and the von Bertalanffy

(1938) growth rate constant (k), (ii) length at maturity (L_m) and asymptotic length (L_∞), and (iii) M and the age of maturity (T_m). Beverton and Holt's primary interest was in estimating M, a parameter that is notoriously difficult to measure, from studies of k, L_m, and T_m, which by comparison, are easily estimated. Although neither Beverton nor Holt used the term, these three life-history ratios (M/k, L_m/L_∞, and $M \times Age_m$) are now commonly referred to as the Beverton–Holt life-history invariants (BH-LHIs). Widely considered to be environmentally influenced constants (Pauly, 1980), the BH-LHIs have been used extensively to parameterize fisheries models (Charnov, 1993; Beddington and Kirkwood, 2005; Gislason *et al.*, 2010). In this study, we use Jensen's (1996) definition of the three BH-LHIs: $M/k = 1.5$, $L_m/L_\infty = 0.66$, and $M \times T_m = 1.65$.

The spawning potential ratio, or spawning per recruit (SPR), is a commonly used index of the relative rate of reproduction (Mace and Sissenwine, 1993; Walters and Martell, 2004) in an exploited stock. Brooks *et al.* (2010) recommend its utility for applying to stocks in data-limited fisheries. The SPR is defined as the proportion of the unfished reproductive potential left by any given level of fishing pressure. It can be conceptualized as the total reproductive potential of all the cohorts in a population at equilibrium, or the lifetime reproductive potential of an average individual passing through a population at equilibrium. By definition, unfished stocks and individuals in an unfished stock have an SPR of 100% ($SPR_{100\%}$) and fishing mortality reduces $SPR_{100\%}$ from the unfished level to $SPR_{X\%}$. Shepherd (1982) used the SPR concept to integrate the separate approaches to fisheries modelling that had developed on opposite sides of the North Atlantic during the 1970s. Generic SPR-based reference points have been developed theoretically through the meta-analysis of quantitatively assessed fisheries and have been recognized in international fisheries law (Restrepo and Powers, 1999; Australian Government, 2007), e.g. ~$SPR_{40\%}$ is generally considered a conservative proxy for maximum sustainable yield (Mace and Sissenwine, 1993; Clark, 2002; Walters and Martell, 2004). Until recently, estimating SPR has required unique population models to be parameterized for each stock using estimates of natural mortality, growth, reproduction, and time-series of abundance or age composition data (e.g. Ault *et al.*, 1998; Walters and Martell, 2004).

This study and the accompanying studies of Hordyk *et al.* (this issue a, b) arose from our interest in developing a simple method for using size composition data to evaluate the SPR of exploited populations (Prince *et al.*, 2008, 2011). Prince *et al.* (2008) observed that the spatial variability of size of maturity in Haliotid populations could be gauged from the shape and appearance of their shells, and that qualitative evaluations of a population's spawning potential can be made based on size composition relative to the visually evaluated size of maturity. This current collection of studies was prompted by a journal editor asking, how the finding of Prince *et al.* (2008) applied to other species? And our research began by addressing the question do all species exhibit the same relationship between size of maturity, relative size composition, and SPR? To this end, we began with the empirical and descriptive study described here, of how SPR relates to the size of maturity, relative body size, and age in 123 species of teleosts, chondrichthyans, invertebrates, and marine mammals. The results presented here suggested to us that there are predictable patterns in life-history ratios M/k and L_m/L_∞ which are related to each species' life-history strategy, unfished size compositions, and the distribution of spawning potential by size. Exploring these results more rigorously Hordyk *et al.* (this issue a) demonstrates that it is the life-history ratios of M/k and

L_m/L_∞ together with F/M that determine the shape of size compositions and the SPR of populations, rather than the individual parameter values as generally assumed. On this basis, Hordyk *et al.* (this issue b) developed and tested a new approach to size-based assessment, which we believe may have great application to data-poor assessment. Returning to the empirical observations made in this study, we postulate that extending our meta-analysis of well-studied species could make it possible to predict characteristic life-history ratios of most exploited populations based on general knowledge of each species life-history strategy, and so make simple size-based assessments possible for many stocks currently considered too data-poor to assess.

Material and methods
Selection of parameter sets
For our meta-analysis, we collected studies of marine and estuarine species for which we could find robust estimates of growth, natural mortality, age/size of maturity or fecundity at age/size, and length–weight relationships. To control the quality of the parameter sets, we applied strict selection criteria. Rather than developing our own criteria *de novo*, we based our criteria on the six criteria developed by Gislason *et al.* (2010), which they define as:

(i) Estimates were rejected if they had been derived from empirical relationships (e.g. Beverton and Holt, 1959; Pauly, 1980) or "borrowed" from studies of similar species.

(ii) Estimates by size or age were rejected if they had been derived from multispecies modelling.

(iii) Parameters were rejected if they were based on an insufficient amount of data, if the authors expressed concern that they could be biased or uncertain, or if the sampling gears and/or procedures for working up the samples were likely to have biased the estimates.

(iv) Estimates of total mortality based on catch-at-length or catch-at-age were accepted as estimates of M, only if the data had been collected from an unexploited or lightly exploited stock over a sufficiently long period to ensure that they reflected mortality and not simply differences in year-class strength, and if growth parameters or ageing methods were considered appropriate.

(v) Estimates derived from tagging data were included only if the following factors had been considered: mortality associated with the tagging operation, tag loss, differences in mortality experienced by tagged and untagged fish, migration out of the study area, and uncertainty regarding tag recovery.

(vi) Estimates derived from regressions of total mortality and effort were included, only if it was credible that total fishing mortality would be proportional to the measure of fishing effort considered, and if extrapolation did not result in excessively large confidence intervals.

While Gislason *et al.*'s focus was solely on ensuring the quality of natural mortality estimates, we found that where other aspects of biology had been studied, these criteria also ensured the quality of estimates for the broader list of parameters of interest to this study (i.e. growth, age/size of maturity or fecundity at age/size, and length weight relationships). To ensure that each species' parameter set described a single population and a similar population density, we also applied a seventh criterion, which we defined as:

(vii) All parameter estimates for a species should be from the same geographic population and from the same period.

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

It should be noted that these criteria biased our selection process towards well-studied populations before or during the early phase of exploitation. Thus, almost all the studies included in our database are of lightly exploited populations. We do not believe our sample is representative of all, or even groups of, marine species. For this reason, we have not attempted to apply statistical techniques of analysis, as we have no expectation that our samples are distributed normally or are representative of any mean condition, parameter value, or relationships. As discussed below, we do not believe such statistical concepts are applicable to a study such as this. In this study, our aim was entirely qualitative, to look for, and to describe patterns of variation that exist in nature. For the quantitative analysis of the patterns we observed, the reader is directed to the accompanying theoretical study of Hordyk *et al.* (this issue a).

SPR model for meta-analysis

We modelled the SPR achieved at any given age for the 123 species to examine patterns in the relationships between age, length, weight, and reproductive output. The SPR is usually calculated by summing the total reproductive output of all age classes and dividing by the number of recruits to obtain a general measure of current rate of reproductive output in relation to the maximum potential reproductive output, i.e. the unfished level. However, here, we are interested in calculating the cumulative percentage of total lifetime reproductive output achieved when an individual reaches each age/size, and how that varies across the widest possible range of marine species. For this purpose, we developed an age-based equilibrium SPR model for each species with an initial cohort size of 1000. The number of survivors, average individual length and weight, and percentage of the total index of reproductive output (expressed variously for the differing species as eggs, pups, calves, or simply mature biomass) achieved for both individuals and cohorts at each successive time-step was calculated. To enable comparisons across species with varying lifespans, sizes, and forms of reproductive output, all were normalized with respect to their maximum value. The maximum age class (t_{max}) was determined to be the first age class with an abundance of $\leq 1\%$ of the initial cohort size (i.e. ≤ 10 individuals), and maximum length (L_{max}), weight (W_{max}), and reproductive output (EP_{max}) were defined as the value estimated for that age class. This is consistent with the results of empirical studies of Hewitt and Hoenig (2005) who note that a range of 1−5% has generally been used to estimating M, and who conclude that 1.5% is most appropriate. In this range, we tested a number of values and found it had little effect on our results.

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

$$N_{t+1} = N_t e^{-M}, \tag{1}$$

where N_t is the number of age t individuals, M the natural mortality, and N_0 is 1000. Reproductive output (EP) was estimated at each age t as:

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

where f_t is the mean fecundity at age t. The cumulative SPR was calculated for each age class t:

$$SPR_t = \frac{\Sigma_{t=0}^{t} EP_t}{\Sigma_{t=0}^{t_{max}} EP_t}, \tag{3}$$

where SPR_t is the proportion of potential lifetime reproductive output achieved at age t. When no fecundity data were available, the reproductive output of a mature age class was assumed proportional to biomass:

$$EP_t = N_t W_t m_t, \tag{4}$$

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

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

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

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

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

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

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

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

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

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

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

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

where α, β, and φ are the constants.

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

$$W_t = aL_t^b, \tag{10}$$

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

$$W_t = a - bL_t + cL_t^2, \tag{11}$$

where a, b, and c are the constants.

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

Where sexual dimorphism was recorded only female parameters were used in the SPR model developed for the species. Our database includes several hermaphroditic species; for these species, the maturity ogive was defined as female maturation ogive, and if occurring after the female stage (which is generally the case), the male stage was considered to contribute to the reproductive potential of the population, and for SPR modelling treated as a continuation of the female phase.

Simulation of length composition

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

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

Results

Figure 1a–d shows the modelled SPR for every species in our meta-analysis as functions of (i) normalized weight (W/W_{max}), (ii) normalized length (L/L_{max}), and (iii) normalized age (t/t_{max}). As described in the methods, W_{max}, L_{max}, and t_{max} are defined as the value attained when modelled cohort abundance declines to ≤1% of initial abundance. In Figure 1d, we standardize the SPR-at-weight trajectories (Figure 1a) with respect to both weight-at-maturity and maximum weight $[(W - W_m)/(W_{max} - W_m)]$ making it evident that much of the crossing of trajectories observed in Figure 1a and b is due to variation in size of maturity. The spectrum of curves observed in Figure 1a–d appears to be determined by the range of M/k ratios observed in our meta-analysis; species with the greatest ratio ($M/k = 3.5$) have trajectories in the upper left of Figure 1a and b, and those with the lowest ratios ($M/k = 0.1$) have trajectories in the bottom right, and this empirical observation is confirmed theoretically by Hordyk *et al.* (this issue a).

Also plotted in Figure 1a–d (black lines) are the relationships expected for species with biological parameters conforming to Jensen's (1996) estimates of the three BH-LHIs ($M/k = 1.5$, $L_m/L_\infty = 0.66$, and $M \times Age_m = 1.65$), and the assumption that reproductive output is proportional to mature weight, which in turn is a cubic function of length. From this, we conclude that the three BH-LHIs proscribe a unique relationship between normalized size, age, and SPR; however, the BH-LHI relationship is apparently a "median" form of the relationships we observe across all 123 species in our meta-analysis rather than an invariant relationship that is applicable to many species as we expected originally might be the case.

As demonstrated by Hordyk *et al.* (this issue a) and illustrated by simulation in Figure 2, the M/k ratio determines the relative shape of
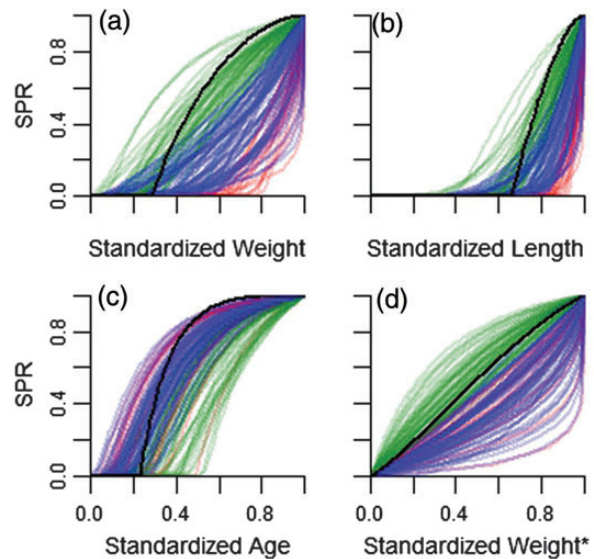

Figure 1. Observed relationships for 123 selected marine species between SPR and (a) standardized weight (W/W_{max}), (b) standardized length (L/L_{max}), (c) standardized age (t/t_{max}), and (d) weight standardized for size of maturity and maximum weight ($W - W_m$)/($W_{max} - W_m$). Green lines denote species with indeterminate growth and $M/k > 1.0$; blue lines denote species with indeterminate growth and $M/k < 1.0$; red lines denote species with determinate growth and $M/k < 1.0$; black lines show the relationship for species conforming with BH-LHI; $M/k = 1.5$, $L_m/L_\infty = 0.66$, and $M \times Age_m = 1.65$.

a population's unfished size composition. Here, we note again our use of the simplifying assumption that M remains constant over the all age and size classes in a population, and the influence that this assumption has on the shape of these simulated size compositions. However, using the rationale of Charnov *et al.* (2013) that adult mortality rates are more likely to tend towards a level of consistency and determine lifetime reproductive output, we observe that unfished populations with $M/k > 1.0$ do not tend to exhibit an adult modal size (Figure 2). This is because adults grow and die too rapidly to accumulate around a species' asymptotic size (Hordyk *et al.*, this issue a). This contrasts with unfished populations of species with $M/k < 1.0$ (Hordyk *et al.*, this issue a) in which adults grow relatively slowly and persist long enough to accumulate around an asymptotic size so that a modal adult size becomes observable, and increasingly prominent as M/k declines (Figure 2).

To assist in our description of the variation we observed around the BH-LHI relationship between normalized size, age, and SPR, we

categorized the species in our meta-analysis with respect to $M/k =$ 1.0, and whether their growth is determinate or indeterminate. Species with indeterminate growth continue growing throughout adult life, although slowing to some extent with increasing size, while species with determinate growth do not grow as adults. These two criteria defined three broad groups or "types" of species in our meta-analysis; Type I, $M/k > 1.0$ and indeterminate growth; Type II, $M/k < 1.0$ and indeterminate growth; Type III, $M/k < 1.0$ and determinate growth (Figure 1). No species with $M/k > 1.0$ and determinate growth were observed in our meta-analysis (see also Hordyk *et al.*, this issue a).

In all, 49 Type I species (green lines) were identified, including 34 teleosts, 10 chondrichthyes, 3 crustaceans, and 2 molluscs. Their trajectories occupy the upper left hand side of Figure 1a−c and the lower right of Figure 1d. Type I species conform to the general shape of the BH-LHI trajectories and have a slightly higher average M/k (1.95, cf. 1.5; Table 1) but slightly lower average $L_{\mathrm{m}}/L_{\infty}$ (0.55,
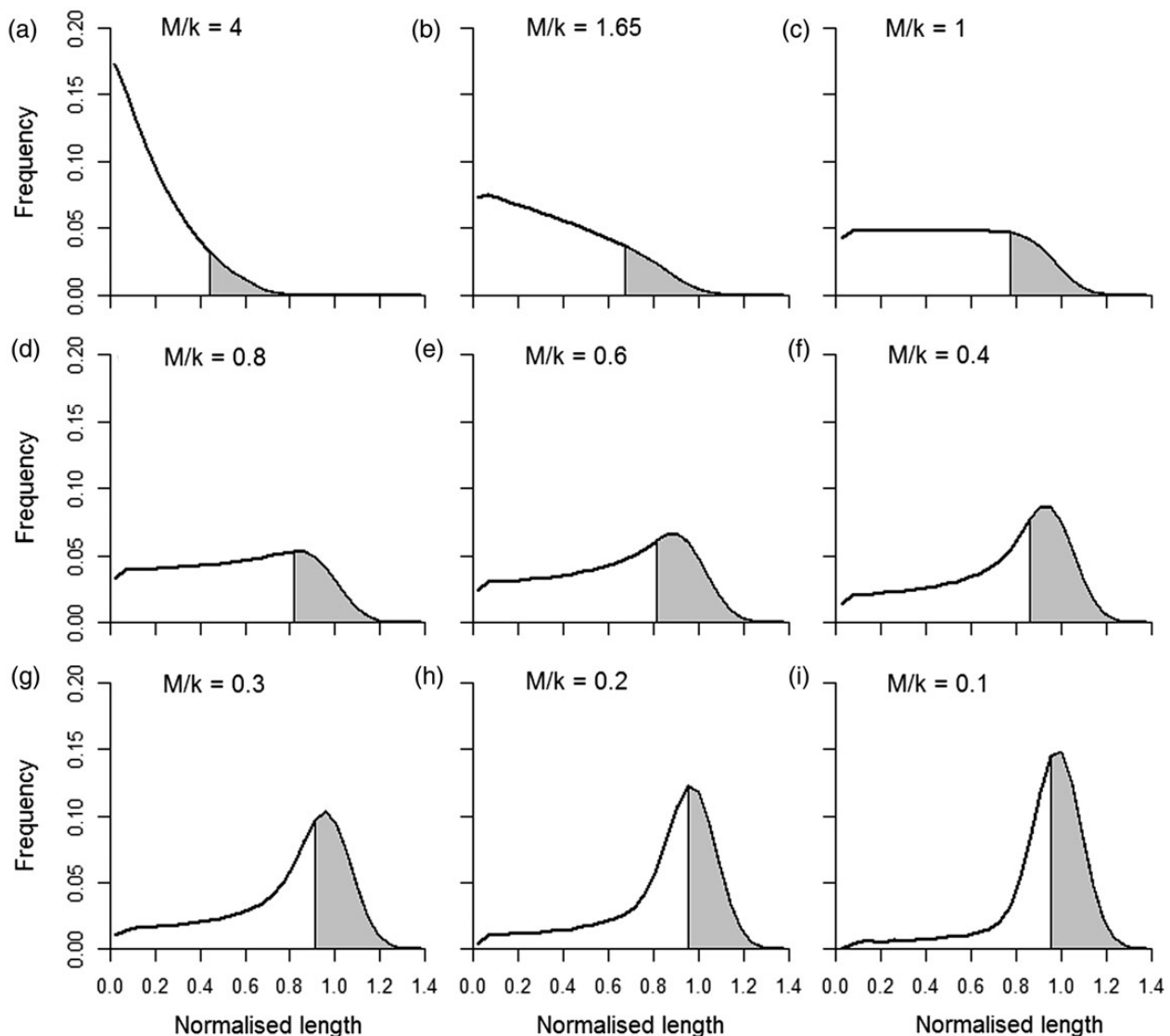

Figure 2. Simulated length frequency histograms illustrating how the size compositions of unfished populations are determined by the M/k ratio for a species. The range of M/k ratios (0.1−4.0) chosen for simulating these histograms was based on the range of ratios observed in the meta-analysis of 123 species. Top row: $M/k = 4.0, 1.65, 1.0$. Middle row: $M/k = 0.8, 0.6, 0.4$. Bottom row: $M/k = 0.3, 0.2, 0.1$. Shading indicates the proportion of the mature, adults in the population, assuming $L_{\mathrm{m}}/L_{\infty} = 3/(3 + M/k)$, as derived from Beverton (1992).

cf. 0.65; Table 1) than those for the BH-LHI. They begin reproduction at relatively small sizes (Figure 1a and b) but at a relatively later stage of their life cycle (Figure 1c) than Types II and III. Unfished Type I populations are numerically dominated by juvenile length classes and do not exhibit an adult modal size (Figure 2; top panels). Most (60–80%) of the reproductive potential in these populations comes from smaller individuals that are <80% of their asymptotic size (Figure 1a and b).

A diverse range of species comprise the Type I category, including coastal bivalves *Gari solida*, *Semele solida*, a crab *Callinectes sapidus*, two spiny lobsters *Panulirus argus* and *P. ornatus*, several carcharhinid *Carcharhinus obscurus* and *C. plumbeus* and triakid sharks, *Mustelus antarcticus* and *Prionace glauca*, and teleosts ranging from low trophic level species such as *Scomber japonicus* and *Cololabis saira* and the clupeid *Brevoortia patronus* to higher trophic level species, such as the rockfish *Sebastes chlorostictus*, *S. melanonstomus* and two apex piscivores, the scombrid tuna *Thunnus alalunga*, and *T. tonggol*.

Type II species (blue curves on Figure 1) are shifted to the right of Type I species in Figure 1a and b and to the left in Figure 1c. They share the indeterminate growth pattern of Type I species. Type III species (red) grow to a determinant asymptotic adult size and reproduce without further growth. Their trajectories are shifted to the extreme right in Figure 1a and b and the extreme left in Figure 1c. The 74 Type II and III species share lower M/k ratios than Type I species (mean = 0.62, cf. 1.95; Table 1). In contrast to Type I species, Type II and III species do not reproduce until growth is almost complete; Type II species produce ∼70% of their SPR at sizes >80% of the asymptotic size, whereas Type III species produce 90% of SPR at sizes >80% of asymptotic size (Figure 1). Unfished populations of Type II and III species are dominated by adult size classes and exhibit distinct adult modes that become more pronounced with lower M/k ratios (Figure 2; middle and lower panels).

The Type II species (blue) form a middle group of 59 species (45 teleosts, 1 elasmobranch, 5 crustaceans, and 8 molluscs) with average L_m/L_∞ similar to the BH-LHI ratio (0.69, cf. 0.66; Table 1), but a lower average M/k than the BH-LHI ratio (0.62, cf. 1.5; Table 1). Type II species include crustaceans, *Nephrops norvegicus*, all the prawns (=shrimp) in our analysis, *Penaeus indicus*, *P. latisulcatus*, and *P. merguiensis*, all three haliotid gastropods *Haliotis rubra*, *H. laevigata*, and *H. iris*, a carcharhinid shark *Rhizoprionodon taylori*, and a range of teleosts including flat-forms

Pleuronectes platessa and *Psettichthys melanostictus*, tropical snappers *Lutjanus malabaricus*, *L. carponotatus*, *L. argentimaculatus*, and the long-lived orange roughy *Hoplostethus atlanticus*.

The 15 Type III species (red) exhibit trajectories that balloon into the bottom right of Figure 1a and b. These species reach maturity (Figure 1c) and a determinant asymptotic size (Figure 1a and b) relatively early in life. Type III species have the largest average L_m/L_∞ ratio (0.88; Table 1) and the lowest average M/k ratio (0.57; Table 1). Besides the five marine mammals in our database, Type III species include two triakid sharks *Galeorhinus galeus* and *Furgaleus macki*, eight teleosts, including the long-lived *Scorpis aequipinnis*, and two short-lived Lethrinidae species.

In Figure 3a, the L_m/L_∞ of each species in our analysis is plotted as a function of M/k. The solid black line $[L_m/L_\infty = 3/(3 + M/k)]$ is derived from Beverton (1992) and Hordyk *et al.* (this issue a), but is originally from Holt (1958) who used this equation to demonstrate that size at maximum biomass ($L_{opt.}$) can be estimated from the ratio of M/k. Many empirical studies observe that length at maturity (L_m) coincides with L_{opt} and various theoretical studies postulate that this is because the evolutionary fitness of a species is maximized by this coincidence (Fryer and Iles, 1972; Roff, 1984; Beverton, 1992). The factor of "3" used in this equation comes from the assumption that weight is proportional to L^3. The dashed and dotted lines plotted in Figure 3 indicate alternative relationships obtained by substituting factors of 2.5 or 3.5 into this equation, which would be equivalent to assuming weight and fecundity are proportional to $L^{2.5}$ and $L^{3.5}$, respectively. These alternative relationships are plotted to provide some scaling of variance around the relationship.

Very few of the species in our meta-analysis fall above the Beverton (1992) curve for the relationship between M/k and L_m/L_∞; most of the outliers are below (Figure 3a). This is primarily because our meta-analysis encompasses all marine species, some of which have fixed rates of reproduction, whereas Beverton (1992) worked almost entirely with teleosts for which fecundity is normally more closely related to adult body size. In Figure 3b, the relationship between M/k and L_m/L_∞ is plotted for the nine teleost families with three or more species in our database and these conform much more closely to the Beverton (1992) relationship (Figure 3b).

In Figure 3b, there is the suggestion that species within families tend to group together on the M/k and L_m/L_∞ spectrum, which

Table 1. Synopsis of the taxa and species in this meta-analysis summarizing the range of parameters used for each species group.

Taxa	# Families	# Species	Max. age (years)	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)

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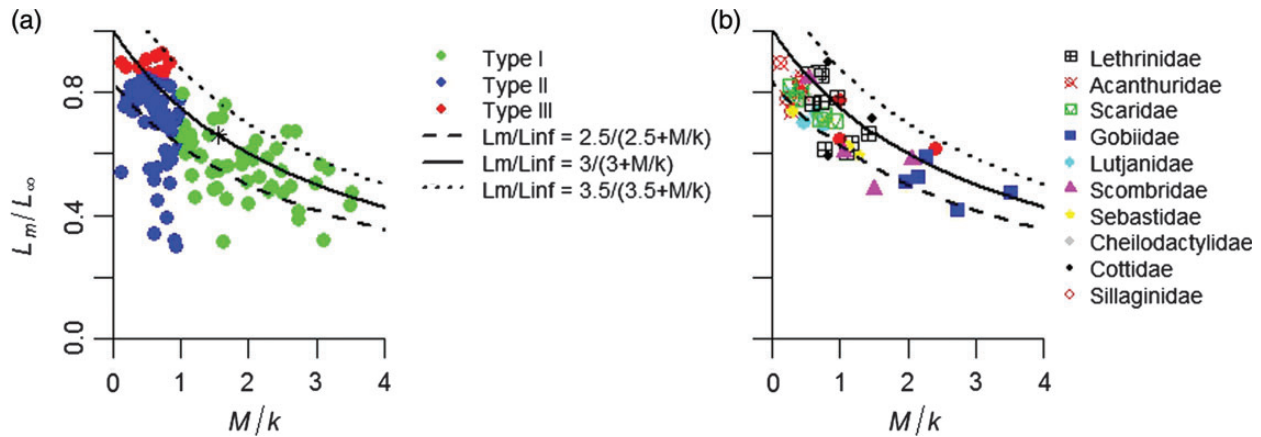
Figure 3. The relationship between relative length of maturity (L_m/L_∞) in (a) the 123 marine species selected for this meta-analysis; and (b) nine teleost families with more than three species plotted against the M/k for each species. In (a), green points denote species with indeterminate growth and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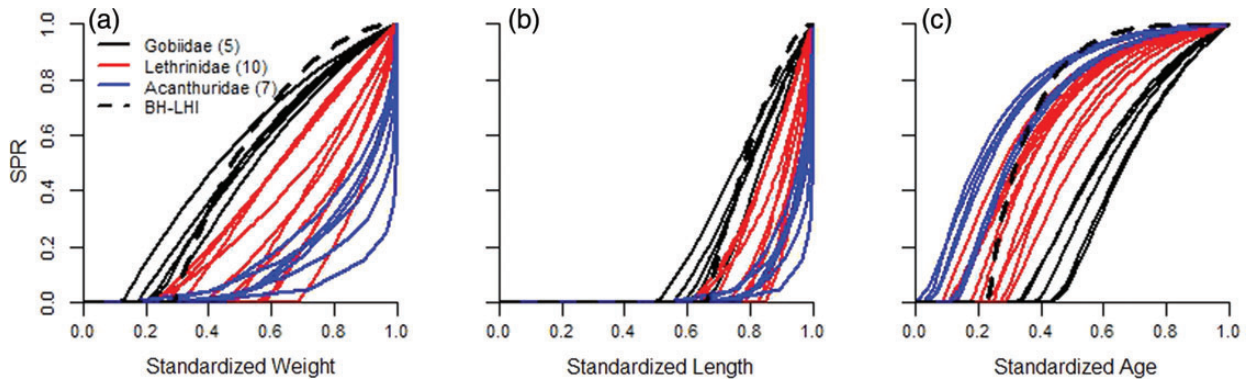

Figure 4. Observed relationships between SPR and (a) standardized weight (W/W_{max}), (b) standardized length (L/L_{max}), (c) standardized age (t/t_{max}) for the three most many teleost families in our meta-analysis; Gobiidae, $n = 5$, green; Lethrinidae, $n = 10$, red; Acanthuridae, $n = 7$, blue. The broken black line show the BH-LHI relationships; $M/k = 1.5$, $L_m/L_\infty = 0.66$, and $M \times Age_m = 1.65$.

in Figure 4 is shown with our three most numerous families to result in their SPR at size and age trajectories grouping into distinctive family bands. Comparison with the plotted BH-LHI trajectories (Figure 4, broken black line) shows that to some extent the BH-LHI relationship describes the weight and length trajectories of the Gobiidae in our study, but not their SPR at age relationship. The BH-LHI relationship overestimates the productivity of the Lethrinidae and Acanthuridae, by suggesting higher than observed SPR at lower sizes for those families, while describing a relationship between SPR and relative age that is intermediate between the Lethrinidae and Acanthuridae relationships in our analysis.

We also examined the predictive power of Pauly's (1980) equation for estimating M empirically by comparing the M/k and L_m/L_∞ ratios of species in our meta-analysis with those derived from Pauly's (1980) equation (Figure 5). The relationship between M/k and L_∞ is plotted for the 109 species in our database with $L_\infty \leq 200$ cm, which excludes marine mammals and large sharks (Figure 5a). The solid lines indicate the estimates of M/k that would be derived using the Pauly equation across the range of k values we observed. The Pauly equation requires an assumption about ambient temperature. For simplicity, we assume $15°C$ but

sensitivity analyses showed that increasing the assumed temperature only raised the plotted lines minimally. The Pauly equation generally produces estimates of $M/k > 1$, especially for species with $L_\infty < 50$ cm. Our database includes a considerable number of teleosts with $L_\infty < 50$ cm and $M/k < 1$, for which the Pauly equation over-estimates M. This pattern is maintained even when the analysis is restricted to the teleost families with three or more species (Figure 5b).

Discussion

In fisheries science, the three BH-LHIs are most commonly used separately to estimate individual parameters for population modelling; generally, they are only linked within studies seeking to relate evolutionary fitness and metabolic parameters to the optimization of life histories (e.g. Jensen, 1997; Charnov et al., 2013). We believe our combination of them to reveal that they imply a unique generalized relationship between normalized size, age, and SPR is relatively novel. Our meta-analysis suggests that rather than approximating some unique relationship between size, age, and reproductive potential that is broadly applicable across species, the BH-LHIs estimate some form of the "median"
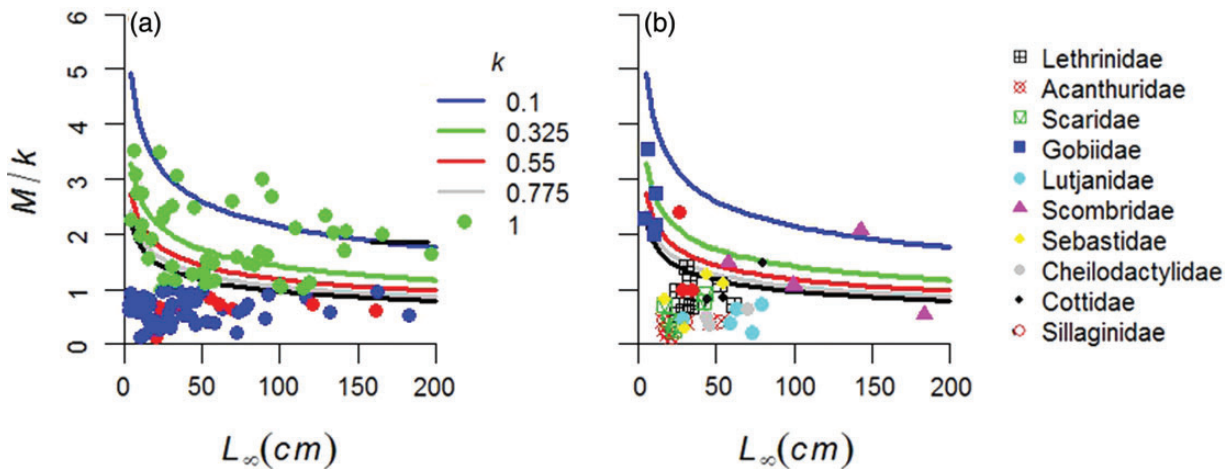
Figure 5. The relationship between asymptotic length (L_∞) and M/k for (a) 109 marine species in our database with $L_\infty \leq 200$ cm and (b) nine teleost families with more than three species. Coloured lines show the relationships estimated from Pauly's (1980) equation assuming the range of *k* observed in this meta-analysis (0.1 – 1.0) and an ambient temperature of 15°C.

relationship for the 123 species in our meta-analysis (Figure 1) that is not necessarily found in any species.

The first formulations of BH-LHI (Beverton and Holt, 1959; Beverton, 1963) were based on North Sea teleosts (clupeids and engraulids) that our analysis has classed as Type I species. Since that time fisheries biology has tended to accept, seemingly by default, that the values derived from those initial studies are relatively constant across much broader suites of species, particularly the ratio of M/k of ∼1.5. This was, however, not an assumption ever made by Holt (1958) nor Beverton (1992), who both conceptualized species as displaying a range of M/k values co-varying with L_m/L_∞ (Figure 3), nor by Pauly (1980), who correlated ambient temperature and adult body size with the M/k ratio for each species.

Apparently confirming these earlier studies, the descriptive meta-analysis we present here illustrates the natural variability observed across marine species. We defined three broad types of marine species with characteristic relationship between size, age, and reproductive potential and ratios of M/k and L_m/L_∞. Our intent in doing so is not to imply basic differences or strong boundaries between our rather arbitrary groupings, but to provide an initial indicative categorization to aid our discussion of the phenomena we observe. Our aim here is to (i) illustrate that predictable patterns in size, age, and SPR appear to exist in nature and (ii) postulate that these predictable patterns might provide an alternative theoretical framework for deriving knowledge of unstudied species from studies of related species.

When we apply the classification of teleost life strategies developed by King and McFarlane (2003) or the more generalized "*r* and *K*" theory of Pianka (1970), which characterizes life-history strategies as either (i) "*r*-strategists" with high population turn-over rates, a tendency for boom and bust dynamics, and invasive "weed-like" characteristics or (ii) "*K*-strategists" with relatively stable population dynamics, lower turnover, and adults that reproduce over many breeding cycles. We conclude that our Type I species which mature at relatively small sizes, reproduce for a relatively short and late part of their life cycle, continue growing relatively rapidly as they reproduce, have unfished populations that are dominated by juvenile size classes, and do not exhibit a modal adult size, are opportunist and intermediate strategists (King and McFarlane, 2003) and tend towards being "*r*-strategists" (Pianka, 1970). While Type II and III

species which mature at relatively high sizes, reproduce for a relatively extended part of their life cycle, while growing slowly or not at all, and have unfished populations that exhibit a modal adult size, are typically periodic and equilibrium strategists (King and McFarlane, 2003) and *K*-strategists (Pianka, 1970). From this, we surmize that, for an unstudied stock, general knowledge of a species typical life-history strategy might be used to estimate a likely set of life-history ratios and the likely relationships between size, age, and SPR those ratios proscribe. We propose that the estimations developed in this way for a relatively unstudied stock will be more accurate than existing standard methods for applying the concept of BH-LHI to data-poor stock assessment.

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

The obvious question at this point is; where do phenotypic plasticity, and density-dependent responses to fishing pressure fit into this conceptualization? Do they invalidate this conceptualization of BH-LHI? The short answer is not at all, and although not studied enough now, we believe that these two phenomena are likely to provide the broader context, which will in time fully validate and extend this concept's application. Implicitly because of the selection criteria used, this meta-analysis is basically a study of unfished, or lightly fished, populations and this limits what

can be demonstrated here. In each of the cases we have used, we would expect that the individual parameter estimates used will have changed as the stocks for which they were estimated have been fished down, just as we expect the individual parameters to vary between geographically isolated populations of each species. For *Cheilodactylus spectabilis*, we know this to have occurred as the population was fished down (Ziegler *et al.*, 2007). We are not proposing a new alternative form of invariance within families, species, or stocks. Rather, we are returning to the spirit of the original formulation of this concept by Holt (1958) which was that the physiological constraints of species and families imply that the life-history ratios will remain more stable across geographical distributions and density ranges than the individual life-history parameters, and so for the purpose of data-poor stock assessment the life-history ratios are expected to be more informative and useful than the more variable individual parameters (S. J. Holt, Pers. Comm.). There is a growing body of literature to support this supposition, and in this context, the body of work by Choat on coral reef fish deserves to be highlighted and should be referred to (e.g. Choat and Robertson, 2001; Gust *et al.*, 2002). While the precedence set by fisheries science, and our selection criteria place a strong emphasis on the quality of component estimates of natural mortality, and our sampling of the literature has been strongly biased towards using lightly fished populations for this analysis, we suspect that exploited marine species do not distinguish between whether a seal or a human eats them. Thus, we expect we would reach similar conclusions if we were to broaden our study to use the ratio of Z/k rather than M/k. On this basis, we postulate that for metabolic and evolutionary reasons species respond to changes in total mortality by minimizing changes in their life-history ratios, rather than the parameters themselves, and that this conceptualization of BH-LHIs may be useful for predicting how stocks are likely respond to fishing pressure, and thus, the likely form and magnitude of density-dependence mechanisms for each species.

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

Our observation that the commonly assumed values of the BH-LHIs define a unique "median" form of the SPR-at-size and age relationships observed in nature also has significant implications. First, the results of empirical studies to more accurately derive single estimates of the BH-LHIs and to develop correlative techniques for estimating individual life-history parameters (e.g. Pauly, 1980; Gislason *et al.*, 2010) will be strongly influenced by the sample of species included in those studies. We suspect that many of these studies are implicitly (and unintentionally) biased against the inclusion of low M/k species. Noting the inherently lower productivity of low M/k species, these species are expected to be more prone to early depletion in poorly managed systems, and less likely to sustain large, valuable fisheries (and thus research programmes) in well-managed systems. This could well have resulted in low M/k species being underrepresented in the literature and meta-analyses, especially if those studies have an implicit (and perhaps unavoidable) focus on research from regions with long histories of heavy exploitation, such as the North Sea, Atlantic, and Southeast Asia (Costello *et al.*, 2012). This might explain the apparent conflict between the Pauly (1980) technique and our meta-analysis (Figure 5). Being mainly based in Australia which has a relatively recent history of fishing and a strong history of research, we had ready access to recent research conducted in lightly exploited regions of Australia and found many studies documenting small bodied low M/k teleost species, which were, apparently, not as well represented in Pauly's (1980) analysis. In this context, the quest to more accurately estimate unique values for the BH-LHI looks somewhat misguided, unless narrowed carefully on taxonomic grounds, as were the original studies of Beverton and Holt (1959) and Beverton (1963).

Another significant implication of our observation that the BH-LHIs define a unique "median" form of the relationships between size, age, and SPR observed in nature is that existing stock assessments, using some derivation of the assumption that $M/k \sim 1.5$, are implicitly overestimating the productivity of stocks with $M/k < 1.5$. This could amount to a serious systematic bias for our field as such techniques are commonly used with long-lived species where the depletion of the older age classes through fishing is thought to have rendered the estimation of M with ageing studies unreliable. Species with $M/k < 1.0$ are most prone to having the older adult classes depleted through fishing and are consequently, more likely to have had a technique based on $M/k \sim 1.5$ applied to them. Even without extending this meta-analysis rigorously down to the level of families, assessments that have used the assumption of $M/k \sim 1.5$ could be improved using the three Types of species we defined here based on life-history strategies and forms of growth.

Conclusions

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

Acknowledgements

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Handling editor: Shijie Zhou