Size structure, not metabolic scaling rules, determines fisheries reference points

Ken H. Andersen and Jan E. Beyer

Center for Ocean Life

National Institute of Aquatic Resources (DTU-Aqua)

Technical University of Denmark

Charlottenlund Castle, DK-2920 Charlottenlund, Denmark.

Corresponding author: kha@aqua.dtu.dk

Abstract

Impact assessments of fishing on a stock require parameterization of vital rates: growth, mortality and recruitment. For "data-poor" stocks vital rates may be estimated from empirical size-based relationships or from life-history invariants. However a theoretical framework to synthesize these empirical relations is lacking. Here we combine life-history invariants, metabolic scaling and size-spectrum theory to develop a general size- and trait-based theory for demography and recruitment of exploited fish stocks. Important concepts are physiological or metabolic scaled mortalities and flux of individuals or their biomass to size. The theory is based on classic metabolic relations at the individual level and uses asymptotic size W_∞ as a trait. The theory predicts fundamental similarities and differences between small and large species in vital rates and response to fishing. The central result is that larger species have a higher egg production per recruit than small species. This means that density-dependence is stronger for large than for small species and has the consequence that fisheries reference points that incorporate recruitment do not obey metabolic scaling rules. This result implies that even though small species have a higher productivity than large species their resilience towards fishing is lower than expected from metabolic scaling rules. Further we show that the fishing mortality leading to maximum yield per recruit is an ill-suited reference point. The theory can be used to generalise the impact of fishing across species and for making demographic and evolutionary impact assessments of fishing, particularly in data-poor situations.

Keywords: Beverton-Holt, recruitment, metabolic theory, size spectrum, data-poor.

Introduction

Most quantitative work on fish stocks relies on the theoretical framework developed by Beverton and Holt (1959). The Beverton-Holt framework is an age-structured matrix formulation of the demography of a stock that is coupled to a von Bertalanffy description of growth (Bertalanffy, 1957) to calculate yield from the fishery and the reproductive potential of the stock. To apply the framework for a specific exploited stock two issues must be confronted: 1) parameters related to growth, mortality, maturation and recruitment of the stock have to be specified. Estimating these parameters requires a well-established biological monitoring program. 2) The framework relies on costly aging that, even for well-studied stocks, is plagued with uncertainties. These two issues make it difficult to apply the Beverton-Holt framework for impact assessment of fishing in a data-poor setting since neither parameters nor the age of fish in catches are known.

Soon after the Beverton-Holt framework was formulated it was realized that there were regularities in the variation of the parameters across fish species (Beverton and Holt, 1959; Pauly, 1980; Beverton, 1992). These regularities make it possible to formulate some of the parameters in terms of "Beverton-Holt life-history invariants", which are non-dimensional parameters that do not vary systematically across species (Charnov and Berrigan, 1991; Charnov, 1993). Examples of life-history invariants are: the ratio between adult natural mortality and the von Bertalanffy growth constant (M/K), or the ratio between size at maturation and asymptotic size. Later, the life-history invariants received a theoretical underpinning, either through life-history optimization theory (Charnov et al., 2001) or community ecology (Andersen et al., 2009). The life history invariants made it possible to formulate the Beverton-Holt theory using only two parameters for a given stock related to growth (L_∞ or K) and recruitment (the "α" parameter in a stock-recruitment relation that designates density-independent survival) (Williams and Shertzer, 2003; Beddington and Kirkwood, 2005; Brooks et al., 2009). This is an important step forward to reduce the number of parameters in a data-poor setting but it still leaves the recruitment parameter α unspecified.

An alternative to rely on life-history invariants is to use empirical relationships of vital rates, typically based on size (Le Quesne and Jennings, 2012). Such relationships can be derived from cross-species analyses of mortality (McGurk 1986, Gislason et al 2010), growth (Kooijman 2000) and even for reproduction (Denney et al 2002, Goodwin et al 2006, Hall et al 2006). The existence of robust empirical relationships between the vital rates of fish suggests that these relationships may be derived from a general theory but so far such a general theory has been lacking. One candidate for a theory is the "metabolic" framework (Brown et al. 2004), which predicts that all mass-rates, such as metabolism, scale with weight as $w^{3/4}$ and specific rates, such as productivity P/B, scale with $w^{-1/4}$. We refer to these two predictions as metabolic scaling rules. A potential problem with the metabolic framework is that is does not explicitly consider structured populations where the ratio between adult size and offspring size is large, as it is the case for fish.

Since information on size is much easier to obtain than information on age, size-spectrum theory has been developed to use body size as the structuring variable instead of age (Beyer, 1989). Further, body size is more important than age for physiology (Winberg, 1956), mortality of individuals (Kerr, 1974), fisheries regulations through gear specifications, and usually also market value. Analyses of biomass as a function of size have demonstrated community-level patterns in the scaling of biomass with body size, in particular the "Sheldon" size spectrum (Sheldon et al, 1972) supported by theoretic arguments (Sheldon et al, 1977; Andersen and Beyer, 2006), as well as how the spectrum responds to fishing (Daan

et al, 2005). It is possible to apply size-based principles to the size-structure of a single population (Andersen and Beyer, 2006). Here we are concerned with how the size-structure of a single population responds to fishing.

The objective of this paper is to formulate a general size-based theoretical framework to calculate demography and recruitment of fished stocks. The framework unites the Beverton-Holt theory with life-history invariants, metabolic scaling rules and size-spectrum concepts. The theory is developed from five assumptions related to the metabolism, life-history and density-dependence. The end result is a theory that requires one parameter only to characterize a stock: the asymptotic size W_∞.

To provide a practical example of the application of the theory for a non-growing population we calculate four relevant fisheries reference points as functions of asymptotic size: the fishing mortalities that maximize yield per recruit F_{msyr} or yield F_{msy}, and the fishing mortalities at which recruitment is impaired F_{lim} or the stock crashes F_{crash}. Reference points are usually calculated on a species by species basis but we show that there are regularities in how the reference points vary with asymptotic size. We discuss the generality of the theory in light of the assumptions and give examples of how the theory can be applied for ecological and evolutionary impact assessments of fishing for data-poor as well as for data-rich stocks.

Methods

The theory is based on size of individuals. We use weight w as a measure of size since it is the natural currency to formulate a mass balance. Table 1 provides a glossary of symbols used with a specification of their relation to the symbols used in classic age-based theory.

The theory rests on five fundamental assumptions on density-dependence and the scaling of consumption, mortality, and reproductive effort with individual size. The assumptions are used to develop an energy budget for an individual fish that leads to formulas for growth and egg production. The individual energy budget is combined with mortality to scale up to population level quantities: stock structure, spawning stock biomass and density-dependent recruitment. Finally fisheries reference points are calculated as functions of asymptotic size.

Assumption #1: available energy and metabolic scaling

The available energy is the energy remaining after assimilation costs and standard metabolism have been deducted from consumed food. The concept of "available energy" corresponds to the "anabolic" term in a classic von Bertalanffy energy budget. Available energy for an individual of weight w is assumed to follow a power-law (Fig. 1a):

$$C(w) = Aw^n \tag{1}$$

where A and n are species-independent constants. The justification for this assumption is that energy (food) has to be absorbed through a surface in the body. The area of a surface scales with weight as $w^{2/3}$ (Bertalanffy, 1957; Kooijman, 2000). The modern "metabolic" interpretation recognizes that the surface may be fractal so the exponent may be higher, e.g. $n = 3/4$ (West et al., 1997). Our formulation of the theory only requires that $0 < n < 1$. For metabolic scaling $n = 3/4$ is used in the practical examples as it conforms with data (see later).

Assumption #2: natural mortality

Natural mortality $\mu_p(w)$ is assumed to be a power-law function with exponent $n - 1$ (Fig. 1b):

$$\mu_p(w) = aAw^{n-1} \qquad (2)$$

where the *physiological level of predation* a is a non-dimensional constant expressing the level of mortality (Beyer, 1989). Since $n = 3/4$, mortality is a decreasing function of size with exponent -1/4. Thus a 1 g fish is exposed to mortality 10 times higher than a 10 kg fish. The assumption further states that growth and mortality are connected through the constant A: a higher consumption leads to a higher risk of predation mortality. The physiological level of predation a is a central parameter and can be understood in two ways: First the formal definition is the ratio between mortality and weight-specific available energy (Beyer, 1989). Second a is approximately proportional to the M/K life-history invariant (the ratio between adult mortality and von Bertalanffy growth rate; Beverton and Holt, 1959; see Table 1). However, a is defined with a mortality declining with size whereas M/K is defined from a constant mortality. The value of a can be determined from empirical M/K relations to be $\approx$ 0.35 (Table 1). Alternatively, (2) can be derived from assumption 1 from mass conservation in the fish community (Peterson and Wroblewski, 1984; Beyer, 1989), which leads to a prediction of the value of a in terms of parameters related to predator-prey interactions (Andersen et al., 2009). Here the assumption is treated as separate from (1) since a for a specific species might deviate from the community average value.

Assumption #3: reproduction

The effort invested in reproduction by mature individuals is proportional to individual weight. This corresponds to assuming that the gonado-somatic index of adults is independent of age and size.

Assumption #4: maturation

Size at maturation w_m is assumed proportional to asymptotic weight: $w_m = \eta_m W_\infty$. The constant of proportionality η_m is one of the Beverton-Holt life-history invariants (Charnov, 1993), which has been demonstrated from cross-species analyses to be between 0.06 and 0.68 with an average value of $\eta_m \approx 0.25$ (Beverton, 1992).

Assumption #5: density dependence

Recruitment is limited by density-dependent processes described by a stock-recruitment relationship (Ricker, 1954; Beverton and Holt, 1959). Such a description of density-dependent regulation is often used to represent density-dependent processes happening early in life (Myers and Cadigan, 1993) but it may just as well represent processes happening at any size or age before fishing and maturation occur or density dependent regulation of reproduction.

Energy budget of an individual

The energy budget of an individual fish determines how growth and egg production varies as a function of size and across species. Such an energy budget can be formulated on the basis of assumption 1, 3 and 4. The available energy Aw^n (assumption 1) is used for activity and the remainder is divided between reproduction (for mature individuals) and somatic growth. Cost of activity has been shown to be approximately proportional to weight when an individual swims at an optimal speed (Ware, 1978). Investment in reproduction for mature individuals is proportional to weight (assumption 3). The remaining energy is used for somatic growth.

We use a smooth function to describe the transition between juveniles and adults to represent that individuals mature at different weights. This "maturity ogive" is described by a

sigmoidal function varying smoothly from 0 to 1 around the size at maturation $\eta_m W_\infty$ (Hartvig et al. 2011; Fig. 1a):

$$\psi_m(w/W_\infty) = \left[1 + \left(\frac{w}{\eta_m W_\infty}\right)^{-u_m}\right]^{-1} \tag{3}$$

where u_m specifies the width of the zone where the transition from 0 to 1 occurs. The specific choice of the function is not important for the results as long as the width of the transition zone is proportional to W_∞. The growth rate (weight per time) can now be written as (Fig. 1a):

$$g(w) = Aw^n - k_a w - \psi_m(w/W_\infty)k_r w, \tag{4}$$

where and k_a and k_r are weight-specific costs of activity and investment into reproduction (time^{-1}). The role of $\psi_m(w/W_\infty)$ is to ensure that investment in reproduction is only taken into account for mature individuals. This aspect may be ignored by setting $\psi_m = 1$ without seriously compromising accuracy, as $(k_a + k_r)w \ll Aw^n$ when $w \ll W_\infty$. Doing so will make the growth function equivalent to the classic von Bertalanffy growth function. We introduce reproduction explicitly to allow application of the theory as a basis for life-history optimization calculations (Day and Taylor, 1997) and quantitative genetics calculations of fisheries induced evolution (Andersen and Brander, 2009). For larvae, $\psi_m = 0$ and $w/W_\infty \approx 0$. This means that their growth rate is approximately Aw^n, which fits larval growth rates well (Beyer, 1989, p. 138).

To formulate (4) in terms of life-history invariants we express the species-specific parameters k_a and k_r in terms of two other parameters: the asymptotic size W_∞ and the fraction of the energy invested into activity and reproduction used for activity ϵ_a. At the size $w = W_\infty$ all available energy is used for activity and reproduction. We can determine this size from $AW_\infty^n = k_a W_\infty + k_r W_\infty$:

$$W_\infty = \left(\frac{A}{k_a + k_r}\right)^{\frac{1}{1-n}}. \tag{5a}$$

We further define ϵ_a as:

$$\epsilon_a = \frac{k_a}{k_a + k_r}. \tag{5b}$$

ϵ_a is a non-dimensional number representing the fraction of the energy invested into activity. That ϵ_a is constant (independent of W_∞) follows from assumption 4 (Charnov et al. 2001). k_a and k_r can now be expressed in terms of W_∞ and ϵ_a by re-arranging (5):

$$k_a = A\epsilon_a W_\infty^{n-1}$$

$$k_r = A(1 - \epsilon_a)W_\infty^{n-1}.$$

Inserting these expressions back into (4) leads to:

$$g(w) = Aw^n \left[1 - \left(\frac{w}{W_\infty}\right)^{1-n}\left(\epsilon_a + (1 - \epsilon_a)\psi_m\left(\frac{w}{W_\infty}\right)\right)\right] \tag{6}$$

This expression for $g(w)$ has two advantages compared to eq. (4). First it is formulated in terms of the trait W_∞ and the species-independent parameters ϵ_a, A and n. Second, it shows directly the three phases of growth. The factor outside the square brackets expresses growth at early life since $w \ll W_\infty$ ensures the square brackets is ≈ 1. In juvenile life $\psi_m(w/W_\infty) \approx 0$ still governs but the costs of activity represented by $\epsilon_a(w/W_\infty)^{1-n}$ cannot be ignored.

The term in the square bracket has decreased to 0.75 when the fish has reached 1/100 of W_∞ with $\epsilon_a \approx 0.8$ (Table 1). In adult life $\psi_m(w/W_\infty) \approx 1$ and (6) is identical to the von Bertalanffy growth equation. When w approaches W_∞ the term in the square brackets $\to 0$ and growth ceases.

Scaling from individuals to a population

The size distribution of individuals within a non-growing stock $N(w)$, often referred to as the size spectrum, is a "density function" with dimension numbers per weight, such that $N(w)\mathrm{d}w$ is the number of individuals in the size range $[w: w + \mathrm{d}w]$. Population-level measures referring to any size range are obtained by integrating over $N(w)$ since we are dealing with continuous size, e.g. the total number of individuals is $\int N(w)\mathrm{d}w$ and the total biomass is $\int N(w)w\,\mathrm{d}w$.

Recruitment is represented by a continuous and constant flux R of individuals entering the population at size w_r. Such a flux, with dimension numbers per time, must equal the number density multiplied by the growth rate, i.e. $R = N(w_r)g(w_r)$. Here R is obtained from a stock-recruitment relationship (see later) and the flux $N(w)g(w)$ at any larger size w simply equals R reduced by the survivorship, i.e.

$$N(w) = \frac{R}{g(w)} \exp\left(-\int_{w_r}^{w} \frac{\mu(\widetilde{w})}{g(\widetilde{w})}\,\mathrm{d}\widetilde{w}\right) \qquad (7)$$

where the exponential term expresses the probability of being alive at size w. With fluxes replaced by numbers this formula is identical to how numbers-at-size are calculated in traditional size-based theory (Beyer, 1989). The inverse of the growth rate measures the time required to grow through a tiny size range so the integral in (7) expresses the cumulative mortality growing from w_r to w when exposed to a total mortality of $\mu(w)$ (see Appendix B for a full derivation that also covers the time-dependent case).

Considering larval fish where $g(w) \approx Aw^n$, eq. (7) gives the important result that the size-spectrum is a power-law $\propto w^{-n-a}$ (Appendix B; Fig. 1c):

$$N(w) = \frac{R}{Aw_r^{-a}}w^{-n-a} \quad \text{for } w \ll W_\infty \qquad (8)$$

This is because mortality divided by growth in (7) in this case becomes a/w giving rise to a survivorship of:

$$P_{w_r \to w} = \left(\frac{w}{w_r}\right)^{-a} \quad \text{for } w \ll W_\infty \qquad (9)$$

where the survival factor w^{-a} combined with the inverse growth factor w^{-n} creates the size spectrum in (8).

Recruitment

The flux of recruits (numbers per time) is described by a Beverton-Holt stock recruitment relationship:

$$R = R_{max} \frac{P_r R_p}{R_{max} + P_r R_p} = R_{max} \frac{\alpha P_r B}{R_{max} + \alpha P_r B}, \tag{10}$$

where R_{max} is the maximum flux of recruits at size w_r at high stock biomass, R_p is the total flux of viable eggs of size w_{egg} and $P_r = P_{w_{egg} \to w_r}$ is the density−independent survivorship from egg size to size at recruitment represented by the initial slope of the recruitment curve. The second expression is obtained using the spawning stock biomass $B = \int \psi_m(w/W_\infty)N(w)w\,dw$ and α, the egg production rate per biomass (numbers· biomass^{-1}time^{-1}), to express $R_p = \alpha B$. α is proportional to the weight-specific investment in reproduction k_r divided by the size of an egg:

$$\alpha = \epsilon_r k_r/w_{egg} = A\epsilon_r(1 - \epsilon_a)W_\infty^{n-1}/w_{egg} \tag{11}$$

where ϵ_r is the efficiency of reproduction, i.e. 1-ϵ_r represents costs of reproduction and egg mortality. The important result is the prediction that α is a decreasing function of asymptotic size with scaling W_∞^{n-1} (Fig. 2a).

The recruitment can be related to the classic "steepness" parameters (Appendix D). Simulations using Ricker recruitment did not yield systematically different results for the reference points hence the Beverton-Holt curve was used in the examples given later.

Yield

Yield is calculated by integrating over the size distribution multiplied by a size-selectivity curve of the fishing operation. In the examples presented later fishing mortality is specified via a trawl selectivity curve $\mu_F = F\psi_F(w/W_\infty)$ where $\psi_F(w/W_\infty)$ is given as in (3) with subscript m replaced by subscript F:

$$Y = F \int_{w_r}^{W_\infty} \psi_F(w/W_\infty)N(w)w\,dw \tag{12}$$

Yield per recruit is defined as yield divided by the biomass flux of recruits, Rw_r. It is therefore a dimensionless quantity and not, as it is sometimes defined, a biomass. Yield per recruit $Y/(Rw_r)$ is calculated from (12) by inserting $N(w)$ from (7) and dividing through by Rw_r. Since R then does not figure on the right-hand-side, yield per recruit is independent of actual recruitment R and is therefore determined solely by the stock structure (7).

In the calculations presented later the yield is instead divided by the biomass flux of recruits to the fishery, i.e. Rw_r is replaced by $R_F w_F$ where $R_F = N(w_F)g(w_F)$ is the flux of individuals to the size $w_F = \eta_F W_\infty$ of 50 % gear selection in the absence of fishing. This calculation of yield per recruit equals the former multiplied by w_r/w_F and divided by the survivorship due to natural mortality to size w_F. Thus the two expressions differ only by a constant but the latter has the advantage that $Y_r = Y/(R_F w_F) > 1$ gives a direct indication of the relation between recruitment to the fishery and the yield per recruit.

Fishing mortality can be written as a non-dimensional parameter by scaling it similarly to the way the physiological mortality a is defined:

$$a_F = FW_\infty^{1-n}/A. \tag{13}$$

This "physiological fishing mortality" introduces a metabolic scaling of fishing mortality by measuring fishing mortality in terms of specific available energy. The physiological scaling of fishing mortality is used to test which aspects of the population dynamics that follow metabolic scaling rules: if fish stock dynamics follow metabolic scaling rules, fish populations should tolerate the same physiological fishing mortality regardless of their asymptotic size.

Reference points

Fisheries reference points are calculated as the fishing mortality (in absolute or physiological units) that maximizes yield or yield per recruit (F_{msy} or F_{msyr}) or which leads to decreased recruitment (F_{lim}) or population collapse (F_{crash}). Specifically, F_{lim} is the fishing mortality where the recruitment is half the maximum recruitment $R = 0.5R_{\mathrm{max}}$, which is the same as the fishing mortality where $\alpha P_r B = R_{\mathrm{max}}$. The four reference points characterize the response of the population to fishing in terms of yield and population state, with and without taking recruitment into account.

To compare the predicted values of the reference point with observations, we have collected values of two reference points, F_{msy} and F_{lim} from ICES's advice from 5 ecosystems (Table 2). Only a small fraction of the assessed stocks had calculations of both reference points, in particular there were only two data points for small species ($W_\infty < 500$ g). The estimation of the reference points were not performed by any standardized procedure. We have converted the fishing mortalities to physiological units using von Bertalanffy growth constants: $a_{F.\mathrm{msy}} = F_{\mathrm{msy}}/(3K)$ and likewise for $a_{F.\mathrm{lim}}$.

Parameter values

Parameter values are determined from cross-species analyses from the literature (Table 1). The growth rate parameter A was determined from a fit between growth curves specified by (6) and observed von Bertalanffy size-at-age specified by K and asymptotic length L_∞. Length was converted to weight by the relationship $W_\infty = qL_\infty^3$ where $q = 0.01$ g cm^{-3}, and K was corrected for temperature by a Q_{10} of 1.83 (Q_{10} is the fractional change when the temperature is increased by 10°C). For details of the fitting procedure see Appendix A.

The dimensional parameter that scales biomass is the maximum recruitment R_{max} (numbers per time). R_{max} is stock-specific and depends on the carrying capacity of the stock in question. R_{max} is not covered by the theory but since reference points are only formulated with respect to relative yield and recruitment, i.e. yield and recruitment divided by R_{max}, this parameter is not required to calculate reference points.

It does not matter how we select the size of recruitment w_r as long as it is before fishing. For simplicity we choose $w_r = w_{\mathrm{egg}}$ implying $P_r = 1$.

Implementation

The calculation of the size distribution, yield and recruitment can be reduced to a few equations that can be implemented in a spreadsheet (Appendix C) or as a web-application (Appendix E).

Results

The important dimensional parameter, i.e. a parameter having units, is the growth constant A,

which has dimensions weight^{1-n} per time (Table 1). A plays the role of a time scale in the theory as it enters all expressions that have dimensions of time: yield (biomass per time), recruitment (numbers per time), and fishing mortalities (time^{-1}). Fitting A to observed von Bertalanffy weight-at-age curves (Fig. 2b) demonstrates that A does not vary systematically as a function of asymptotic size despite a large variation in growth between species with similar asymptotic size.

The size distribution of the stock is determined by performing the integral (7) either analytically (Appendix B) or numerically (Appendix C). To visualize the size spectrum we follow the idea of Sheldon et al. (1972) and plot the total biomass in logarithmic size bins, e.g. from 1-10 g, from 10-100 g etc. This is achieved by multiplying the number density spectrum by w^2 to form $w^2 N(w)$ (see Andersen and Beyer 2006, Appendix A) (Fig. 1c+d). Since the size spectrum of juveniles scales as w^{-n-a} (8) the total biomass in a logarithmic bin scales as $w^{2-n-a} \approx w^{0.90}$; an increasing function of size. The increase in biomass with size is because the gain in biomass from consumption (the exponent $2 - n$) exceeds the loss to predation (exponent $-a$). The bins may be set up such that the last bin contains the spawning stock biomass per recruit, which then scales as $B/R \propto W_\infty^{2-n-a}$. Hence, in the absence of fishing, larger species (large W_∞) have a higher spawning stock biomass per recruit than smaller species. When the stock is subject to fishing the biomass of larger species is being diminished more by a given F than smaller species (Fig. 1c). This is because fishing mortality acts over a longer time-span for large species than for small species (the time to grow through a logarithmic size bin is proportional to $w/g(w) \propto w^{1-n}$ so the time fishing acts is $\approx W_\infty^{1-n}$). Therefore large species experience a larger cumulative fishing mortality than small species. If the fishing mortality is measured as the physiological fishing mortality a_F then the relative impact of fishing on the stock structure is independent of W_∞ (Fig. 1d and analytical calculations in Appendix B).

Yield per recruit to the fishery, $Y/(R_F w_F)$, is calculated directly from the stock structure using (7) and (12). It has a maximum at $F = F_{\mathrm{msyr}}$ and F_{msyr} decreases as a function of asymptotic size (Fig. 3a). To test whether metabolic scaling rules hold for yield per recruit, it is plotted as a function of the physiological fishing mortality (Fig. 3b). In this case all the curves lie on top of one another, i.e. there is one universal yield per recruit curve for a given set of life-history parameters, independent of W_∞. The yield per recruit reference point therefore obeys metabolic scaling rules.

The yield per recruit curve is fairly flat around the maximum for the standard set of parameters. For stocks with a relatively small natural mortality the maximum becomes better defined but also occurs at a smaller fishing pressure. For a high natural mortality the maximum occurs at higher fishing pressures, and may even lie beyond the point where the stock crashes.

Egg production of the stock is determined by multiplying the spawning stock biomass per recruit $B/R \propto W_\infty^{2-n-a}$ (increasing with W_∞) with the investment in reproduction $k_r \propto W_\infty^{n-1}$ (decreasing with W_∞), yielding $R_p/R \propto W_\infty^{1-a} \approx W_\infty^{0.65}$; an increasing function of W_∞. The increasing spawning stock biomass per recruit is therefore more important for egg production than the decreasing investment into reproduction. As a result larger species have a higher egg production per recruit than smaller species and consequently lie higher on the stock-recruitment curve and experience stronger density dependence (Fig. 4). This result only depends on the value of a which is expected to be less than 1 since if it was larger than 1 it would not be an optimal life-history strategy for fish to produce many small eggs (Andersen et al 2008). Further, if $a = 1$ then all species would have the same R_p/R, however, as will be

evident later, that level of mortality would crash the population. The result is therefore insensitive to the values of the other parameters and is essentially determined by assumptions (1) and (2). Small species lie low on the stock-recruitment curve and do not experience strong density dependence. As seen earlier (Fig. 1c), larger species are harder hit by a given fishing mortality so the impact of fishing on recruitment is therefore stronger for large species than for medium sized species (Fig. 5a). For very small species the egg production is on the rising part of the recruitment curve even in the absence of fishing, so fishing also has a strong impact on these species. If F is scaled to physiological units a_F the impact of fishing still depends on the asymptotic size (Fig. 5b). Thus recruitment does not obey metabolic scaling rules.

Yield from the fishery is determined by a combination of the size structure of the stock and recruitment (Fig. 6). Yield is roughly a parabolic function of fishing mortality as predicted by classic surplus production theory. For the largest species the yield curve coincides with the yield per recruit curve until the fishing mortality leading to maximum yield (Fig. 6; thick line). For higher fishing mortalities yield becomes recruitment limited and the yield is smaller than the yield per recruit. For the smallest species the yield per recruit curve is different from the yield per recruit curve at all fishing mortalities as these species are recruitment limited even in the absence of fishing (Fig. 6; thin line).

Fisheries reference points are determined either by stock structure (yield per recruit; F_{msyr}) by recruitment (F_{lim} and F_{crash}), or by yield (F_{msy}). Plots of reference points as a function of fishing effort synthesize the previously presented results (Fig. 7): the impact of a given F on the stock structure is larger on big species than on small species (Fig. 1c). On the other hand very small species are expected to be recruitment limited even in the absence of fishing (Fig. 4) and consequently only tolerate approximately the same F as large species (Fig. 6a). In general $F_{\text{crash}} \gg F_{\text{msy}}$, i.e. stocks are expected to tolerate fishing mortalities much higher than F_{msy} albeit with a penalty in yield. Determining reference points using the physiological fishing mortality makes them monotonous functions of W_∞, roughly proportional to $\ln(W_\infty)$, except F_{msyr} which is independent of W_∞ (Fig. 7b). This is because only F_{msyr} obeys metabolic scaling rules. The most conspicuous result is the lack of metabolic scaling for the reference points that depend on recruitment and yield. The absence of a metabolic scaling is also present in the reference points currently used for selected ICES stocks which appear to be almost independent of asymptotic size (Fig. 8).

The values of the life-history parameters that are used in the calculation of the reference points vary quite significantly around the default values in Table 1 see e.g. Fig 2b. To account for this variation we have selected sets of parameters at random from distributions that represent the range of variation of the parameters and for each set calculated the reference points (Fig. 8). The analysis demonstrates that the reference points vary roughly a factor of two around the value found using the default parameters. This variation is surprisingly small considering the quite large variation in the parameters and the sensitivity of survivorships to variations in natural mortality a (eq. 9).

The most important parameter determining the value of the reference points is the natural mortality, a (Fig. 9). There is an obvious negative relation between natural mortality and the maximum fishing mortality F_{crash} that a stock can tolerate. What is less obvious is that the fishing mortality leading to the maximum yield F_{msy} is an increasing function of a as long as a is small (significantly smaller than the default value of $a = 0.35$). The fishing mortality that leads to maximum yield per recruit F_{msyr} is a good predictor of F_{msy} for small values of a because the stock is not recruitment limited, i.e. $R \approx R_{\text{max}}$. For higher natural mortalities

fishing at F_{msy} leads to a reduction in recruitment such that F_{msyr} is no longer a good predictor of F_{msy}. F_{msyr} is a particularly ill-suited reference point for stocks with a high natural mortality, as it may well be larger than both F_{lim} and F_{crash}.

Discussion

We have made a physiological reformulation of the classic Beverton-Holt single-species theory for assessing the impact of fishing on a fish stock. The theory builds on the Beverton-Holt theoretical framework but draws on modern elements from life-history theory, size-spectrum theory and metabolic theory. The basal assumptions are similar to the Beverton-Holt framework with two adjustments: natural mortality is size-dependent (Beyer, 1989) and the growth function is bi-phasic with an explicit representation of effort spent on reproduction (Lester et al., 2004).

The physiological formulation is similar to the "metabolic" formulation of population dynamics (Brown et al., 2004) due to the reliance on a central assumption of consumption scaling as a power-law with size. In contrast to the metabolic theory the size-based framework explicitly considers a structured population. Because of the "metabolic" scaling assumption (1) many relationships can be described as power laws with scaling exponents n or $n-1$, e.g. P/B (Andersen et al. 2009) and yield-per-recruit. However, the added complexity introduced by the structured population leads to two counter-intuitive predictions that will be discussed below: 1) egg production per recruit in an unfished population is an increasing function of W_∞ and 2) reference points do not obey metabolic scaling rules.

Density dependence

Egg production per recruit scales as $W_\infty^{1-a} \approx W_\infty^{0.65}$. As it increases with asymptotic size there is a systematic variation in the degree of density dependence as a function of W_∞: large species have strong density dependence ($R_p/R_{\mathrm{max}} \gg 1$) while small species have a more linear stock-recruitment curve ($R_p/R_{\mathrm{max}} \lesssim 10$). In other words: large species have approximately constant recruitment while small species have a linearly increasing stock recruitment-relationship. This qualitative result is in accordance with the pattern of density-dependence observed in the Barents Sea (Dingsør et al, 2007) and with cross-species analysis across systems (Goodwin et al, 2006). The difference in density dependence between small and large species can be used to hypothesize that there are systematic differences in the impact of fishing and environmental changes on recruitment. Because recruitment of large species is saturated (when they are not heavily fished) they are insusceptible to conditions that influence survival at early life. They will however be sensitive to environmental changes that influence the carrying capacity of the stock characterized by R_{max}. In contrast, small species are predicted to be on the rising part of the stock-recruitment curve and are susceptible to conditions influencing egg survival. Hence, environmental changes can be expected to lead to large year-to-year fluctuations in recruitment of small species. Further, fishing will impact recruitment directly leading to recruitment overfishing.

Reference points

The difference in density dependence between species highlights the importance of accounting for recruitment when reference points are estimated – purely relying on demographics, i.e. using constant recruitment, does not guarantee a reliable assessment of the fishing mortality at maximum sustainable yield. The predicted reference points were compared to "observed" reference points used in practical management. The estimation procedure for these observed reference points varied between stocks and it should be kept in

mind that the estimations in all cases are quite uncertain. Nevertheless, it is clear that the observed reference points do not vary with W_∞ as predicted by metabolic scaling rules. Metabolic scaling rules are therefore unsuited to parameterize unstructured models, like surplus production models and EcoPath (Christensen and Pauly, 1992). The only reference point that obeys metabolic scaling rules is $F_{\mathrm{msyr}} \propto W_\infty^{-1/4}$ since it does not rely on recruitment. F_{msyr} is often used as a reference point (e.g. Le Quesne and Jennings, 2012). For large species F_{msyr} may be a reasonable predictor of F_{msy} if natural mortality is low but for small species F_{msyr} is an unsuitable reference point since it may even be higher than F_{crash}.

Assumptions

How does these two central predictions depend on the assumptions? Assumption 5 states that density-dependence is regulated by processes happening early in life, represented by a stock-recruitment relationship. This has been a standard procedure since Ricker (1954) and Beverton and Holt (1959) and is supported by data for some well-studied stocks (Elliott 1989). However, this procedure has come under pressure due to the increasing amount of evidence of density dependent control by growth (Lorenzen and Enberg, 2002), maturation (Persson et al. 1998) or cannibalism (Persson et al 2003). To understand how our results rely on assumptions of growth, mortality and density dependent control (assumption 1, 2 and 5) it is instructive to consider the F_{crash} reference point. When the population is unfished density-dependent control is at its maximum. As F increases the density dependent regulation of growth, recruitment and mortality needed to keep the unfished population in balance is gradually replaced by the impact of fishing. Eventually, at $F = F_{\mathrm{crash}}$ where the population is at the brink of extinction, density dependent regulation is completely absent. Since there is no density dependent regulation at F_{crash}, the shape of F_{crash} as a function of W_∞ is independent on *how* density dependence operates, i.e. on whether density dependence is due to growth, mortality or the stock-recruitment relation. Instead F_{crash} is determined by the *amount* of density-dependent regulation that is substituted by fishing mortality before the population crashes. The amount of density-dependent regulation is measured by the egg production per recruit from density-independent processes, which was found to be $R_p/R \propto W_\infty^{1-a} \approx W_\infty^{0.65}$. If the egg-production per recruit would have been independent of W_∞, the amount of density dependent control in the unfished state would be independent of W_∞ and F_{crash} would follow metabolic scaling rules. Since egg-production does depend on W_∞, we conjecture that the two conclusions about recruit production and reference points would be the same with other types of density dependent control than the (convenient) stock-recruitment relationship. Which assumptions, then, determines egg-production per recruit? These are essentially the assumptions related to growth and mortality; the "n" exponent in (1) and the "$n-1$" exponent and the "a" constant in (2). A recent comprehensive data-analysis of mortality (Gislason et al. 2010) suggested that mortality does not follow the metabolic law with exponent $n-1$ but instead scales with w and W_∞ as $\mu \propto w^{-1/2} W_\infty^{1/6}$ (Charnov et al. 2012). Using this assumption makes egg production per recruit almost independent of asymptotic size (Gislason et al 2008) and following the logic rolled out above this implies that F_{crash} approximately obeys the metabolic scaling rule. However, this result is in violation of the data from reference points that we have collected, which clearly do not obey the metabolic scaling rule. This apparent contradiction may be understood by accepting that mortality and growth measured on natural populations are composed of density-independent and density-dependent contributions. About 60 % of the populations analysed by Gislason et al. (2010) were from unfished populations where density-dependent control presumably is strong. Therefore, if the Charnov et al. (2012) mortality scaling were to be applied to determine fisheries reference points, the density-dependent contribution needs to be explicitly

subtracted first. Partitioning of growth and mortality into density-independent and density-dependent processes is no simple matter, as it requires analysing time-series of abundance, growth and mortality in conjunction with a model of density-dependence (Lorenzen and Enberg, 2002; Lorenzen 2008). In summary: our specification of growth and mortality represent density *in*dependent processes and all density-dependence is parameterized into the stock-recruitment relationship. We argue that a different representation of density-dependence would yield qualitatively similar functional relationships between reference points and asymptotic size. We call for further empiric examinations of the nature of density-dependent regulation (sensu Lorenzen and Enberg 2002; Lorenzen, 2008) and theoretic examinations of the consequence of different types of density-dependence on reference points.

Applications

Since the theory only relies on asymptotic size it is convenient for use as a starting point in data-poor situations where the asymptotic size can be estimated as the largest fish caught. If a size-distribution of the catch is known, the fishing mortality can be estimated which may be compared to the reference points calculated from the "default" life-history invariant parameters. If additional information from the specific stock is available, e.g. gonado-somatic index, mortality, etc., the predictions will improve. The theory therefore provides a framework that can be applied for genuine data-poor situations, where only the size-distribution of the catch is known, as well as for data-rich situations where default life-history invariants can be replaced by more accurate stock-specific estimates. A promising way to improve the assessment of the life-history parameters is to use the "Robin Hood" approach by borrowing information from phylogenetic related data-rich stocks (Smith et al., 2009). In addition to being a useful starting point in data-poor situations, the theory can be applied to obtain insight into the response of fish stocks to fishing in general. As an example, we used the theory to predict how species with small and large asymptotic size are expected to have systematic differences in density dependence and therefore systematic differences in their fisheries reference points. Other related applications would be to test the impact of different types of size-selection, like the "balanced" selection (Garcia et al. 2012; Law et al.., 2012) or gill-net selectivity, or to examine the relative importance of young vs. old individuals for recruitment to test the "BOFF" hypothesis across life-histories (Morgan 2008). The calculations have been performed for a stock in demographic equilibrium, but the theory can be applied out of equilibrium by using the time-dependent McKendric-von Foerster equation (B1), e.g. to test how fishing influences the stability of population dynamics as a function of W_∞. The theory can be used for life-history optimization calculations or quantitative genetics calculations of fisheries induced evolution (Jørgensen et al. 2007, Andersen and Brander, 2009). Further, the single-species model provides the basis for multi-species models where mortality and growth are calculated dynamically based on the abundance of predators and available food (Andersen and Ursin, 1977; Andersen and Beyer, 2006). This approach can be realized either in trait-based models (Pope, et al., 2006; Andersen and Pedersen, 2010) or in species-based models (Hall et al., 2006). Finally the theory can be applied in a practical fisheries management context for determining fisheries reference points, as a basis for statistical stock-assessment models, or for making impact assessment of fisheries management measures, e.g. rebuilding and recovery plans or changes in gear size regulations. Such management applications may cover any data situation from the poorest to situations where life-history parameters are well known.

Acknowledgements

References

Andersen, K. H. and Beyer, J. E. (2006). Asymptotic size determines species abundance in the marine size spectrum. *The American Naturalist*, 168:54–61.

Andersen, K. H. and Brander, K. (2009). Expected rate of fisheries-induced evolution is slow. *Proceedings of the National Academy of Science U.S.A.*, 106(28):11657–11660.

Andersen, K. H., Beyer, J. E., Pedersen, M., Andersen, N. G., & Gislason, H. (2008). Life-history constraints on the success of the many small eggs reproductive strategy. *Theoretical population biology*, *73*(4), 490-497.

Andersen, K. H., Farnsworth, K., Pedersen, M., Gislason, H., and Beyer, J. E. (2009). How community ecology links natural mortality, growth and production of fish populations. *ICES Journal of Marine Science*, 66:1978–1984. doi:10.1093/icesjms/fsp161.

Andersen, K. H. and Pedersen, M. (2010). Damped trophic cascades driven by fishing in model marine ecosystems. *Proceedings of the Royal Society of London B*, 277:795–802.

Andersen, K. P. and Ursin, E. (1977). A multispecies extension to the Beverton and Holt theory of fishing, with accounts of phosphorus circulation and primary production. *Meddelelser fra Danmarks Fiskeri- og Havundersøgelser*, 7:319–435.

Bagge, O., Thurow, F., Steffensen, E., and Bay, J. (1994). The Baltic cod. *Dana*, 10:1–28.

Beddington, J. and Kirkwood, G. (2005). The estimation of potential yield and stock status using life–history parameters. *Philosphical Transactions of the Royal Society of London B*, 360(1453):163–170.

Bertalanffy, von L. (1957). Quantitative Laws in Metabolism and Growth. *Quarterly Review of Biology*, (3):217–231.

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

Beverton, R. J. H. and Holt, S. J. (1959). A review of the lifespans and mortality rates of fish in nature and the relation to growth and other physiological characteristics. In Ciba foundation colloquia in ageing. V. The lifespan of animals, pages 142–177. Churchill, London.

Beyer, J. E. and Lassen, H. (1994). The effect of size-selective mortality on the size-at-age of Baltic herring. *Dana*, 10:203–234.

Beyer, J. E. (1989). Recruitment stability and survival – simple size-specific theory with examples from the early life dynamic of marine fish. *Dana*, 7:45–147.

Brooks, E. N., Powers, J. E., and Cortés, E. (2009). Analytical reference points for age-structured models: application to data-poor fisheries. *ICES Journal of Marine Science*, 67(1):165–175.

Brown, J., Gillooly, J., Allen, A., Savage, V., and West, G. (2004). Toward a metabolic theory of ecology. *Ecology*, 85(7):1771–1789.

Charnov, E. L. (1993). *Life history invariants*. Oxford University Press, Oxford, England. 25

Charnov, E. L. and Berrigan, D. (1991). Evolution of life history parameters in animals with indeterminate growth, particularly fish. *Evolutionary Ecology*, 5:63–68.

Charnov, E. L., Turner, T. F., and Winemiller, K. O. (2001). Reproductive constraints and the evolution of life histories with indeterminate growth. *Proceedings of the National Academy of Science U.S.A.*, 98(16):9460–9464.

Charnov, E.L., Gislason, H. and Pope, J.G. (2012) Evolutionary assembly rules for fish life histories. *Fish and Fisheries*: doi: 10.1111/j.1467-2979.2012.00467

Christensen, V. and Pauly, D. (1992) Ecopath II—a software for balancing steady-state ecosystem models and calculating network characteristics. *Ecological modeling* 61(3) 169-185.

Daan, N., Gislason, H., Pope, J. G., and Rice, J. C. (2005). Changes in the North Sea fish community: evidence of indirect effects of fishing?. *ICES Journal of Marine Science* 62(2), 177-188.

Day, T. and Taylor, P. D. (1997). Von Bertalanffy's growth equation should not be used to model age and size at maturity. *The American Naturalist*, 149(2): 381–393.

Denney, N., Jennings, S., and Reynolds, J. (2002). Life-history correlates of maximum population growth rates in marine fishes. *Proceedings of the Royal Society of London B*, 269:2229–2237.

Dingsør, G.E., Ciannelli, L., Chan, K.-S., Ottersen, G. and Stenseth, N.C. (2007) Density dependence and density independence during the early life stages of four marine fish stocks. *Ecology* 88(3): 625-634.

Elliott, J.M. (1989)   Mechanisms Responsible for Population Regulation in Young Migratory Trout, *Salmo trutta*. I. The Critical Time for Survival. *Journal of Animal Ecology*, (58)3 987-1001

Garcia, S.M., Kolding, J., Rice, J., Rochet, M.-J. , Zhou, S. et al. (2012) Reconsidering the Consequences of Selective Fisheries. *Science* 335: 1045-1047.

Gislason, H., Pope, J.G., Rice, J.C. and Daan, N. (2008) Coexistence in North Sea fish communities: implications for growth and natural mortality. *ICES Journal of Marine Science* 65, 514–530.

Gislason, H., Daan, N., Rice, J. C., and Pope, J. G. (2010). Size, growth, temperature and the natural mortality of marine fish. *Fish and Fisheries*, 11(2):149–158.

Goodwin, N. B., Grant, A., Perry, A. L., Dulvy, N. K., and Reynolds, J. D. (2006). Life history correlates of density-dependent recruitment in marine fishes. *Canadian Journal of Fisheries and Aquatic Science*, 63(3): 494–509.

Gunderson, D. R. (1997). Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. *Canadian Journal of Fisheries and Aquatic Science*, 54(5): 990–998.

Hall, S. J., Collie, J. S., Duplisea, D. E., Jennings, S., Bravington, M., and Link, J. (2006). A length-based multispecies model for evaluating community responses to fishing. *Canadian Journal of Fisheries and Aquatic Science*, 63: 1344–1359. doi:10.1139/F06-039.

Hartvig, M., Andersen, K. H., and Beyer, J. E. (2011). Food web framework for size-structured populations. *Journal Theoretical Biology*, 272(1):113–122.

Jørgensen C., et al. (2007) Managing evolving fish stocks. *Science* 318:1247–1248.

Kaljuste, O. (1999). Changes in the growth and stock structure of Baltic sprat (*Sprattus sprattus balticus*) in the Gulf of Finland in 1986–97. *Proceedings of the Estonian Acadademy of Science, Biology and Ecology*,

48(4):296–309.

Kerr, S. (1974). Theory of size distribution in ecological communities. *Journal Fisheries Research Board of Canada*, 31(12):1859–1862.

Kooijman, S. A. L. M. (2000). *Dynamic Energy and Mass Budgets in Biological Systems*. Cambridge University Press, Cambridge, U.K.

Law, R., Plank, M. J., & Kolding, J. (2012). On balanced exploitation of marine ecosystems: results from dynamic size spectra. *ICES Journal of Marine Science* 69(4), 602-614.

Le Quesne, W.J.F. and Jennings, S. (2012) Predicting species vulnerability with minimal data to support rapid risk assessment of fishing impacts on biodiversity. *J. Applied Ecology.* 49:20-28.

Lester, N. P., Shuter, B. J., and Abrams, P. A. (2004). Interpreting the von Bertalanffy model of somatic growth in fishes: the cost of reproduction. *Proceedings of the Royal Society of London B*, 271:1625–1631.

Lorenzen, K. and Enberg, K. (2002). Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proc. R. Soc. Lond. B Biol. Sci.* 269: 49–54.

Lorentzen, K. (2008) Fish population regulation beyond "stock and recruitment": the role of density-dependent growth in the recruited stock. *Bulletin of Marine Science* 83(1): 181–196.

McGurk, M. D. (1986). Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. *Mar. Ecol. Prog. Ser*, *34*(3), 227-242.

Morgan, M. (2008). Integrating reproductive biology into scientific advice for fisheries management. *Journal of Northwest Atlantic Fisheries Science 41*, 37:51.

Moses, M. E., Hou, C., Woodruff, W. H., West, G. B., Nekola, J. C., Zuo, W., and Brown, J. H. (2008). Revisiting a model of ontogenetic growth: estimating model parameters from theory and data. *The American Naturalist*, 171(5):632–645.

Myers, R. A. and Cadigan, N. G. (1993). Density-dependent juvenile mortality in marine demersal fish. *Canadian Journal of Fisheries and Aquatic Science*, 50(8):1576–1590.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *Journal Conseil Internatineux Exploration du Mer*, 39(2):175–192.

Persson, L., Leonardsson, K., de Roos, A.M., Gyllenberg, M. And Christensen, B. (1998) Ontogenetic scaling of foraging rates and the dynamics of a size-structured consumer-resource model, *Theoretical Population Biology* (54)3 270--293

Persson, L., de Roos, A.M., Claessen, D., Byström, P., Lövgren, J., Sjögren, S., Svanbäck, R., Wahlström, E. And Westman, E. (2003) Gigantic cannibals driving a whole-lake trophic cascade. *Proceedings of the National Academy of Sciences* (100)7 4035-4039.

Peterson, I. and Wroblewski, J.S. (1984) Mortality Rate of Fishes in the Pelagic Ecosystem. *Can. J . Fish. Aqua. Sci.*, 41: 1117-1120.

Pope, J. G., Rice, J. C., Daan, N., Jennings, S., and Gislason, H. (2006). Modelling an exploited marine fish community with 15 parameters – results from a simple size-based model. *ICES Journal of Marine Science*, 63:1029–1044.

Ricker, W. E. 1954. Stock and recruitment. *J. Fish. Res. Board Can*. 11: 559–623.

Sheldon, R., A. Prakash, and W. Sutcliffe (1972). The size distribution of particles in the ocean. *Limnology and Oceanography* 17:327– 340.

Sheldon, R. W., Sutcliffe Jr, W. H., & Paranjape, M. A. (1977). Structure of pelagic food chain and relationship between plankton and fish production. *Journal of the Fisheries Board of Canada*, *34*(12), 2344-2353.

Shin, Y.-J. and Cury, P. (2004). Using an individual-based model of fish assemblages to study the response of size spectra to changes in fishing. *Canadian Journal of Fisheries and Aquatic Science*, 61:414–431.

Smith, D., Punt, A., Dowling, N., Smith, A., Tuck, G., and Knuckey, I. (2009). Reconciling approaches to the assessment and management of data-poor species and fisheries with Australia's harvest strategy policy. *Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science*, 1:244–254. doi:10.1577/C08-041.1.

Ware, D.M. (1978) Bioenergetics of pelagic fish: theoretical change in swimming speed and ration with body size. *J. Fish. Res. Board. Can.* 35:220-228.

West, G. B., Brown, J. H., and Enquist, B. J. (1997). A general model for the origin of allometric scaling laws in biology. *Science*, 276:122–126.

West, G. B., Brown, J. H., and Enquist, B. J. (2001). A general model for ontogenetic growth. *Nature*, 413:628–631.

Williams, E. H. and Shertzer, K. W. (2003). Implications of life-history invariants for biological reference points used in fishery management. *Canadian Journal of Fisheries and Aquatic Science*, 60:710–720.

Winberg, G. G. (1956). Rate of metabolism and food requirements of fishes. *Journal Fisheries Research Board of Canada*, 194:1–253.

Appendix A. Fitting growth parameters to obtain A

The growth function (6) contains two species-independent constants that must be determined: the exponent for the consumption n and the growth constant A. Growth in fishes is usually described by a von Bertalanffy growth equation based on measurements of length and age. The von Bertalanffy equation corresponds to (6) provided that $n = 2/3$, $\psi_m = 1$ and an isometric relation between weight and length l: $w \propto l^3$. In that case length-at-age t is: $l(t) = L_\infty(1 - e^{-Kt})$. We have collected values of von Bertalanffy growth constants K and L_∞ for species with asymptotic lengths between 3 and 400 cm, and corrected them to a common temperature of 10°C using a Q_{10} of 1.83 as described by Kooijman (2000), where Q_{10} describes the relative change of K when the temperature is changed 10°C (Fig. 2b).

The growth curve generated by (6) is not a von Bertalanffy growth curve because of the switch in allocation of energy around the size of maturation. However the growth curve generated by (6) (for given values of A and n) can be fitted quite well with a standard von Bertalanffy growth curve to determine the two constant K_{fit} and $L_{\infty fit}$. We have done this by calculating length-at-age from numerical solutions of (6) at ten ages between age 1 and the age where individuals reach 95 % of the asymptotic length (the results are not sensitive to the choice of these two ages) (Fig. A1). We have then used a least-squares optimization to find the value of A that minimizes the difference between the observed $K_{obs.i}$ and fitted $K_{fit.i}$ values of K for the ith observation as: $\min_{A}\{\sum_i(\log(K_{obs.i}) - \log(K_{fit.i}))^2\}$. Using a value of $n = 2/3$ gave a value of $A = 5.2\ g^{0.25}\text{yr}^{-1}$ with $r^2 = 0.47$. Using $n = 3/4$ gave a better fit: $r^2 = 0.58$ and $A = 4.47\ g^{0.25}\text{yr}^{-1}$. The best fit was with $n = 0.81$ leading to $= 4.46\ g^{0.25}\text{yr}^{-1}$, $r^2 = 0.63$. We have used $n = 3/4$ as it conforms best with metabolic theory. The fitted values of K lie on a straight line in a log-log plot as a function of L_∞ (Fig. 2b). Using $n = 3/4$ gave a relation between the von Bertalanffy parameters which was $K \propto L_\infty^{-0.78}$.

In summary: if an exponent $n = 3/4$ is used for the growth function the relation between the K and L_∞ is approximately $K \propto L_\infty^{-0.78}$, in good agreement with other investigations (Shin and Cury, 2004 Appendix B). Since K varies systematically with asymptotic size it is not an appropriate measure of growth rate, because it becomes difficult to ascertain directly whether the species grows fast or slow without first compensating for the variation with asymptotic size. We therefore encourage A as a measure of growth rate instead of K, which is commonly used.

The value of n does not matter for the qualitative results of the theory but it will impact the exact results of e.g. reference points. Using $n = 2/3$ is the obvious choice as it conforms to the classic use of the von Bertalanffy growth equation in fisheries science (it is also used in our previous works: Andersen et al. 2009; Andersen and Brander, 2009), while $n = 3/4$ would conform to modern metabolic theory (West et al., 2001). Metabolic theory bases the scaling of the growth rate on the scaling of standard metabolism, which is known to be high for fish, around 0.86 (Winberg, 1956). However, metabolic theory does not account for how activity metabolism scales with size, and an empirical assessment of n based on standard metabolism is not sufficient (Moses et al., 2008). Our fitting of growth curves demonstrated that $n = 3/4$ actually gave a better fit to the dataset on growth parameters than $n = 2/3$. To finally settle the matter on the value of n requires a data-analysis that is based on the raw length-at-age data in the full size range and not just the von Bertalanffy growth parameters. We therefore call for a cross-species estimation of n based on raw size-at-age data.

Appendix B. Determining the size-spectrum from growth and mortality

Knowing the growth rate (6) and mortality (2) the size spectrum can be determined as a

solution to the McKendric-von Foerster equation:

$$\frac{\partial N(w)}{\partial t} + \frac{\partial g(w)N(w)}{\partial w} = -\mu(w)N(w), \tag{B1}$$

where $\mu(w)$ is the total mortality. This equation is equivalent to a standard life-table approach just written in continuous time for a size-structured population. In steady state $\partial N/\partial t = 0$ and (B1) can be written as:

$$\frac{\partial g(w)N(w)}{\partial w} = -\frac{\mu(w)}{g(w)}g(w)N(w), \tag{B2}$$

which emphasizes the central role of the ratio between mortality and growth reflected in the a parameter in (2), which is the ratio between mortality and specific available energy. The concept of a "flux" is central in size-based theory. A flux is the biomass or number of individuals passing through a given size per time. For example, the flux of number of individuals through the size w is $g(w)N(w)$ (numbers per time), which is equivalent to number-at-size in classic size-discrete theory (Beyer 1989). Dividing by this flux on both sizes of eq. (B2) yields:

$$\frac{d \ln[g(w)N(w)]}{dw} = -\frac{\mu(w)}{g(w)}$$

with the solution:

$$\frac{N(w)}{R} = \frac{1}{g(w)} \exp\left(-\int_{w_r}^{w} \frac{\mu(\tilde{w})}{g(\tilde{w})} d\tilde{w}\right) = \frac{1}{g(w)} P_{w_r \to w} \tag{B3}$$

where R is the flux of recruits (numbers per time) at the size w_r:

$$R = g(w_r)N(w_r)$$

Mathematically R acts as a boundary condition for (B1) at w_r. The exponential term in (B3) is the survivorship $P_{w_r \to w}$ which in general must be solved numerically (Appendix C). It can be solved analytically for the case of von Bertalanffy growth ($\psi_m(w/W_\infty) = 1$) and size-independent (or none) fishing (Beyer 1989, Andersen et al. 2008). Such analytical solutions are useful for checking the accuracy of numeric calculations and for understanding the results of the theory. To demonstrate this we make an analytical calculation of the stock structure in Fig. 1c+d below. For juvenile fish ($\psi_m(w/W_\infty) = 0$) the exponential term in (B3) becomes

$$P_{w_1 \to w_2} = \left(\frac{w_2}{w_1}\right)^{-a} \left[\frac{1 - \epsilon_a \left(\frac{w_2}{W_\infty}\right)^{1-n}}{1 - \epsilon_a \left(\frac{w_1}{W_\infty}\right)^{1-n}}\right]^{\frac{a+a_F/\epsilon_a}{1-n}}, w_2 < w_m \tag{B4}$$

Thus when growth is governed by $g(w) = Aw^n[1 - \epsilon_a(w/W_\infty)^{1-n}]$ and mortality by the physiological mortalities a and a_F the number flux $R_2 = N(w_2)g(w_2)$ at size w_2 equals the number flux or recruitment at size w_1: $R_1 = N(w_1)g(w_1)$ multiplied by $P_{w_1 \to w_2}$. Note that the approximate survivorship (9) is recovered from (B4) when $w_1 \ll W_\infty$ and $w_2 \ll W_\infty$ which makes the term in the square bracket become ≈ 1.

Fig. 1c+d depicts the biomass density on a logarithmic size scale, i.e. the biomass $w^2 N(w)$. Mathematically this is because the biomass in a small size interval

$wN(w)\mathrm{d}w$ is proportional to $w^2N(w)\mathrm{d}\log w$. Starting with a biomass $w_1^2N(w_1)$ at w_1 we want to calculate the biomass $w_2^2N(w_2)$ at w_2. This is obtained directly from $R_2 = R_1P_{w_1\to w_2}$. Dividing by growth rate and multiplying by weight squared yields

$$w_2^2N(w_2) = \left(\frac{w_2}{w_1}\right)^{2-n-a}\left[\frac{1 - \epsilon_a\left(\frac{w_2}{W_\infty}\right)^{1-n}}{1 - \epsilon_a\left(\frac{w_1}{W_\infty}\right)^{1-n}}\right]^{\frac{a+a_F/\epsilon_a}{1-n}-1}w_1^2N(w_1)$$

where the first factor represents a biomass spectrum which explains why the biomass in Fig. 1c starts by increasing almost linearly with slope $2\text{-}n\text{-}a = 0.90$. In Fig. 1 the start biomass at $w_1 = 0.01W_\infty$ is set to 1. At the start of fishing $w_F = 0.05W_\infty$ the biomass has inceased by a factor of $5^{0.90} = 4.257$ which is reduced by 7% to 3.955 by the square-bracket factor with a_F=0. Considering now $w_1 = 0.05W_\infty$ the biomass at $w_2 = 0.25W_\infty$ will again increase by a factor of $5^{0.90} = 4.257$ which is reduced by 13% to 3.688 by the square-bracket factor with a_F=0. Thus, at the size of maturation $w_m = 0.25W_\infty$ (vertical dotted line in Fig. 1), the biomass has increased by a factor of $3.955\cdot 3.688 = 14.6$ in the absence of fishing. However, if fishing occurs with a_F=0.5 then this unfished biomass at w_m is reduced by the bracket to the power of $a_F/((1\text{-}n)\,\epsilon_a) = 2.5$ or by a factor of 0.408. Thus the biomass at w_m (vertical dotted line in Fig. 1d) increases to only $14.6\cdot 0.408 = 5.95$ when fishing takes place at a_F=0.5. Alternatively, expressing fishing by F, the fishing exponent of the square-bracket becomes $W_\infty^{1-n}F/(A(1\text{-}n)\,\epsilon_a) = 0.8333W_\infty^{0.25}$ for F=0.75 per year. For example, W_∞= 10 kg produces a power of 8.333 thereby reducing the biomass to 5% of the unfished biomass at w_m ($14.6\cdot 0.050 = 0.74$ cf. vertical dotted line crossing thick dashed line in Fig. 1c).

Similarly calculations for mature fish can take place based on the von Bertalanffy growth equation which produces the biomass equation above with ϵ_a replaced by 1 since the cost of reproduction also must be incorporated. Such analytical results will deviate slightly from correct numerical calculations because we are not considering smooth gear selection and maturity ogives.

Recruitment

The flux of eggs, R_p (numbers/time), is traditionally written as being proportional to the spawning stock biomass $R_p = \alpha B$. The spawning stock biomass B is the integral of the biomass density $N(w)w$ over the mature individuals. Dividing by the flux of recruits to size w_r, R (numbers/time), yields the spawning stock biomass per recruit (time·weight):

$$\frac{B}{R} = \int_{w_r}^{W_\infty} \psi_m\left(w/W_\infty\right)\frac{N(w)}{R}\,w\,\mathrm{d}w \tag{B5}$$

The egg production R_p is found by multiplying the spawning stock biomass by α (eq. 11 in main text):

$$\frac{R_p}{R} = \alpha\frac{B}{R} = \epsilon_r(1 - \epsilon_a)AW_\infty^{n-1}/w_{egg}\frac{B}{R} \tag{B6}$$

Combining (B6) with the Beverton-Holt recruitment relationship (10) and rearranging gives the recruitment:

$$\frac{R}{R_{max}} = 1 - \frac{R}{P_{w_{egg}\to w_r}R_p} = 1 - \frac{W_\infty^{1-n}w_{egg}}{\epsilon_r(1 - \epsilon_a)AP_{w_{egg}\to w_r}B/R} \tag{B7}$$

where B/R is found from (B5) using (B3) and the survivorship $P_{w_{egg} \to w_r} \approx (w_r/w_{egg})^{-a}$ becomes one since we here are considering recruitment R in numbers of eggs so $w_r = w_{egg}$.

Appendix C. Numerical solution procedure

Finding the size spectrum and the yield is a matter of solving equations (B3), (B5), (B7), and (12). The integrals involved in the expressions can be approximated by sums that are readily implemented in a spreadsheet. The procedure to determine the yield is a follows:

1. First construct a series of m weight classes w_i logarithmically distributed between w_r and W_∞: $w_i = \exp[\ln(w_r) + (i-1)\Delta]$ where $\Delta = (\ln W_\infty - \ln w_r)/(m-1)$. For the numerical calculations presented in the paper we used $m = 1000$.

2. Define the physiological mortality at each grid point as the mortality divided by specific growth:

$$a_i = \frac{\mu_p(w_i) + \mu_F(w_i)}{g(w_i)} w_i$$

where $\mu_p(w_i)$ and $g(w_i)$ are given by (2) and (6). Note that here the fishing mortality is written as $\mu_F(w)$ since it may vary differently with size than the particular form of trawl selectivity used in the main text.

3. Approximate N/R from (B3) as a discrete cumulative sum:

$$\frac{N_i}{R} \approx \frac{1}{g(w_i)} \exp\left(-\sum_{j=2}^{i} \frac{a_{j-1}}{w_{j-1}} \delta_j\right) \quad \text{for } i \geq 2 \tag{C1a}$$

where $\delta_j = w_j - w_{j-1}$. For the first grid point $N_1/R = 1/g(w_1)$ and for the last $N_m = 0$. The approximation (C1a) is the direct numerical approximation of the integral in (B3) by a sum. An alternative, and more accurate, approximation is to write $N_i = N_{i-1} P_{w_{i-1} \to w_i} g(w_{i-1})/g(w_i)$. The survivorship $P_{w_{i-1} \to w_i}$ can be approximated by (9) to give:

$$\frac{N_i}{R} \approx \frac{1}{g(w_i)} \prod_{j=2}^{i} \left(\frac{w_j}{w_{j-1}}\right)^{-a_{j-1}} = \frac{1}{g(w_i)} \exp\left[-\Delta \sum_{j=2}^{i} a_{j-1}\right] \quad \text{for } i \geq 2$$

$$\tag{C1b}$$

Also in this case the first grid point is $N_1/R = 1/g(w_1)$. This approximation makes it possible to reduce the number of weight classes.

4. Approximate the spawning stock biomass per recruit as B/R from (B5):

$$\frac{B}{R} \approx \sum_{i=1}^{m-1} \psi_m(w_i) \frac{N_i}{R} w_i \delta_{i+1} \tag{C2}$$

5. Calculate the relative recruitment R/R_{max} from (B7):

$$\frac{R}{R_{max}} = 1 - \frac{W_\infty^{1-n} w_{egg}}{\epsilon_r(1 - \epsilon_a)A} \frac{1}{P_{w_{egg} \to w_r}} \frac{R}{B} \tag{C3}$$

where the survivorship $P_{w_{egg} \to w_r} = 1$ if $w_r = w_{egg}$. If not, the approximate formula (9) for the survivorship should be sufficient, or the full formula (B4) can be applied. If

$R/R_{\text{max}} < 0$ the population is crashed.

6. Approximate the yield from (12) (here scaled with the maximum biomass flux of recruits):

$$\frac{Y}{R_{max}w_r} \approx F \frac{R}{R_{max}w_r} \sum_{i=1}^{m-1} \psi_F(w_i) \frac{N_i}{R} w_i \delta_{i+1}. \tag{C4}$$

7. Yield per recruit can be calculated from (C4) by multiplying with $R_{\text{max}}/R_{\text{F}}$ and with w_r/w_F where:

$$\frac{R_{\text{F}}}{R_{\text{max}}} = \frac{N(w_F)g(w_F)}{R_{\text{max}}} = \frac{N(w_F)}{R} \frac{R}{R_{\text{max}}} g(w_F)$$

with $N(w_F)/R$ and R/R_{max} calculated from (C1) and (C3) without fishing mortality, alternatively by using a size of recruitment to the fishery where $\psi_F(w_F) = 0$.

Appendix D. Steepness parameter

The Beverton-Holt stock-recruitment function is frequently characterized by the "steepness" parameter h. The steepness parameter is defined as the proportion of recruitment, relative to the recruitment at the equilibrium with no fishing, when the spawner abundance or biomass is reduced to 20% of the un-fished level. The steepness can be calculated as:

$$h = \frac{1 + R_p/R_{max}}{5 + R_p/R_{max}}$$

It is a monotonous function of asymptotic size with larger species having a higher steepness than smaller species (Fig. D1).

Appendix E. Web-based implementation

The model has been implemented as an interactive web-based application written in java-script. The application solves the full dynamic version of the model (B1) using finite-difference methods (Hartvig et al. 2011, App. G). It also demonstrates how a variation of the recruitment over the season can be implemented and the impact on the size-distribution of species of different asymptotic sizes. The application can be accessed at http://www.stockassessment.org/spectrum/

Table 1. Parameters and symbols used in the model and their relation to von Bertalanffy parameters K and L_∞, adult mortality M, and individual length l. $q = 0.01$ g cm^{-3} is the constant of proportionality between length^3 and weight.

Symbol	Parameter or symbol	Value$^{\$\$}$ (range*)	Relation to "classic" parameters
A	Growth constant (eq. 1)¶	4.5 g^{1-n}yr^{-1} ($\sigma = 0.5$)	$A = 3\, q^{1-n} K L_\infty^{3(1-n)}$
n	Exponent for consumption (eq. 1,2)¶	3/4	
a	Physiological mortality (eq. 2)§	0.35 (c.v. = 0.5)	$a \approx M/(3K)\eta_m^{1-n}$
W_∞	Asymptotic size (weight) (eq. 5a)	Stock specific	$W_\infty = qL_\infty^3$
u_m, u_F	Width of switching functions (eq. 3)	10	
ϵ_a	Fraction of energy for activity$^{\$}$ (eq. 5b)	0.8	
η_m	Size at maturation rel. to W_∞ (eq. 3)**	0.25 (c.v. = 0.3)	$\eta_m = (L_m/L_\infty)^3$
ϵ_r	Recruitment efficiency (eq. 11)†	0.1 ($\sigma = 0.5$)	
w_{egg}	Weight of an egg (eq. 11)	1 mg	
η_F	Start of fishing rel. to W_∞	0.05 ($\sigma = 0.5$)	
w	Individual weight (eq. 1)	weight	$w = ql^3$
$\mu_p(w)$	Predation mortality (eq. 2)	1/time	
k_a and k_r	Specific investment into activity and reproduction	1/time	
$g(w)$	Growth rate (eq. 6)	weight/time	
$N(w)$	Abundance spectrum (eq. 7)	numbers/weight	
$P_{w_1 \to w_2}$	Survivorship from w_1 to w_2 (eq. 9, B4)	-	
B	Spawning stock biomass (eq. B5)	biomass	
α	Recruitment parameter (eq. 11)	numbers biomass^{-1}time^{-1}	
w_r	Weight at recruitment (eq. B5)	weight ($= w_{egg}$)	
R_p	Egg production (physiological recruitment) (eq. 10, B6)	numbers/time	
R	Recruitment (eq. 10, B7)	numbers/time	
R_{max}	Maximum recruitment (eq. 10)	numbers/time	
Y, Y_r	Yield and yield per recruit (eq. 12)	biomass/time and -	
F	Fishing mortality	time^{-1}	
a_F	Physiological fishing mortality (eq. 13)	-	$a_F \approx F/(3K)$

* Ranges specified by σ are normal distributed on log-transformed variables. Ranges specified by c.v. are normal distributed with c.v. being the coefficient of variation, and constrained to be positive.

$^{\$\$}$Note that we distinguish between dimensions of *weight*, which refer to individual weight, and *biomass,* which equals numbers·weight.

§The value of a is determined from its relation to the M/K life history invariant (Andersen et al, 2009). The value of a used in

Andersen et al. (2009) was $a = 0.2$, but here the value has been increased to comply better with the recent dataanalysis of natural mortality on fish by Gislason et al (2010).

$Fitted to data by Gunderson (1997), see Fig. 2a.

¶See Appendix A. Notice that A is represented by $\hbar$ in some of our earlier works.

**Beverton (1992).

†See (Hartvig et al, 2011, Appendix E).

Table 2. Reference points and physiological parameters for the stocks used in Fig. 8.

Species	W_∞ (kg)	K (yr^{-1})	F_{lim} (yr^{-1})	F_{msy} (yr^{-1})
North Sea				
Cod [a]	23	0.16	0.86	0.19
Herring [a]	0.42	0.35	-	0.25
Haddock [a]	2.7	0.1	1.0	0.3
Plaice [a]	1.25	0.15	0.74	0.25
Saithe	30	0.05	0.6	0.3
Sole [a]	1.1	0.35	-	0.22
Baltic Sea, ICES area 25				
Cod [b]	22	0.15	0.96	0.3
Herring [c]	0.1	0.53	-	0.16
Sprat [d]	0.015	0.55	-	0.35
Irish Sea				
Cod [a]	18	0.22	1	0.4
Sole [a]	0.85	0.26	0.4	0.16
Barents Sea				
Cod [a]	22	0.1	0.74	-
Haddock [a]	9	-	0.77	0.35
Saithe [a]	9	-	0.58	-
Bay of Biscay				
Sole	-	-	0.58	0.26
Anglerfish [a]	11	0.18	-	0.28

All reference points are from the 2011 reports of stock assessments conducted within ICES. Growth estimates are from: a: Denney et al. (2002); b: Bagge et al. (1994); c: Beyer and Lassen (1994); d: Kaljuste (1999).
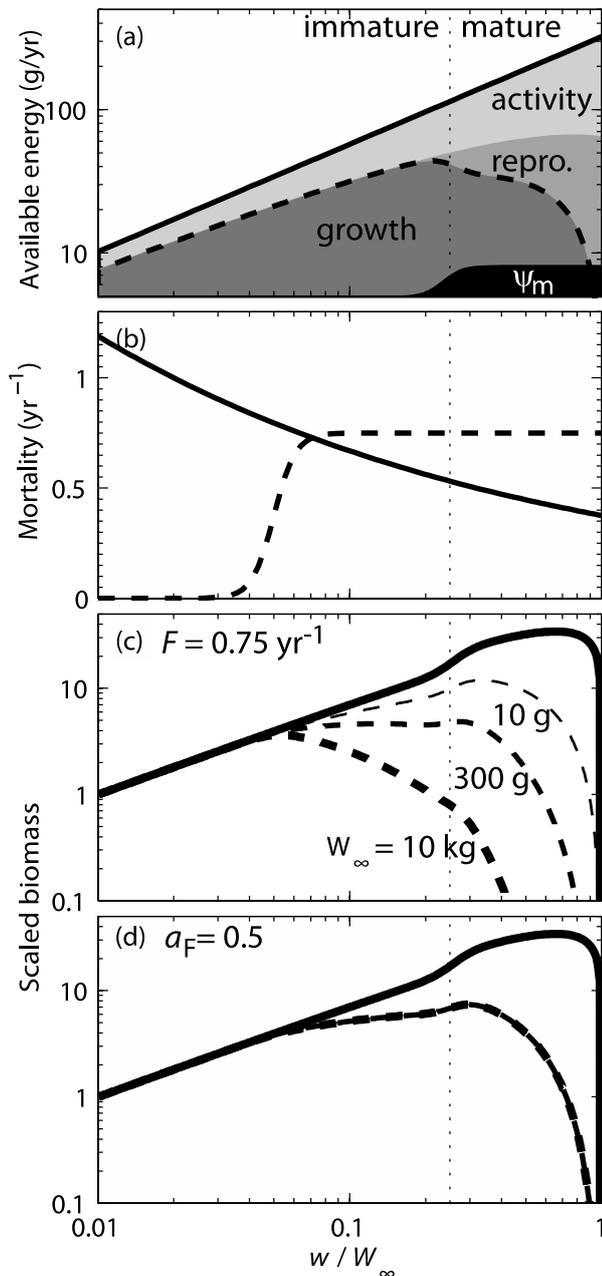
Figure 1. Growth (a), mortality (b), and stock structure (c+d) of a fish population as a function of size divided by asymptotic size. a) Available energy (solid line) of a fish with asymptotic size 300 g is used for activity (light grey), reproduction (medium grey) and somatic growth (dark grey). The boundary of the black patch illustrates the maturity ogive $\psi_m(w)$ (not to scale) that switches between zero and 1 around the size of 50% maturation (vertical dotted line). Growth rate (dashed) increases with size until the size at maturation after which it declines as energy is invested in reproduction. b) Natural mortality is a decreasing function of size (solid line). Fishing mortality is modeled as a trawl selectivity increasing smoothly around $w = 0.05W_\infty$ (dashed line). c+d) Stock structure shown as biomass spectra $w^2 N(w)$ for species with $W_\infty = 10$ g, 300 g and 10 kg (thin, medium, and thick lines) for unfished (solid lines) and fished situations (dashed lines). The soft kink in the spectra around the size at maturation is due to the decline in growth rate around the size of maturation. In panel (c) fishing mortality is constant for all asymptotic size groups at $F = 0.75$ yr^{-1} while in panel (d) fishing mortality is scaled with metabolism as a physiological fishing mortality $a_F = 0.5$ corresponding to $F \approx 1.3, 0.54$ and 0.23 yr^{-1} for the three species. In that case the fished spectra for all three species are identical and therefore lie on top of one another. The spectra are scaled such that they coincide at $w = 0.01W_\infty$.
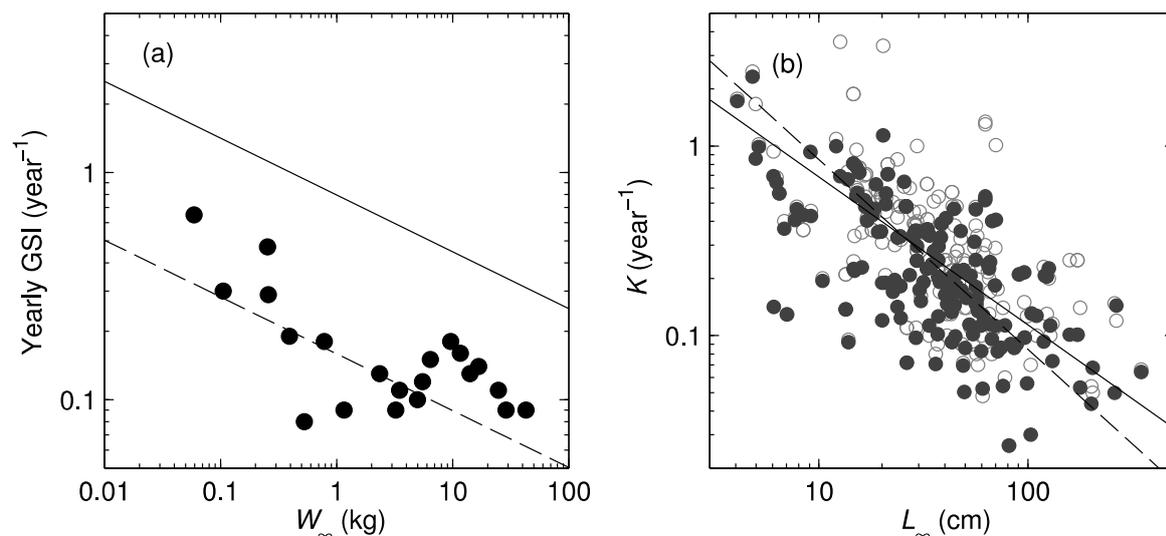
Figure 2. a) Yearly weight-specific allocation to egg production as a function of asymptotic size (black circles; data from Gunderson, 1997), compared to the maximum possible allocation per weight to reproduction $k_a + k_r$ (solid line), and the actual allocation $k_r \propto W_\infty^{-1/4}$ (dashed line). b) von Bertalanffy growth constant K as a function of asymptotic length, corrected from raw data points (open circles) to a temperature of 10°C (grey points). Fits to a standard von Bertalanffy growth function using $n = 2/3$ (dashed line; $r^2 = 0.47$), and to (4) using $n = 3/4$ (solid line; $K \propto L_\infty^{-0.78}$; $r^2 = 0.58$). For details of the fitting procedure, see Appendix A. Data points are from Gislason et al. (2010) and Kooijman (2000).
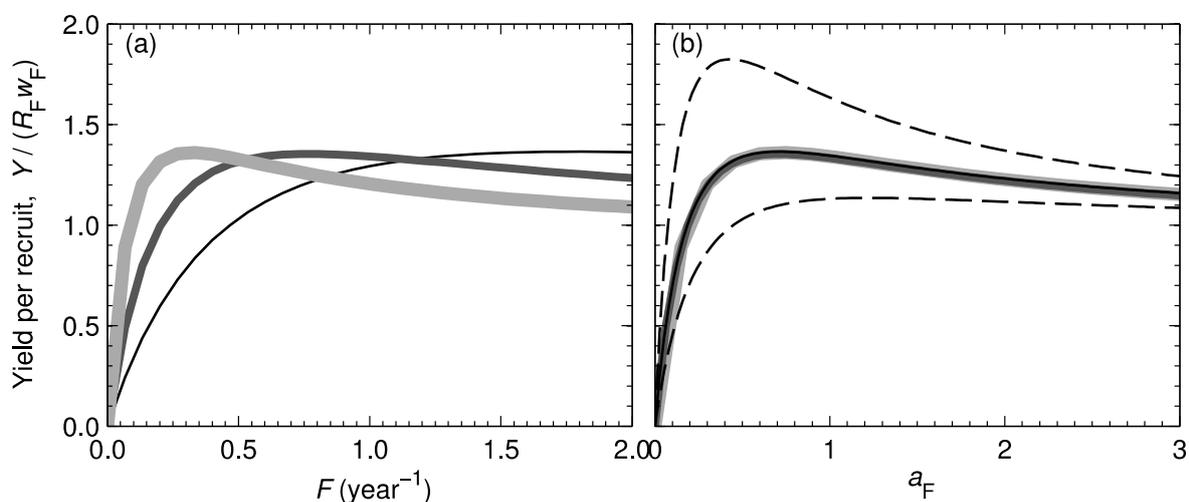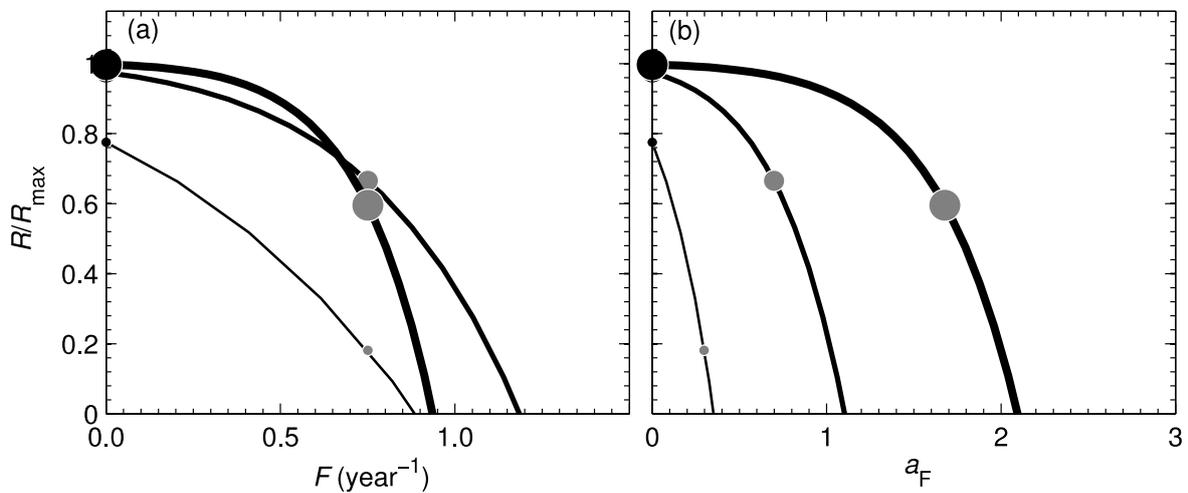

Figure 3. Yield per recruit to the fishery as a function of fishing mortality measured in absolute units (a) and physiological units (b) for species with $W_\infty = 10$, 300 g and 10 kg (thin, medium and thick lines). Dashed lines on (b) are for high and low natural mortality ($a = 0.45$ and 0.25). Note that all yield per recruit curves from panel (a) coincide in panel (b).
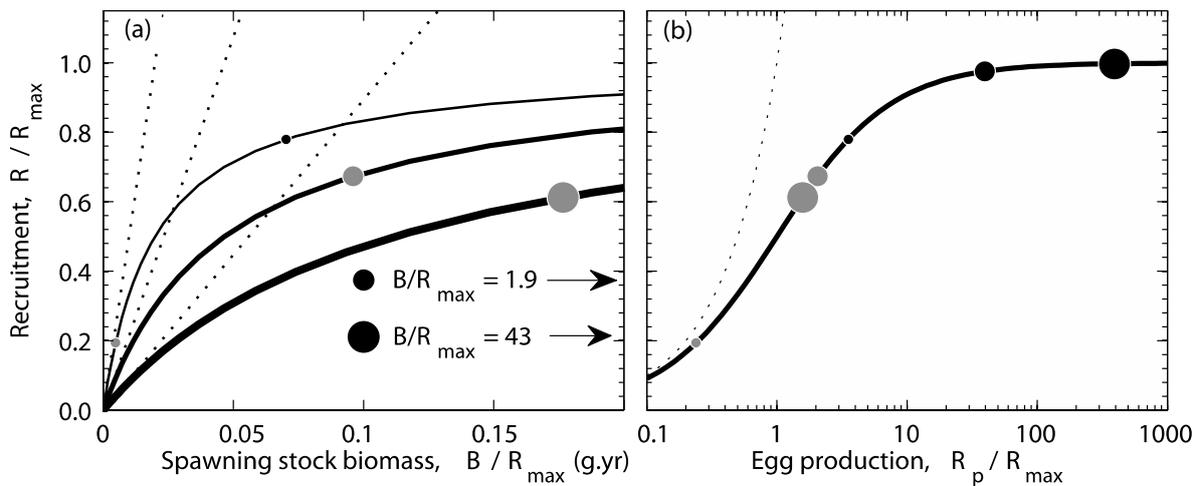
Figure 4. Recruitment for species with W_∞ = 10 g, 300 g and 10 kg (thin, medium and thick lines and symbols) for an un-fished situation (black symbols) and fished with $F = 0.75$ yr^{-1} (grey symbols). a) Beverton-Holt recruitment curves as function of spawning stock biomass $B/R_{\mathbf{max}}$. Note that the spawning stock biomasses for the two largest species in the un-fished situation are so large that they are outside the panel ($B/R_{max} = 1.9$ and 43 g· yr for W_∞ = 300 g and 10 kg). The thin dotted lines represent the initial slopes α of the recruitment curves. b) Beverton-Holt recruitment curves as a function of egg production (physiological recruitment) R_p on a logarithmic axis.

Figure 5. Recruitment as a function of fishing mortality in absolute units (a) and physiological units (b) for species with W_∞ = 10 g, 300 g and 10 kg (thin, medium and thick lines and symbols). The grey symbols correspond to a fishing mortality of $F = 0.75$ yr^{-1}.
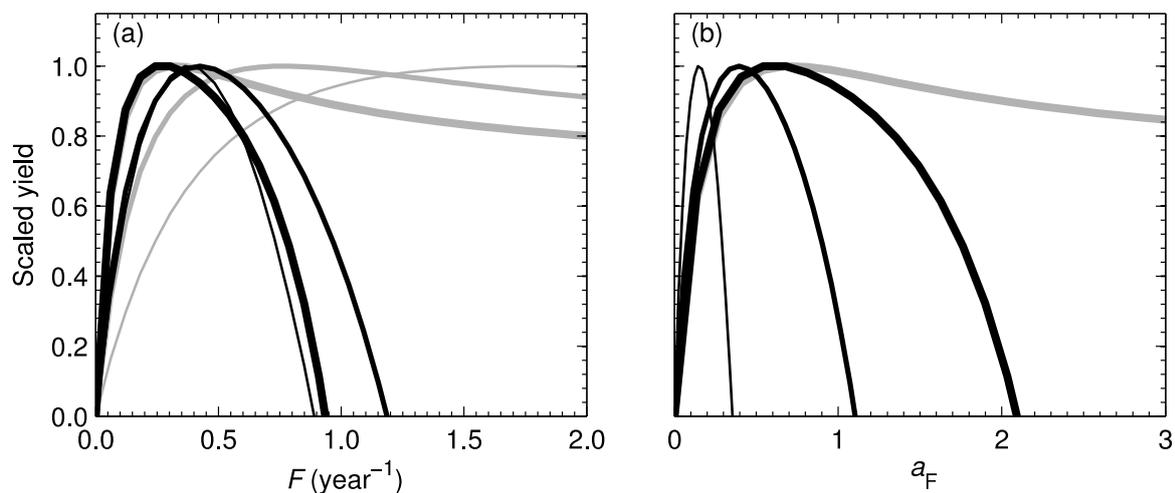
Figure 6. Yield as a function of fishing mortality for species with $W_\infty = 10$ g, 300 g and 10 kg (thin, medium and thick black lines), and yield per recruit (grey lines), as a function of fishing mortality measured in absolute units (a) and physiological units (b). Both yield and yield per recruit are scaled by the maximum yield or yield per recruit. The three yield per recruit curves in panel (b) coincide just as in Fig. 3b.
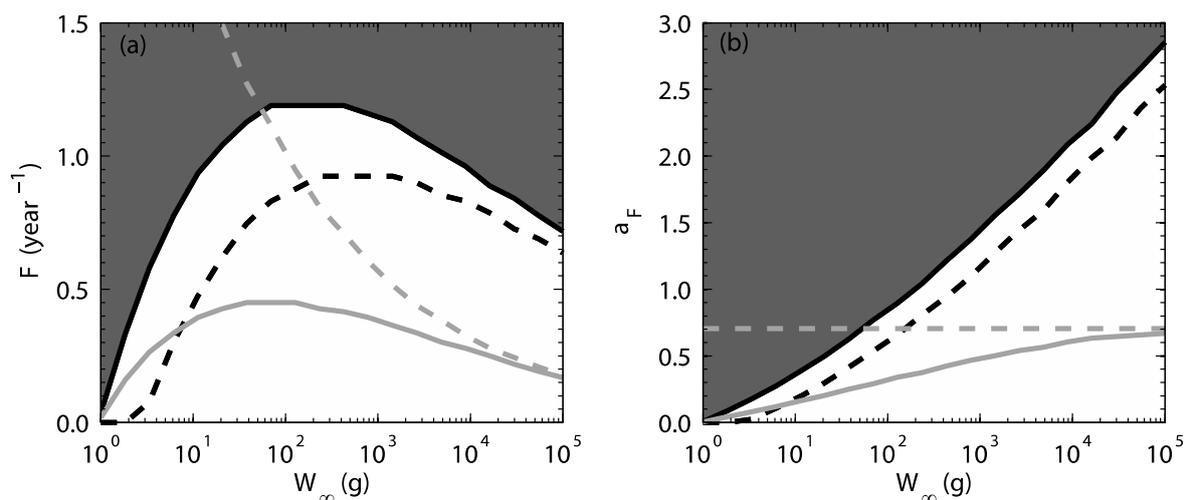

Figure 7. Fisheries reference points as a function of fishing mortality measured in absolute units (a) and physiological units (b). Reference points: F_{msy} (fishing mortality at maximum yield; solid grey), F_{msyr} (fishing mortality at maximum yield per recruit; dashed grey), F_{crash} (fishing mortality where the population goes extinct; solid black), F_{lim} (fishing mortality at 50% reduced recruitment; dashed black). The grey area is where the stock has crashed.
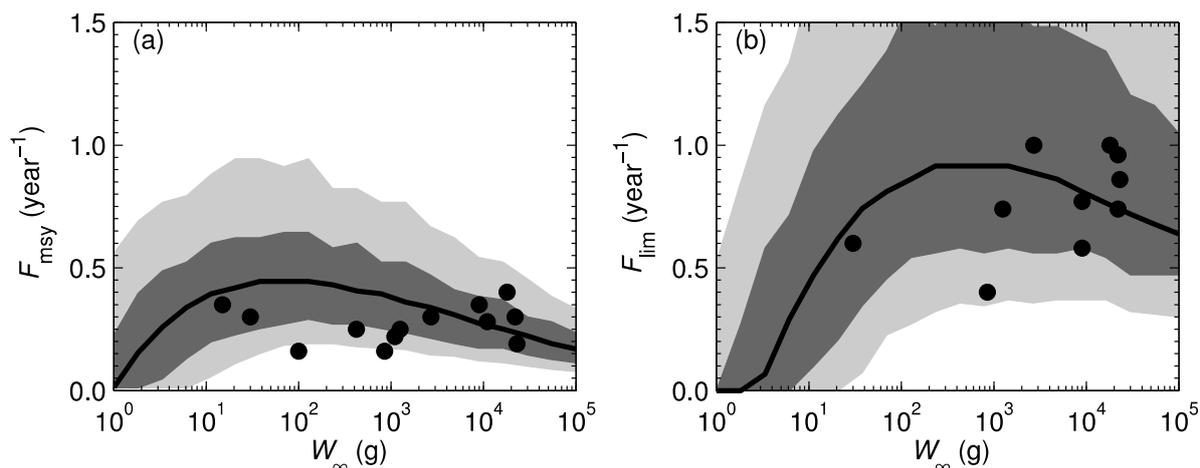
Figure 8. Fisheries reference points F_{msy} (a) and F_{lim} (b) as functions of asymptotic size. Filled circles are currently used reference points from selected ICES stocks (Table 2). The grey areas represent results from calculations of the references points using parameters drawn at random from the distributions specified in Table 1. Light grey shows the 90 % fractile of the results, dark grey shows the 75 % fractile domain
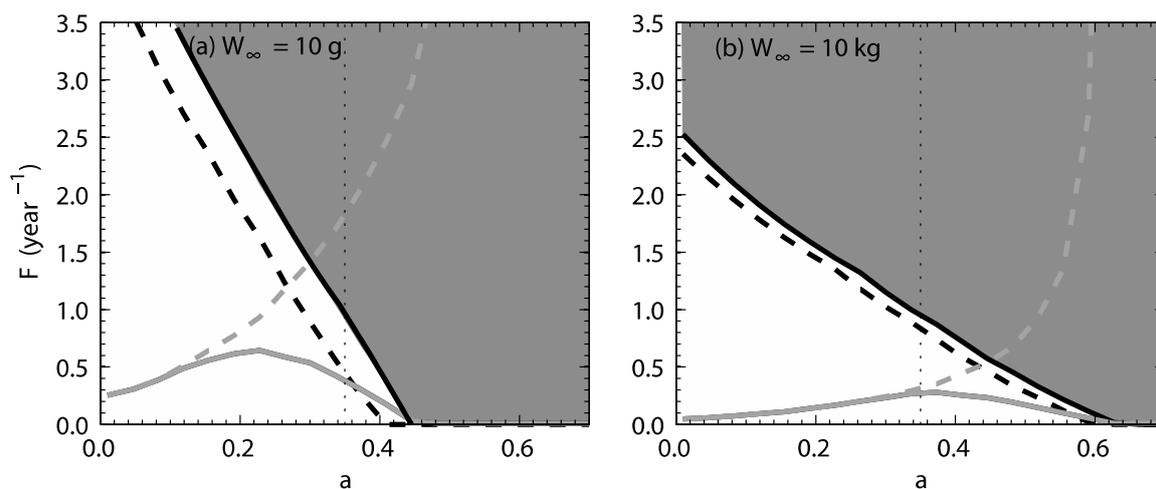

Figure 9. Fisheries reference points as a function of the physiological rate of natural mortality a for a species with $W_\infty = 10$ g (a) and 10 kg (b). Reference points: F_{msy} (solid grey), F_{msyr} (dashed grey), F_{crash} (solid black), F_{lim} (dashed black). The vertical dashed line is the value of a used to construct e.g. Fig. 7 and 8. The grey area is where the stock has crashed.
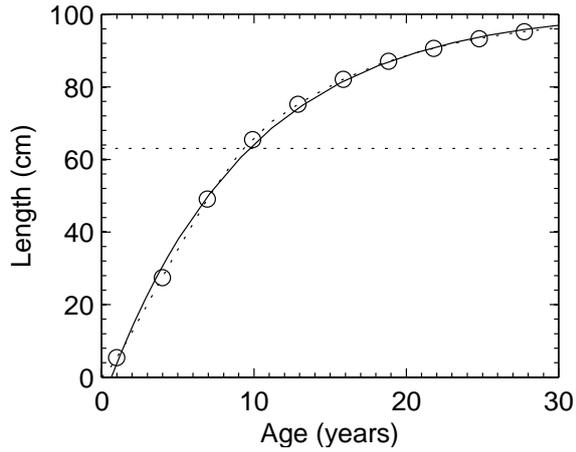
Figure A1. Example of the fit of a von Bertalanffy growth curve (solid line) to the growth curve described by Eq. (4) (dotted line) using 10 data points (circles). The example is for a species with asymptotic length $L_\infty = 100$ cm. The horizontal dotted line is at the length of 50 % maturation.
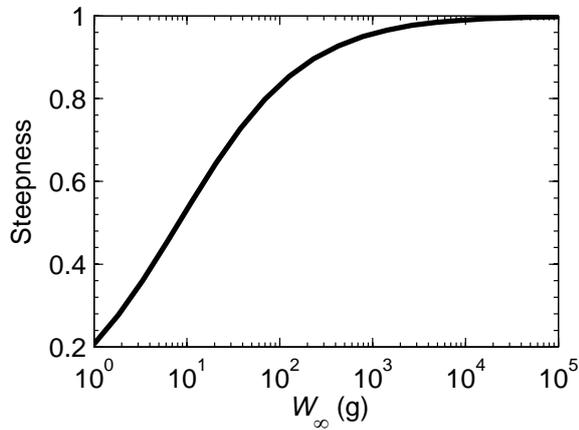

Figure D1. Steepness as a function of asymptotic size.