

A generic solution to the assessment of small-scale and data-poor fisheries.

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Summary

1. The complexity and cost of existing fishery assessment techniques prohibits their application to 90% of fisheries globally. Simple, cost-effective, generic approaches are needed for small-scale and data-poor fisheries that support the majority of the world's fishing communities but cannot currently be quantitatively assessed.
2. This paper synthesises and extends a body of existing fisheries theory to derive a new basis for size-based assessment of spawning potential using minimal information.
3. The relationships between spawning potential and normalized size in 123 marine species selected for meta-analysis conformed closely to theoretically derived relationships, making apparent poorly recognized relationships between the three Beverton-Holt Life History Invariants.
4. Primarily used individually to estimate poorly studied parameters for population modeling, the so-called 'Invariants' (L_m/L_∞ , M/k , $M \times Age_m$) actually vary together according to each species' life history strategy, reflecting the stage at which energy is transferred from somatic growth into reproduction and determining population size structure.
5. Species and groups of species with similar life history strategies share typical ratios of M/k and L_m/L_∞ and their populations have similar relative size compositions. Characterising the typical ratios of species' makes it possible to assess spawning potential directly from simple size studies.

6. *Synthesis and Applications:* In the absence of the detailed biological studies, time series abundance data and age based assessment modeling required by current fisheries assessment techniques, this study makes it possible to assess fisheries using generic knowledge of a species' life history strategy and, data on size of maturity and size composition. Requiring only the two simplest cheapest forms of data required by current techniques this approach makes assessment possible in many fisheries where low value, small scale and/or lack of institutional capacity previously prevented assessments.

Introduction

A persistent challenge for sustainable fisheries is the scale, complexity and cost of fishery assessment (Walters & Pearse 1996; Hilborn *et al.* 2005; Beddington & Kirkwood 2005; Mullon *et al.* 2005). Current assessment techniques require considerable technical expertise, detailed biological knowledge and time-series data on catch, effort and/or surveyed abundance (Walters & Martell 2004) resulting in an annual cost of \$US50,000 to millions 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, directly supporting 14 - 40 million fishers, and indirectly supporting approximately 200 million people are un-assessable by current methods (Andrew *et al.* 2007).

Considerable uncertainty surrounds the status of unassessed stocks (Costello *et al.* 2012; Hilborn & Branch 2012; Pauly 2013) so that overfishing may go unrecognized until stocks collapse, and making third-party certification of sustainability unattainable. Even where fishing communities want to change fishing practices the technical difficulty and expense of current assessment techniques prevents science-based harvest strategies being developed and implemented. A new certifiable assessment methodology is needed for application to the small-scale and data-poor fisheries (Andrew *et al.* 2007; Pauly 2013).

Spawning Potential Ratio or Spawning Per Recruit (*SPR*) is an index of the relative rate reproduction (Mace & Sissenwine 1993; Walters & Martell 2004) in an exploited stock and is defined as the proportion of the unfished reproductive potential left by any given level of fishing pressure (F). By definition, unfished stocks have an *SPR* of 100% ($SPR_{100\%}$) and fishing mortality (F) reduces SPR_{100} from the unfished level to SPR_F . Shepherd (1982) used the *SPR* concept to synthesize different approaches in fisheries and integrated separate approaches to biomass and age structured modeling that had developed on opposite sides of the North Atlantic during the 1970s. The concept of *SPR* is internationally recognized in fisheries law (Restrepo & Powers 1999, Australian Government 2007) and generic *SPR* reference points for management have been developed through the meta-analysis of quantitatively assessed fisheries (Mace & Sissenwine 1993; Walters & Martell 2004).

The apparent correlation of biological parameters across species, known as life history invariants, has been widely used in the life sciences to provide generic parameter estimates for population models (Charnov 1993) and were first described in fisheries by Beverton and Holt (1959) amongst the Clupeids and Engraulids (herring and anchovy-like bony fishes) stocks of the North Sea (Beverton 1963). They observed correlations between the instantaneous natural mortality rate (M) and the von Bertalanffy (1938) growth rate constant (k), between M and the age of maturity (T_m), and between length of maturity (L_m) and asymptotic length (L_∞). 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 observable. These three correlations, now referred to as Beverton-Holt Life History Invariants (BH-LHI), are widely considered environmentally influenced constants and have been used extensively to parameterize fisheries bio-energetic and assessment models (Pauly 1980; Beddington & Kirkwood 2005; Charnov 2008; Gilsason *et al.* 2010). In this study we refer to Jensen's (1996) bio-energetically based estimates of the three BH-LHI; $L_m/L_\infty = 0.66$, $M/k = 1.5$ and $M \times \text{Age}_m = 1.65$.

Here, we use the *SPR* concept to link principals of BH-LHI with life history strategy theory and propose a new generalized size based assessment of *SPR* directly from knowledge of size composition, size of maturity and assumptions about the ratios of M/k and L_m/L_∞ . Our theoretical advance shows that size compositions and *SPR* can be estimated directly from the undifferentiated ratios of M/k and L_m/L_∞ . While our meta-analysis of 122 marine species shows that patterns in M/k and L_m/L_∞ can be categorised in relation to taxonomic grouping and life history strategy. The so-called

'Invariants' (M/k and L_m/L_∞) vary together in relation to the life history strategy of species. This provides a means by which likely ratios of M/k and L_m/L_∞ and thus size composition can be derived from parallel published studies, making size based assessments of SPR possible for fish stocks where only size data exist. Until now the estimation of *SPR* has required unique population models parameterised for each stock with estimates of natural mortality, growth, reproduction and time series, or age composition data (e.g. Ault *et al*, 1998; Walters & Martell 2004). Relying on only size at maturity and size composition data, together with knowledge of a species' life history strategy derived from the literature our technique has the potential to reduce the costs of assessing each stock down to <\$US10,000.

Materials and Methods

Selection of Parameter Sets

For our meta-analysis we collected estimates of growth, natural mortality (M), reproduction and length-weight relationships for marine and estuarine species (Table 1). Parameters were only included if they met the six criteria (1-6 below) defined by Gislason *et al.* (2010) and an additional criterion (7) we defined:

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

2. Estimates by size or age were rejected if they had been derived from multi-species modeling.
3. 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.
4. 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 time 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.
5. 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.
6. 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.”

The criterion we applied in addition to Gislason *et al.*'s was:

7. All estimates should be from the same geographic population, and gathered over a similar time to ensure they described the parameters of a single stock.

Using these selection criteria, we collated the data for a total of 123 species, including representatives from teleosts, invertebrates, chondrichthyans, and marine mammals (Table 1). The data covered a wide range of species from very short-lived species such as prawns (= shrimp, e.g. *Penaeus indicus*) to long-lived species such as orange roughy, *Hoplostethus atlanticus* (Tables 1 & S1).

SPR model for meta-analysis

SPR at size and age was modeled for each of these species using the procedure described below. The SPR models for each species were used to examine patterns in the relationships between age, length, weight and SPR across all 123 species.

For this purpose an age-based equilibrium model of spawning potential ratio was developed for each species. These models used an initial cohort size of 1,000 and then estimated numbers surviving, average individual length and weight, and reproductive output for both individuals and cohorts at each successive time step. To enable comparisons to be made across all species, age, length, weight and SPR were all normalized with respect to their maximum value, which we defined for all as being the value estimated for the first modeled age class with abundance $\leq 1\%$ of the initial cohort size (i.e. ≤ 10 individuals).

Where sexual dimorphism was recorded SPR models utilized female parameters.

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

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

where N_t is number of individuals at age t , M is natural mortality, and N_0 is 1000.

Egg production (EP) was estimated at each age t :

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

where EP_t is the spawning stock biomass of individuals at age t , and N_t is number in cohort at age t , M is natural mortality, and f_t is mean fecundity at age t .

Spawning Potential Ratio (SPR) was calculated for each age class t :

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

where SPR_t is the proportion of potential lifetime spawning biomass at age t , and t_{max} the age when cohort reaches 1% of initial size. When no fecundity data was available, reproductive output of a mature age class was assumed proportional to biomass:

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

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

A broad range of formulations to describe growth, 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, to smooth the functions being estimated we converted the unit of time to the next lowest unit (i.e. years to months, or months to weeks).

Five growth models were used to describe the growth for the 123 selected species (Table S1). The three parameter von Bertalanffy growth function (VBGF) was used to describe the growth of 117 species:

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

where L_t is mean length at age t , L_∞ is asymptotic length, k the growth coefficient, and t_0 is the theoretical age at zero length. The Schnute growth function was used for 3 species:

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

where L_t is length at age t , T_1 and T_2 are reference ages, y_1 and y_2 length at each reference age respectively, and A and B are constants $\neq 0$. The Gompertz growth function was used for 1 species:

$$L_t = W_0 e^{G(1-e^{-gt})} \quad (7)$$

where L_t is length at age t , and W_0 , G & g are constants. Two generic length models were used to for 2 species:

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

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

where α , β and ϕ are constants.

Length-weight relationships were described for all but two species by:

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

where W_t is mean weight at age t , L_t is mean length at age t , and a and b are constants. Polynomial regressions were reported for the length weight relationships for 2 species:

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

where W_t is mean weight at age t , L_t is mean length at age t , and a , b and c are constants.

When data on fecundity at length, weight, or age relationships were not available, reproductive output was assumed to be proportional to the biomass of an individual or cohort, based on the reported maturity ogive for each species (Equation 4). When no maturity ogive was available, the estimated length at maturity (L_0 , L_{50} , L_{100}) was used. Size-fecundity relationships were available for 24 species. In the absence of size-fecundity relationships, individual egg production was assumed to be

proportional to individual weight for teleosts (86 species), and size-independent for elasmobranches and mammals (13 species).

Simulation of Length-Composition

An age-based model was developed to simulate the variation seen in length frequency composition data from a theoretical unfished population as the ratio of M/k varies. For these simulations von Bertalanffy growth ($L_{\infty} = 1$, $CVL_{\infty} = 0.1$, $t_0 = 0$) in arbitrary units was assumed, with L_{∞} distributed normally among individuals, and with the variance in mean length of the cohort, a function of mean cohort length (Sainsbury 1980). The size composition simulation model was run with nine values of M/k (4.0, 1.65, 1.0, 0.8, 0.6, 0.4, 0.3, 0.2, & 0.1) spanning the range observed for the species in our meta-analysis. To achieve the desired ratios of M/k for each simulation M was fixed at 0.2 and the k was determined by back-calculating from the assigned value of M/k for that simulation. Because of the normal variation associated with length at age, some individuals are at lengths greater than 1, thus the length composition was calculated for lengths between 0 and 1.4. A maturation ogive was constructed for each length class, multiplying this ogive by the frequency of each length class estimates the number mature individuals in each length class. For indicative purposes only a constant proportional length-at-maturity of 0.66 was assumed.

Results

Theoretical Development

Considering these analyses mathematically we begin with the assumption that the number of individuals in a cohort decreases with constant natural mortality (M). Maximum age (t_{max}) is defined as the age when number of individuals in the cohort reaches 1% of initial size:

$$t_{max} = \frac{-\log(0.01)}{M} \quad (12)$$

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

$$L_t = L_{\infty} \left(1 - e^{(-kt)}\right) \quad (13)$$

where L_t is length at age t , L_{∞} hypothetical length at infinite age, and k is the growth coefficient. If we are interested in relative growth, i.e. length as a proportion of L_{∞} , Equation 13 becomes:

$$L_t = 1 - e^{(-kt)} \quad (14)$$

We can also standardize age as a proportion of t_{max} so that relative age (x) is defined as t/t_{max} for t from 0 to t_{max} . Note here that the vectors t and t_{max} are integers, and the number of time-steps in the vector t (and therefore the vector x) is defined by M in Equation 12. Length at standardized age x is then given by:

$$\begin{aligned}
L_x &= 1 - e^{\left(-k \frac{-\log(0.01)}{M} x\right)} \\
&= 1 - e^{\left(\log 0.01 \frac{k}{M} x\right)} \\
&= 1 - 0.01^{\left(\frac{xk}{M}\right)} \quad \text{for } 0 \leq x \leq 1
\end{aligned} \tag{15}$$

Thus, as plotted in Figure 1a, species with the same ratio of M/k share the same standardized growth curve. Note that as M/k decreases, the biological significance of L_∞ becomes increasingly vague; species with $M/k < 2$ tend to grow towards an asymptote, where L_∞ is probably a reasonable proxy for the largest expected size (L_{max}). However, in species with $M/k > 2$ extremely few individuals reach the asymptote and the value of L_∞ is less indicative of the largest individuals in the population.

Eggs-per-recruit at size as function of M/k

The number of individuals in a cohort at age t subject to constant M can be modeled as:

$$N_t = N_0 e^{-Mt} \tag{16}$$

When working with per-recruit models $N_0 = 1$. The von Bertalanffy equation can be re-arranged to give age t at length L_t :

$$t = \frac{1}{K} \log\left(\frac{1}{1 - L_t}\right) \quad \text{for } 0 \leq L_t < 1 \tag{17}$$

Substituting this into Equation 16:

$$\begin{aligned}
 N_t &= e^{-M \frac{1}{k} \log\left(\frac{1}{1-L_t}\right)} \\
 &= e^{-\frac{M}{k} \log\left(\frac{1}{1-L_t}\right)} \\
 &= (1 - L_t)^{\frac{M}{k}} \quad \text{for } 0 \leq L_t \leq 1
 \end{aligned} \tag{18}$$

Assuming that maturity is knife-edge at L_m , and that weight is proportional to L^3 , relative spawning biomass (SB) at size L_t can be given by:

$$\begin{aligned}
 SB_{L_t} &= 0 && \text{for } 0 \leq L_t < L_m \\
 &= (1 - L_t)^{\frac{M}{k}} L_t^3 && \text{for } L_m \leq L_t \leq 1
 \end{aligned} \tag{19}$$

The relative length where spawning biomass is maximized can be found by setting to zero the first derivative of the previous equation, which gives:

$$L_{B_{\max}} = \frac{3}{3 + \frac{M}{k}} \tag{20}$$

This result, although derived differently, is equivalent to Holt's (1958) equation for L_{opt} , which is used to calculate the length at which yield-per-recruit is maximized.

Optimal life-history theory suggests that, in order to maximize fitness, size at maturity (L_m) should occur when potential egg production is at a maximum (Beverton, 1992). This suggests that L_m should be equivalent to $L_{B_{\max}}$, and provides a theoretical relationship between L_m/L_∞ and M/k that can be used to estimate M/k from knowledge of L_m/L_∞ .

If we assume that fecundity is proportional to weight, than Equation 19 also describes the relationship between relative length and relative egg production. This relationship is demonstrated in Figure 1b for the range of M/k we observed in our meta-analysis.

SPR-at-size_as Function of M/k

Spawning Potential Ratio (SPR) at size can be thought of as the proportion of total cumulative life-time egg production a cohort has achieved at any proportion of its asymptotic size. SPR -at-size (SPR_{L_t}) can be defined as:

$$SPR_{L_t} = \frac{\sum_0^{L_t} SB_{L_t}}{\sum_0^1 SB_{L_t}} \quad \text{for } 0 \leq L_t \leq 1 \quad (21)$$

As plotted in Figure 2, these equations show that the relationships between relative size (2a – length; 2b - weight) and SPR are determined by the ratio of M/k rather than the absolute values of either parameter. Implicit in this result is that unfished size compositions are primarily determined by each species' ratios of M/k . This we make explicit with Figure 3 depicting simulated unfished size compositions for the range of M/k ratios observed in our meta-analysis (0.1 – 4.0). Note that $M/k \sim 1.0$ represents a break point in the characteristic size composition of unfished populations; populations with $M/k > 1.0$ tend to have a concave shaped size structure and are dominated by juveniles (unshaded), while $M/k < 1.0$ populations tend to convex shaped size compositions and domination by adults (shaded).

Meta-analysis

Our meta-analysis of 123 marine species shows that these modelled *SPR*-at-size curves accurately represent the relationships observed in nature. Figure 4a-d plots the *SPR* for every species in our meta-analysis as functions of; (a) normalized weight (= weight/weight_{max}), (b) normalized length (= length/length_{max}) and (c) normalized age (= age/age_{max}). In Figure 4d we standardise the estimated *SPR*-at-weight trajectories (Figure 4a) with respect to both weight of maturity ($W_m=0.0$) and maximum weight ($W_{max}=1.0$) making it evident that much of the 'complication' or crossing of trajectories observed in Figures 4a & b is due to variation in size of maturity. The spectrum of curves observed in Figure 4a-d is determined by the range of M/k ratios in our meta-analysis, species with the greatest ratio ($M/k = 3.5$) have trajectories in the upper left of Figure 4a,b,d and those with the lowest M/k species ($M/k = 0.1$) having trajectories in the bottom right. Figure 4d closely resembles the derived *SPR*-at-weight trajectories plotted in Figure 2b, although the scaling differs slightly. This is because in Figure 4d weight is standardized with respect to both weight-at-maturity ($W_m=0$) and maximum weight ($W_{max}=1.0$), while in Figure 2b weight is standardized to maximum weight alone ($W_{max}=1.0$) but all size classes are assumed mature.

Also plotted in Figures 4a-d are the relationships expected for species conforming to BH-LHI (black lines). We derive these curves using Jensen's (1996) BH-LHI estimates ($L_m/L_\infty = 0.66$, $M/k = 1.5$ 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. We believe that these 'BH-LHI curves' (black lines) are a previously unrecognized extension of the principal of BH-LHI. Previously, these three invariants have been used almost exclusively to provide estimates of individual parameters for population modeling. We believe this to be the first time they have been combined to define a specific relationship between *SPR*, size and age. Having established that together the BH-LHI infer an invariant relationship between normalized size/age and *SPR* it is evident from Figure 4 that they actually define some form of 'median' of the *SPR*-at-size and age trajectories observed in nature.

Continuing our meta-analysis we use $M/k = 1.0$, the point at which the shape of unfished size compositions change from convex to concave (Figure 3) to delineate between species, together with whether or not the growth of a species is determinate or indeterminate. Species with indeterminate growth continue growing throughout adult life, although slowing with increasing size, while species with determinate growth do not grow as adults. In this way we define three broad sub-groups or 'Types' of species in our meta-analysis (Figures 4-6; blue, green, red) differing in extent to which reproduction is deferred to when body size and age approach their maxima (Figure 4).

Type I species (green lines) form the most numerous group in our meta-analysis (49 species comprising 34 teleosts, 10 chondrichthyes, 3 crustaceans and 2 molluscs), their trajectories occupy the upper left hand side of figures 4a-c) and the lower right of figure 4d. Type I species conform roughly to the BH-LHI trajectory with a

relatively high average M/k (1.95, cf. 1.5; Table 1) but slightly lower average L_m/L_∞ (0.55, cf. 0.65; Table 1). They begin reproduction at relatively small sizes (Figure 4a&b) but at a relatively later stage of their life cycle (Figure 4c) than Types II & III. Unfished Type I populations are numerically dominated by juvenile length classes (Figure 3; top panels). Most of the spawning potential in unfished Type I populations comes from smaller individuals, 60-80% being produced by individuals that have achieved at <80% of their asymptotic size (Figure 4a&b).

A diverse range of species comprise Type I including; coastal bivalves (*Gari solida*, *Semele solida*), a crab (*Callinectes sapidus*), two spiny lobsters (*Panulirus argus*, *P. ornatus*), several Carcharhinid and Triakid sharks (*Carcharhinus obscurus*, *C. plumbeus*, *Mustelus antarcticus*, *Prionace glauca*), and a wide range of teleosts, from low tropic level species such as chub mackerel (*Scomber japonicus*), Pacific saury (*Cololabis saira*) and the Clupeid Gulf menhaden (*Brevoortia patronus*) to higher trophic level species, such as two rockfish, *Sebastes chlorostictus*, *S. melanostomus* and two apex piscivores, the Scombrid tunas *Thunnus alalunga*, and *T. tonggol* (Table S1). Applying King and McFarlane's (2003) classification of teleost life strategies, we conclude that our Type I bony fish are Opportunist and Intermediate Strategists. We can also use Pianka's (1970) 'r and K' theory, which characterizes life history strategies as either; 'r-strategists' with populations with relatively high turn-over rates, a tendency for boom and bust population dynamics, and invasive 'weed-like' characteristics, or 'K-strategists' with relatively stable population dynamics, lower rates of turnover and adults that reproduce over many breeding

cycles. Applying Pianka's life history categorization we label Type I species as 'r-strategists'.

Type II species (blue) are shifted to the right of Type I species in Figure 4a&b, and to the left in Figure 4c. They share the indeterminate growth pattern of Type I species; individuals continue growing throughout adult life, although growth slows with age as energy is increasingly diverted from growth to reproduction. Type III species (red) grow to a determinant asymptotic adult size, and reproduce over many breeding cycles without further growth, their trajectories are shifted to the extreme right in Figure 4a&b, and the extreme left in Figure 4c. The 74 Type II and III species share lower M/k ratios than Type I species (0.62, cf. 1.95; Table 1). In contrast to Type I species, Type II & III species do not reproduce until growth in length and weight is almost complete; Type II species produce approximately 70% of SPR at sizes of >80% of the asymptotic size, while Type III species produce 90% of SPR at sizes >80% of asymptotic size. Unfished populations of Type II and III species are numerically dominated by adult size classes (Figure 3; mid & lower panels). Type II and III species can be classed as Periodic and Equilibrium Strategists, or K -strategists.

The Type II species (blue), K -strategist with indeterminate growth, form a middle group of 59 species (45 teleosts, 1 elasmobranch, 5 crustaceans, and 8 molluscs) with average L_m/L_∞ similar to BH-LHI (0.69, cf. 0.66; Table 1;), but lower average M/k (0.62, cf. 1.5; Table 1). Type II species include a range of crustaceans, *Nephrops norvegicus*, and all of the prawns (=shrimp) in our analysis (*Penaeus indicus*, *P.*

latisulcatus, *P. merguensis*), all three haliotid gastropods (*Haliotis rubra*, *H. laevigata*, *H. iris*), a Carcharhinid shark (*Rhizoprionodon taylori*), and a range of teleosts including flat-forms (*Pleuronectes platessa*, *Psettichthys melanostictus*), most tropical snappers (*Lutjanus malabaricus*, *L. carponotatus*, *L. argentimaculatus*) and the very long-lived orange roughy (*Hoplostethus atlanticus*) (Table S1).

The 15 Type III species (red) in our analysis exhibit a spread of trajectories that balloon into the bottom right of Figure 4a&b. By a relatively early stage of their life cycle these species have grown through to maturity (Figure 4c) at a determinant asymptotic size and stop growing (Figure 4a&b). Type III species have the largest relative average L_m/L_∞ (0.88; Table 1) and lowest average M/k (0.57; Table 1). Besides the five marine mammals in our database, Type III comprises two Triakid sharks (*Galeorhinus galeus*, *Furgaleus macki*), eight teleosts, including the long lived *Scorpius aequipinnis*, and two relatively short-lived *Lethrinidae* species (Table S1).

In Figure 5a the L_m/L_∞ of each species is plotted as a function of the species M/k . The dashed black line ($L_m/L_\infty = 3/(3 + M/k)$) is derived from Beverton (1992), but is originally from Holt (1958) who used the equation to demonstrate that size at maximum biomass ($L_{opt.}$) can be estimated from M/k . The factor of '3' comes from the assumption that weight is proportional to L^3 . The two dotted lines indicate the relationships assuming weight and fecundity = $L^{2.5}$ and $L^{3.5}$. This equation establishes that Beverton & Holt recognized M/k and L_m/L_∞ as covariates, while also accepting that their relative invariance within species groups. Very few of the species in our meta-analysis fall above the Beverton & Holt curve, most of the

outliers are below. This appears to be primarily because our meta-analysis encompasses all marine species, some of which have fixed rates of reproduction, while Beverton & Holt worked almost entirely with teleosts for which fecundity is related to body size. In Figure 5b the M/k and L_m/L_∞ for the 9 most common teleost families (3 or more species) in our database are plotted, these data conform much more closely to the Beverton (1992) relationship. Figure 5b also demonstrates that species within a family share similar combinations of M/k and L_m/L_∞ and thus can be expected to exhibit similar SPR-at-size trajectories (Equation. 19 & Figures 2 & 4d) and relative size distributions (Figure 3).

Continuing our comparison with seminal works on data-poor assessment, in Figure 6 we plot our data in relation to Pauly's (1980) equation for empirically estimating M . The relationship between M/k and asymptotic length (L_∞) is plotted for the 109 species in our database with asymptotic length ≤ 200 cm, this excludes all the marine mammals and larger sharks. The plotted lines indicate the estimates of M/k that would be derived using the Pauly (1980) equation across the range of k values we observed. For the Pauly (1980) equation an assumption of ambient temperature is essential. To simplify this illustration we assume 15°C but sensitivity analyses we conducted 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 . Even narrowing the analysis to include just the 9 most common teleost families with 3 or more species does not change this to any great extent.

Discussion

We believe our linkage of the three Beverton-Holt Life History Invariants to define a specific relationship between standardised size and *SPR* (Figure 4a-d; black line) to be a previously unnoticed extension of the BH-LHI principal. In fisheries science the BH-LHI are most commonly used separately to estimate individual parameters for population modeling, generally they are only linked within bio-energetic models (e.g. Jensen 1997; Charnov, Gislason & Pope 2012). In the context of bio-energetic modeling Charnov (2008) noted that because species re-allocate energy from allometric growth to reproductive output, the relationships of growth and reproduction to size, are the inverse of each other, based on this, Charnov presciently postulated that allometric growth might be used to estimate reproductive output. Here we have confirmed Charnov's insight using the fisheries assessment concept of *SPR*.

In some respects, our groupings of species into three broad types of *SPR*-at-size relationships corresponding to categories of life history strategy and growth patterns, may seem 'biologically' counter-intuitive to many fisheries biologists. For example; we group two species of Scombrid tuna with forage fish and two species of rockfish (*Sebastes*); and prawns with abalone, and some teleosts; while we distribute sharks across all three Types. Fisheries scientists are not accustomed to thinking of the BH-LHI as variables, nor with linking M/k and size of maturity to life history strategies. The first formulations of BH-LHI (Beverton & Holt 1959;

Beverton 1963) were based on North Sea studies of teleost species that our analysis has classed as Type I species. Since that time fisheries biology has tended to accept, seemingly by default, that the invariants derived from those initial studies are relatively constant across much broader suites of species, particularly $M/k \sim 1.5$. This was, however, not an assumption implied by the later works of Beverton (1992) who clearly conceptualized species having a range of M/k values co-varying with L_m/L_∞ , or Pauly (1980) whose multivariate meta-analysis correlated ambient temperature and adult body size with each species' M/k ratio (Figures 5 & 6).

Confirming, but also building on the work of Beverton and Pauly we show that M/k and L_m/L_∞ are natural covariates. The so-called 'Invariants' vary together, matching patterns of growth and reproduction to different life history strategies. Their relative invariance is due to their co-varying according to the stage at which each life strategy transfers energy from allometric growth into reproduction. Accepting this conceptualization, tuna are simply 'scaled-up' anchovies, and prawns are 'scaled-down' faster versions of fish, lobsters and abalone. While we have crudely defined three broad types of marine species with characteristic ratios of M/k and L_m/L_∞ we do not mean to imply anything fundamental about this rough categorisation, rather our intention here is to illustrate that predictable patterns exist in nature that can be used to advantage. Together with Beverton's (1992) equation our results suggest that with further meta-analysis of life history strategies and ratios of M/k and L_m/L_∞ amongst well studied species, the expected size structure and *SPR*-at-size trajectories of poorly studied species might be inferred

from taxonomic affiliation and likely life history strategy, opening the way to simple assessments of *SPR* based on size of maturity and size composition.

Extending the principal of BH-LHI in this way has great potential for reducing the complexity and cost of assessment. By necessity, quantitative fisheries assessment currently places great emphasis on measuring the rate of change over time in biomass, age and size structure. Accurate data on pre-exploitation size and age structures are of immense value because they provide a baseline against which current size and age structures can be assessed, however they are almost never available. In studies that will be published elsewhere, we are using the equations derived here to estimate size structure for both unfished and fished populations making 'snapshot' assessments of *SPR* possible directly from current size composition and size of maturity. The approach to size based assessment we are developing has great similarities to earlier length based approaches (Fournier & Breen 1982, Pauly & Morgan 1987, Somerton & Kayabashi 1990; Ault *et al.* 1998). However those earlier approaches relied on M , k , L_m and L_∞ being estimated individually for each assessed stock, a level of biological information knowledge that makes more complex age-structured modeling feasible so that previous size based techniques have been little used in recent times. Our breakthrough is to recognize that it is the ratios of M/k and L_m/L_∞ that determine size structure and the distribution of spawning potential in populations, rather than the individual parameters, as well as to establish a generic basis for estimating these ratios from our general knowledge of species and related species.

Concluding Discussion

This study extends the principle of Beverton-Holt Life-History Invariants beyond providing estimates of individual parameters for stock assessment models. This extension proceeds from a strong basis in the literature (e.g. Charnov 2008), making it somewhat surprising that it has not been noticed before. Our novel use of *SPR* to integrate bioenergetics, life history strategy theory and fisheries assessment apparently provides the required conceptual key. This new conceptualization of BH-LHI can greatly simplify fisheries assessment making it possible to estimate *SPR*, a measure of reproductive output and important fisheries management performance indicator, from simple size studies.

We believe that many, if not most, exploited marine species can already be catalogued in terms of M/k and $Size_m/Size_\infty$ using information about their life-history strategy and biological parameters available in the literature for the species in question, or related species. With a catalogue of *SPR*-at-size curves for marine species made available to all via the world-wide web through inclusion on a website like Fishbase (Froese & Pauly 2000) our technique could make the assessment of many stocks possible with just taxonomic identification, estimates of local size of maturity, and representative size composition data.

Clearly, the approach we describe will not be applicable for every fishery in the world; we are not so bold with our claims. Our approach relies on fishing pressure changing the adult size composition of a population. Thus our approach may be

difficult to apply to low M/k species with deterministic growth (Type III species in this analysis) because the relatively uniform size of adults in those populations will mitigate against fishing pressure changing adult size composition. Likewise, fishing has little impact on the adult size composition when species are only exploited as larvae or juveniles, limiting the application of our technique to these fisheries as well.

Nevertheless, requiring only the two simplest, and cheapest forms of data required by current assessment techniques this new approach will make assessment possible in many fisheries where low value, small scale and/or lack of institutional capacity previously prevented assessments. By providing the basis for generic, simple, cost-effective, scientifically based assessment for most fisheries this approach has the potential to change the nature of fisheries assessment globally.

References

- Andrew, N.L., Bène, C., Hall, S.J., Allison, E.H., Heck, S., & Ratner, B.D. (2007) Diagnosis and management of small-scale fisheries in developing countries. *Fish & Fisheries*, **8**, 277-240.
- Ault, J.S., Bohnsack, J.A. & Meester, G.A. (1998) A retrospective (1979-1996) multipseices assessment of coral reef fish stocks in the Florida Keys. *Fisheries Bulletin*, **96**, 395-414.

Australian Government (2007) *Commonwealth Fisheries Harvest Strategy Policy Guidelines*. Department of Agriculture, Fisheries and Forestry, Canberra.

Beddington, J.R., Kirkwood, G.P. (2005) The estimation of potential yield and stock status using life-history parameters. *Philosophical Transactions of the Royal Society Series B*, **360**, 163-170.

Beverton, R.J.H. (1963) Maturation, growth and mortality of Clupeid and Engraulid stocks in relation to fishing. *Rapports et Procès-Verbaux Réunion du Reun. Conseil international pour l'Exploration de la Mer*, **154**, 44-67.

Beverton, R.J.H. (1992) Patterns of reproductive strategy parameters in some marine teleost fishes. *Journal of Fish Biology*, **41**, 137-160.

Beverton, R.J.H., Holt, S.J. (1959) A review of the lifespans and mortality of fish in nature and the relation to growth and other physiological characteristics. *Ciba Foundation Colloquium on Ageing*, **5**, 142-177.

Charnov, E.L. (1993) *Life history invariants*. Oxford University Press, New York.

Charnov, E.L. (2008) Fish growth: Bertalanffy k is proportional to reproductive effort. *Environ. Biology of Fish*, **83**, 185-187.

Charnov, E.L., Gislason, H. & Pope, J.G. (2012) Evolutionary assembly rules for fish life histories. *Fish & Fisheries*, **(vol?)**, 1-12

Costello, C., Ovando, D., Hilborn, R., Gaines, S.D., Deschenes, O., Lester, S.E. (2012) Status and solutions for the world's unassessed fisheries. *Science*, **338**, 517-520.

Froese, R., Pauly, D. (2000) *FishBase 2000: concepts, design and data sources*.

ICLARM, Laguna.

Fournier, D.A., Breen, P.A. (1983). Estimation of abalone mortality rates with growth analysis. *Transactions of the American Fisheries Society*, **112**, 403-411.

Gislason, H., Daan, N., Rice, J.C., Pope, J.G. (2010) Size, growth, temperature and the natural mortality of marine fish. *Fish and Fisheries*, **11**, 149-158.

Hilborn, R., Branch, T.A., (2013) Does catch reflect abundance? *Nature*, **494**, 303-306.

Hilborn, R., Orensanz, J.M., Parma, A.M. (2005) Institutions, incentives and the future of fisheries. *Philosophical Transactions of the Royal Society Series B*, **360**, 47-57.

Holt, S. J. (1958). The evaluation of fisheries resources by the dynamic analysis of stocks, and notes on the time factors involved. *ICNAF Special Publication, I*, 77-95.

Jensen, A.L. (1996) Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Canadian Journal of Fisheries and Aquatic Sciences*, **53**, 820-822.

Jensen, A.L. (1997) Origin of the relation between K and L_{inf} and synthesis of relations among life history parameters. *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 987-989.

King, J.R., McFarlane, G.A. (2003) Marine fish life history strategies: applications to fishery management. *Fisheries Management and Ecology*, **10**, 249-264.

Mace, P., Sissenwine, M. (1993) How much spawning is enough? *Risk evaluation and biological reference points for fisheries management* (eds S. Smith, J. Hunt & D. Rivard), pp. 101-118. Canadian Special Publication in Fisheries and Aquatic Sciences **120**.

Mahon, R. (1997) Does fisheries science serve the needs of managers of small stocks in developing countries? *Canadian Journal of Fisheries and Aquatic Sciences*, **54**, 2207-2213.

Mullon, C., Freon, P., Cury, P. (2005) The dynamics of collapse in world fisheries. *Fish & Fisheries*, **6**, 111-120.

Pauly, D. (1980) On the interrelationship between mortality, growth parameters and mean temperature in 175 fish stocks. *Journal du Conseil international pour l'Exploration de la Mer*, **39**, 175-92.

Pauly D. and Morgan G.R. (1987). Length-based methods in fisheries research. ICLARM. Conference Proceedings 13, 468p.

Pauly, D. (2013). Does catch reflect abundance? *Nature*, **494**, 303-305.

Pianka, F.R. (1970) On *r*- and *K*- selection. *Amer. Nat.* **104**, 593-597.

Restrepo, V.R., Powers, J.E. (1999) Precautionary control rules in US fisheries management: specification and performance. *ICES Journal of Marine Science*, **56**, 846-852.

Sainsbury, K. J. (1980) Effect of individual variability on the von Bertalanffy growth equation. *Canadian Journal of Fisheries and Aquatic Sciences*, **37**, 241-247.

Shepherd, J.G. (1982) A versatile new stock-recruitment relationship for fisheries, and the construction of sustainable yield curves. *Journal du Conseil international pour l'Exploration de la Mer*, **40**, 67-75.

Somerton, D.A. & Kayabashi, D.R. (1990). A measure of overfishing and its application on Hawaiian bottomfishes. Southwest Fisheries center Administrative Report H-90-10.

Von Bertalanffy, L. (1938) A quantitative theory of organic growth. *Human Biology*, **10**, 181-213.

Walters, C., Martell, S.J.D. (2004) *Fisheries, Ecology and Management*. Princeton University Press, New Jersey.

Walters, C., Pearse, P.H. (1996) Stock information requirements for quota management systems in commercial fisheries. *Reviews in Fish Biology & Fisheries*, **6**, 21-42.

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Table 1. A synopsis of the taxa and species in this meta-analysis summarizing the range of parameters used for each species group. Online Supporting Information contains a table listing the parameters used for each species and supporting sources.

Taxa	# Families	# Species	Max. age (yrs)	Max. length (m)	<i>M/k</i> 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)

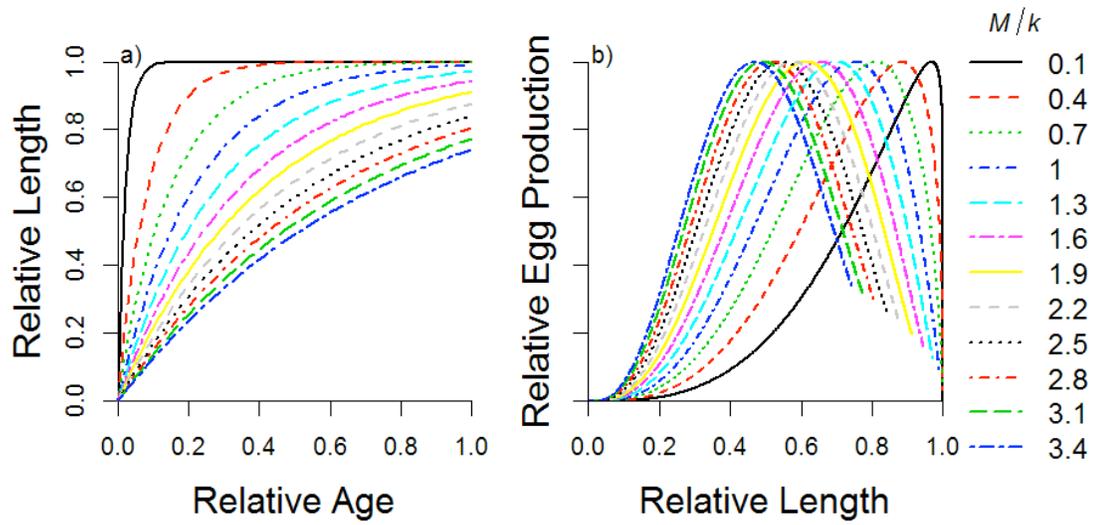


Figure 1

Modeled relationships between (a) relative length ($L_{\infty}=1.0$) and relative age ($Age_{max}=1.0$); and (b) relative egg production and relative length ($L_{\infty}=1.0$) for a range (0.1 – 3.4) of M/k values.

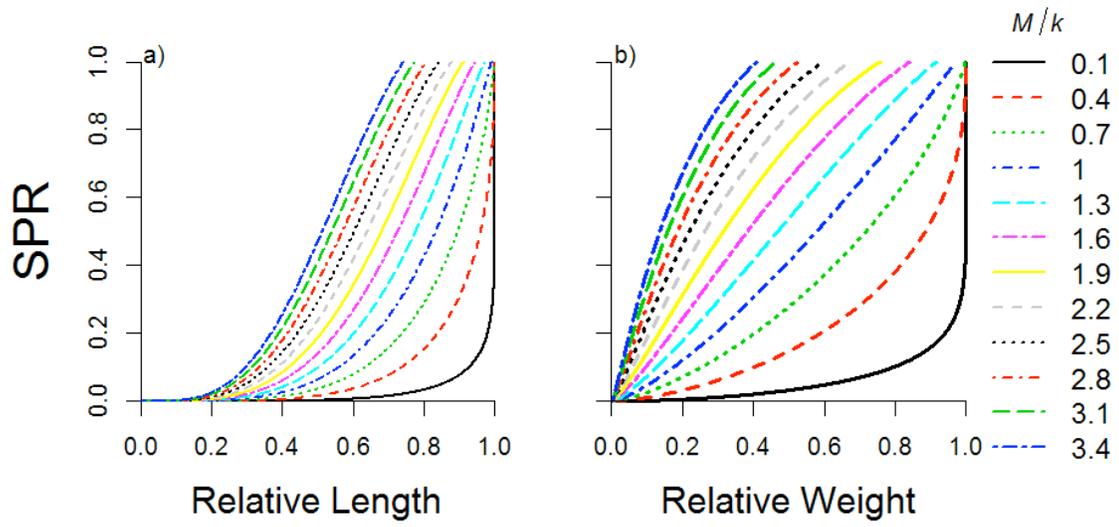


Figure 2

Modeled relationships between SPR and (a) relative length ($L_{\infty}=1.0$), and (b) relative weight ($W_{\infty}=1.0$) for a range (0.1 – 3.4) of M/k values.

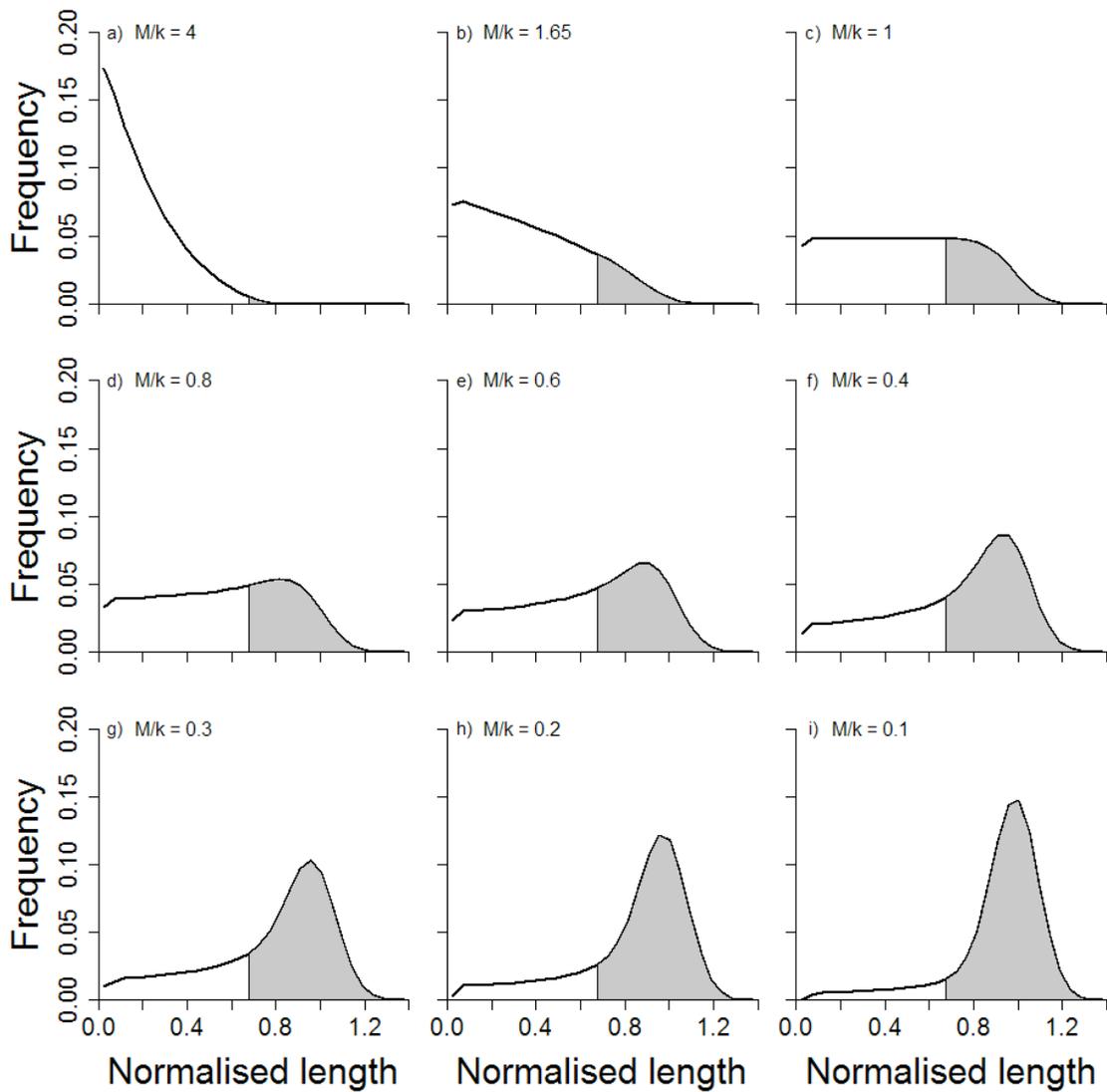


Figure 3

Simulated length frequency histograms illustrating how size composition of unfished populations is determined by a species' M/k ratio. The range of M/k ratios observed in this meta-analysis has been simulated. Top row: $M/k = 4.0, 1.65, 1.0$. Middle row: $M/k = 0.8, 0.6, 0.4$. Bottom row: $M/k = 0.3, 0.2, 0.1$. For these simulations von Bertalanffy growth ($L_\infty = 1, CVL_\infty = 0.1, t_0 = 0$) in arbitrary units was assumed, with L_∞ distributed normally among individuals, variance in mean cohort length assumed to be a function of mean cohort length (Sainsbury 1980). Shading indicates adults assuming $L_m/L_\infty = 0.66$. The skew on the size composition changes from left to right with decreasing M/k with ~ 1.0 being the transition from juvenile to adult dominated size structure.

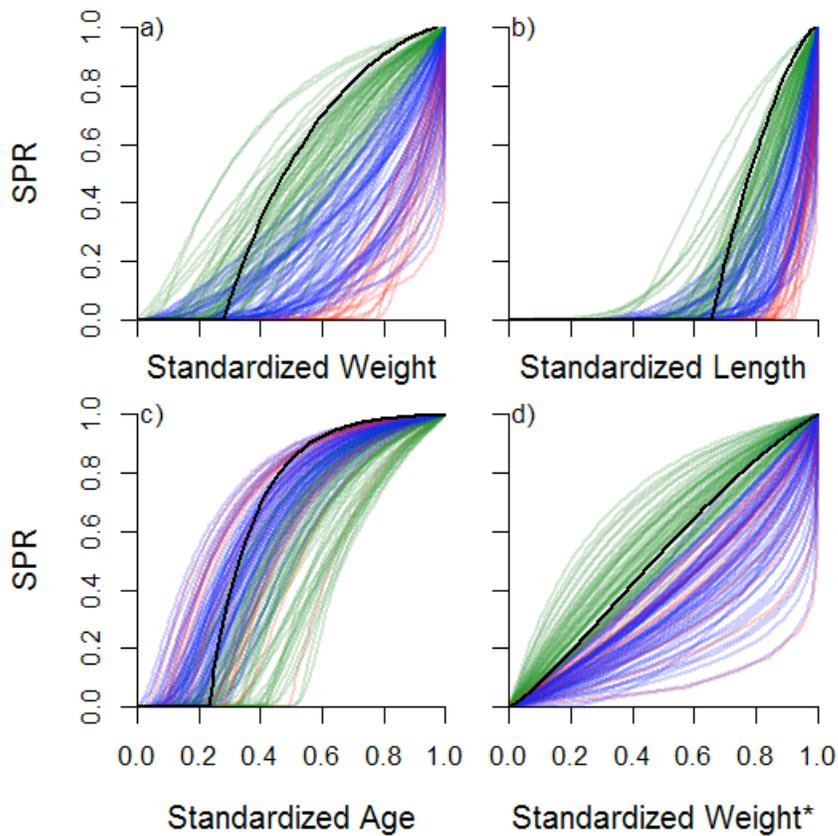


Figure 4.

Observed relationships for 123 selected marine species between *SPR* and (a) standardised weight ($\text{weight}_{\text{max}}=1.0$), (b) standardised length ($\text{length}_{\text{max}}=1.0$), (c) standardised age ($\text{age}_{\text{max}}=1.0$), and (d) weight standardised for size of maturity ($\text{weight}_m=0$) and maximum weight ($\text{weight}_{\text{max}} = 1.0$). Green lines denote species with indeterminate growth & $M/k > 1.0$; blue lines denote species with indeterminate growth & $M/k < 1.0$; red lines denote species with determinate growth & $M/k < 1.0$; black lines show the relationships determined by Beverton-Holt Life History Invariants, indeterminate growth, $L_m/L_\infty = 0.66$, $M/k = 1.5$ & $M \times \text{Age}_m = 1.65$.

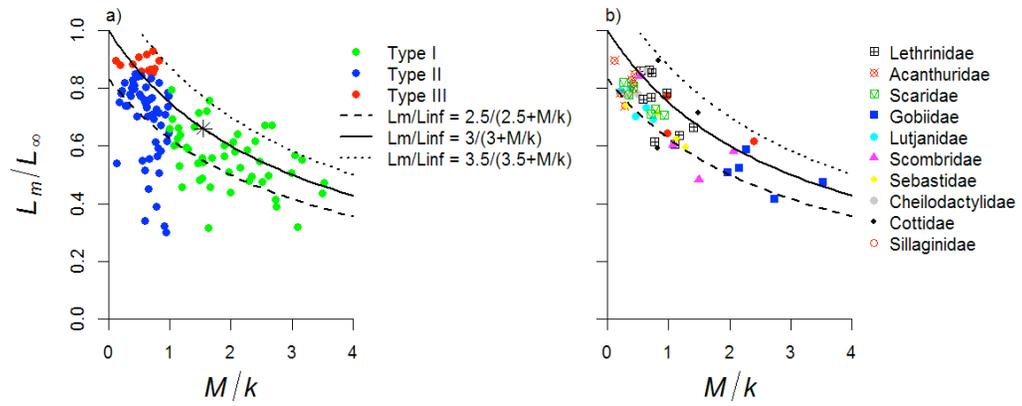


Figure 5

Length of maturity (L_m) in the 123 marine species selected for this meta-analysis, plotted against M/k of each species. Green points denote species with indeterminate growth & $M/k > 1.0$; blue points denote species with indeterminate growth & $M/k < 1.0$; red points denote species with determinate growth & $M/k < 1.0$;

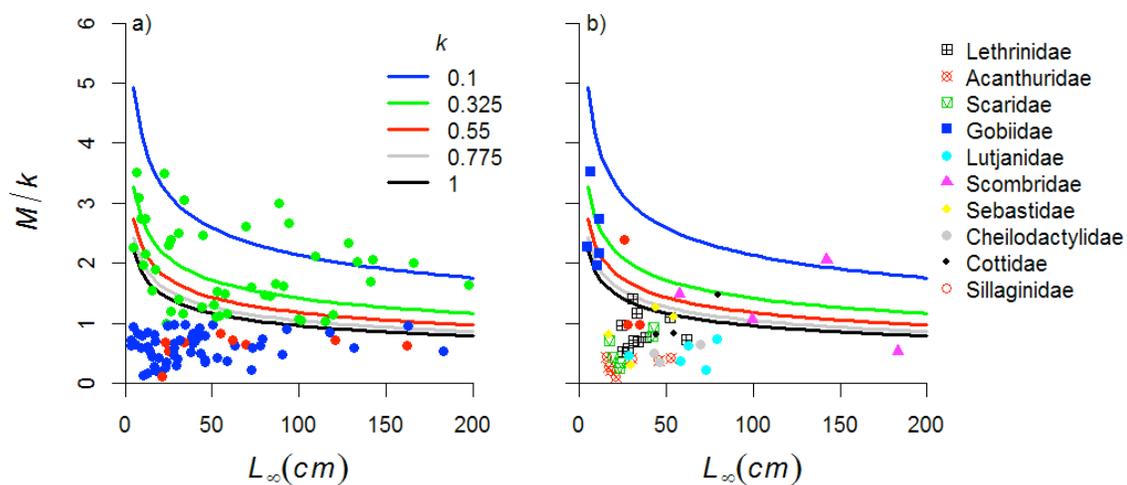


Figure 6

The M/k of 109 marine species with asymptotic size ≤ 200 cm in this meta-analysis plotted as a function of asymptotic length (L_{∞}). Coloured lines from Pauly's (1980) equation with various values for k and temperature assumed to be 15°C .