Reproductive ecology and scientific inference of steepness: a fundamental metric of population dynamics and strategic fisheries management

Marc Mangel[1], Jon Brodziak[2] & Gerard DiNardo[2]

[1]Center for Stock Assessment Research and Department of Applied Mathematics and Statistics, MS E-2, University of California, Santa Cruz, CA 95064, USA; [2]Pacific Islands Fisheries Science Center, Honolulu, HI, USA

Abstract

The relationship between the biomass of reproductively mature individuals (spawning stock) and the resulting offspring added to the population (recruitment), the stock–recruitment relationship, is a fundamental and challenging problem in all of population biology. The steepness of this relationship is commonly defined as the fraction of recruitment from an unfished population obtained when the spawning stock biomass is 20% of its unfished level. Since its introduction about 20 years ago, steepness has become widely used in fishery management, where it is usually treated as a statistical quantity. Here, we investigate the reproductive ecology of steepness, using both unstructured and age-structured models. We show that if one has sufficient information to construct a density-independent population model (maximum per capita productivity and natural mortality for the unstructured case or maximum per capita productivity, natural mortality and schedules of size and maturity at age for the structured model) then one can construct a point estimate for steepness. Thus, steepness cannot be chosen arbitrarily. If one assumes that the survival of recruited individuals fluctuates within populations, it is possible, by considering the early life history, to construct a prior distribution for steepness from this same demographic information. We develop the ideas for both compensatory (Beverton–Holt) and over-compensatory (Ricker) stock–recruitment relationships. We illustrate our ideas with an example concerning bluefin tuna (*Thunnus thynnus/ orientalis*, Scombridae). We show that assuming that steepness is unity when recruitment is considered to be environmentally driven is not biologically consistent, is inconsistent with a precautionary approach, and leads to the wrong scientific inference (which also applies for assigning steepness any other single value).

Keywords Bayesian prior, early life history, reproductive ecology, scombrids, steepness, stock–recruitment relationship

Introduction

Understanding the relationship between the biomass of reproductively mature individuals (spawning stock) and the resulting offspring added to the population (recruitment), the stock recruitment relationship, is a fundamental and challenging problem in all of population biology. For example, strategic fisheries management requires estimates of biological reference points that often critically depend upon the nature of the stock–recruitment relationship (Brodziak 2002). The recovery of threatened or endangered populations is in large part determined by the resilience of reproduction. The Beverton–Holt stock recruitment relationship (Beverton and Holt 1957/1993) is widely used in stock assessments of marine fishery resources and is an important feature of several modeling packages that are used for stock assessments. In some assessments of Pacific tuna (Scombridae spp.) and billfish (*Xiphiidae*, Istiophoridae) stocks, the available data are insufficient to directly estimate spawner recruitment relationship. In such cases [and others, e.g. Pacific rockfish (*Sebastes* spp. Scorpaenidae)] it has become common practice to use the steepness of the stock recruitment relationship in lieu of the entire relationship.

Steepness was popularized by Mace and Doonan (1988), who defined it as the fraction of recruitment from an unfished population (R_0) when the spawning stock biomass is 20% of its unfished level (B_0); its antecedents can be found in Goodyear (1977, 1980) and Kimura (1988) and references there-in. Mace and Doonan (1988) assumed that production follows a Beverton–Holt stock recruitment relationship so that when spawning biomass is B the resulting recruitment $R(B)$ is

$$R(B) = \frac{B}{\alpha + \beta B} \tag{1}$$

where α and β are parameters. In the form of Equation (1) these parameters have clear, if somewhat unnatural interpretations. That is, $\frac{1}{\alpha}$ is the maximum per capita production of recruits (i.e., the limit of $\frac{R(B)}{B}$ for small B) and $R(B)$ approaches $\frac{1}{\beta}$ as B increases. If B_0 and R_0 denote the unfished spawning biomass and recruitment at that spawning biomass and h denotes steepness (Mace and Doonan (1988) use Δ) then

$$R_0 = \frac{B_0}{\alpha + \beta B_0} \tag{2}$$

$$hR_0 = \frac{0.2B_0}{\alpha + 0.2\beta B_0} \tag{3}$$

which can be used to relate α and β to steepness

$$\alpha = \frac{B_0}{R_0}\frac{1-h}{4h} \tag{4}$$

$$\beta = \frac{5h-1}{4hR_0} \tag{5}$$

In the intervening years, a tradition has developed in which one estimates the parameters of the unfished stock (B_0 and R_0) and specifies the steepness, after which the parameters in Equation (1) can be determined from Equations (4 and 5). In many cases, particularly data poor situations, it is common to use plausible values of steepness in the absence of alternative information. This is an implicit Bayesian approach, even if it is not acknowledged as such. In other cases, it is argued that recruitment is mainly determined by the environment and h is set equal to 1 (e.g. Aires-da-Silva and Maunder 2007; Maunder 2007). For example, Maunder (2007) assumes $h = 1$ in the stock assessment for yellowfin tuna (*Thunnus albacares*, Scombridae), conducts a sensitivity analysis with $h=0.75$, and reports that the best estimate

when treating steepness as a free parameter is $h = 0.54$. This approach of fixing h and conducting a sensitivity analysis is commonly used, but clearly there is need to better understand the reproductive biology (*sensu* Morgan (2008)) of steepness. Our approach is very much in the spirit of Winemiller and Rose (1992), who recognize that organisms are not simply data points, but the result of natural selection on trade-offs among important demographic variables, and of McAllister *et al.* (2001) who used a combination of Bayesian and demographic methods to infer the maximum per capita growth rate in a Schaefer model.

Determining probable values of steepness for marine species is a very important research topic. Stock–recruitment steepness is intrinsically related to the resilience of a species to harvesting and effectively determines the average productivity of fishery resources within a stationary environmental regime. Steepness itself must be firmly rooted in the evolutionary ecology of the species and reproductive biology of a stock must surely be important for its management (Morgan 2008). Currently, we lack an explanatory theory to predict steepness based on the evolutionary ecology and associated life history parameters of a species, information that is more readily available and less expensive to generate than assessment data.

The topic of estimating steepness has been addressed through meta-analyses of stock–recruitment data for several species and taxa. For example, Myers *et al.* (1999) estimated a family level median steepness for the scombrids, using data for six species, at 0.52 with 20 and 80 percentiles 0.30 and 0.72 respectively; their median estimate for swordfish (*Xiphias gladius* Xiphiidae) was 0.88. Although Myers *et al.* (1999) was a breakthrough, the statistical approach is limited to commercially-exploited species for which there are sufficient data to conduct an assessment. Such species represent a modest fraction of the potential fishery resources worldwide. Thus, while Myers *et al.* (1999) provided a useful empirical basis for developing an informative prior belief about the steepness of some species for analyzing population dynamics, many other species were not considered and indeed could not be considered if the analyses were repeated today. Furthermore, there are other concerns with the meta-analyses (cf. Osenberg *et al.* 1999): lack of representativeness of the selected stocks, bias towards temperate fishes, lack of independence of stock response to the impact of environmental

variation on recruitment. Dorn (2002) developed a hierarchical Bayesian method for computing a prior for steepness for west coast groundfish species. Munch *et al.* (2005) show how to find a posterior distribution for steepness using Bayesian nonparametric methods and Punt *et al.* (2005) use parametric Bayesian methods to make inferences about steepness for data-poor stocks using information on steepness from data-rich stocks. He *et al.* (2006) use a stochastic simulation to construction a prior for steepness based on long-term persistence of the stock.

In this paper, we provide a new look at the evolutionary ecology and reproductive biology of steepness and its theoretical basis. We develop a practical framework for estimating the probable value of steepness based on life history parameters and show the importance of understanding early life history in the context of steepness.

We use scombrids to illustrate the framework for estimating the probable value of steepness because they are commercially-valuable, highly productive, and intensively-exploited fishery resources for which it is often assumed that $h = 1$ in stock assessments because "recruitment is environmentally driven". This assumption implies an ecologically optimistic compensatory response in the stock–recruitment dynamics at low fish stock sizes and can lead to unrealistic expectations about stock resilience at high harvest rates. More technically, setting $h = 1$ attributes a probability of one to the event of 100% of R_0 at 20% of B_0. The same is true, of course, for any other value of h – that one attributes a probability of one to the recruitment associated with that value of steepness. We argue that an alternative, more consistent scientific inference (*sensu* Jeffreys 1931) is that if recruitment is truly solely environmentally driven, then the prior on steepness should be uniform or close to it (details are provided below).

In the next section, we begin with a production model, for which one is required to know maximum per capita productivity and natural mortality to be able to construct steepness. We then consider the age-structured model, for which one additionally needs to know the probability of maturity and fecundity as a function of age (for simplicity, we assume that fecundity is proportional to mass). We show the conditions under which the age-structured result collapses to the production model. We then discuss sources of stochasticity and uncertainty, focusing on variation in mortality rates of

recruited individuals. We use a Monte Carlo simulation to estimate maximum productivity from early life history (egg to recruited) stages. We illustrate our analysis using data on bluefin tuna. We construct priors for steepness based on reproductive ecology and then fit these to transformed beta-densities. Finally, we discuss extensions of the method. In Appendix 1, we show how our approach can be applied to over-compensatory stock–recruitment relationships such as the Ricker and in Appendix 2 we show that adding process uncertainty to the stock–recruitment dynamics allows one to produce a distribution of recruitment but the fundamental flaw of fixed steepness remains; we also compute the likelihood of a recruitment deviation sufficiently large to lead one to conclude that steepness is 1, conditioned on the true value of steepness and the standard deviation of log-normally distributed recruitment deviations.

Methods

We begin with a production model, which might be used in the analysis of a data-poor fishery, and then consider an age structured model (which is more data-intensive).

The production model

We work with a biomass production model (MacCall 2002). We let $B(t)$ denote the total biomass at time t and assume that the fraction of males at birth is r, so that spawning (i.e. female) biomass at any time is $(1 - r)B(t)$. If M is the rate of natural mortality and F is the rate of fishing mortality then the dynamics of biomass are

$$\frac{\mathrm{d}B}{\mathrm{d}t} = \frac{\alpha_p(1-r)B}{1+\beta(1-r)B} - (M+F)B \tag{6}$$

where α_p is subscripted to note *production* and has units of new biomass per existing spawning (female) biomass per time, so that it is a rate, comparable to the rate of natural mortality M or of fishing mortality F. Clearly, if we were just interested in statistical estimation of parameters, rather than a more complete scientific inference, $1 - r$ could be folded into α_p and β. However, by keeping $1 - r$ out of the parameters, we are explicitly able to connect total biomass with spawning biomass – thus providing a biologically more mechanistic interpre-

tation. Note that we assume it is only the female biomass that affects density dependence. As will be seen below, all of our conclusions about steepness are identical if we replace $\beta(1 - r)B$ in Equation (6) by βB.

The steady state biomass at fishing mortality rate F is

$$\overline{B}(F) = \frac{1}{\beta(1-r)}\left(\frac{\alpha_p(1-r)}{M+F} - 1\right) \tag{7}$$

so that

$$B_0 = \frac{1}{\beta(1-r)}\left(\frac{\alpha_p(1-r)}{M} - 1\right) \tag{8}$$

We thus see that existence of a steady state requires that the Beverton number (*sensu* Mangel 2005) $\frac{\alpha_p(1-r)}{M} > 1$ and that density dependence scales the overall size of the steady state. Thus, the parametrization in Equation (6) separates the roles of α and β in shape and scale when determining B_0. The separation becomes even clearer when we consider steepness.

According to its definition, steepness is

$$h = \frac{0.2\alpha_p(1-r)B_0/[1+0.2\beta(1-r)B_0]}{\alpha_p(1-r)B_0/[1+\beta(1-r)B_0]} \tag{9}$$

from which we obtain

$$h = 0.2 \times \frac{1+\beta(1-r)B_0}{1+0.2\beta(1-r)B_0} \tag{10}$$

However, in light of Equation (8)

$$\beta(1-r)B_0 = \left[\frac{\alpha_p(1-r)}{M} - 1\right] \tag{11}$$

so that we find

$$h = \frac{\alpha_p(1-r)}{4M+\alpha_p(1-r)} \tag{12}$$

which can also be rewritten as

$$h = \frac{\frac{\alpha_p(1-r)}{M}}{4+\frac{\alpha_p(1-r)}{M}} \tag{13}$$

Note that as α_p gets larger and larger, h increases towards 1 and that as $\alpha_p(1 - r)$ declines towards M (but in light of Equation (8) must be larger than M), h declines towards 0.2, as it must. This equation was derived by Myers *et al.* (1999) using a discrete-time Ricker model without considering sex ratio. For the production model, it is also easy to show that

the maximum per capita rate of increase in biomass, analogous to r in the Schaefer model (McAllister *et al.* 2001) is $\frac{4Mh}{1-h}$, thus connecting steepness to more classical measure of population growth.

The age structured model

In a standard age-structured model with Beverton–Holt recruitment, $N(a,t)$ denotes the number of individuals of age a alive at time t. For the recruited class

$$N(0,t) = \frac{\alpha_s B_s(t)}{1 + \beta B_s(t)} \qquad (14)$$

where $B_s(t)$ is the spawning biomass at time t and α_s has units of *new individuals/spawning biomass* and is subscripted with s to denote that this is a structured model. Assuming that fecundity of an individual is proportional to its mass, spawning biomass is

$$B_s(t) = (1 - r) \sum_{a=1}^{a_{\max}} N(a,t) W_f(a) p_{f,m}(a) \qquad (15)$$

where $W_f(a)$ is the mass of a female at age a and $p_{f,m}$ is the probability that a female of age a is mature and $a_{\max}$ is the maximum age that an individual can attain (with suitable modification of the dynamics of the last age class, we can incorporate a 'plus' group into this formulation).

For ages $a > 0$ we have

$$N(a,t) = N(a-1, t-1) e^{-Z(a-1)} \qquad (16)$$

where $Z(a - 1)$ is the total mortality at age $a - 1$, given by the sum of natural mortality $M(a - 1)$ and fishing mortality $F(a - 1)$ at age. Since neither of the mortality rates depend upon time the population will reach a steady state and a stable age distribution.

We let B_0 and R_0 denote the values of spawning biomass and associated recruitment respectively in this steady state and in the absence of fishing and $\overline{N}(a)$ the number of individuals of age a in this steady state so that

$$\overline{N}(a) = S(a) \times R_0 \qquad (17)$$

where $S(a)$ is survival from age 0 to age a, i.e. $S(a) = \prod_{i=0}^{a-1} e^{-M(i)}$. In the steady state, Equation (14) becomes

$$R_0 = \frac{\alpha_s B_0}{1 + \beta B_0} \qquad (18)$$

where

$$B_0 = (1 - r) \sum_{a=1}^{a_{\max}} \overline{N}(a) W_f(a) p_{f,m}(a) \qquad (19)$$

We now define

$$\overline{W}_f = \sum_{a=1}^{a_{\max}} S(a) W_f(a) p_{f,m}(a) \qquad (20)$$

which has the interpretation of the expected surviving mature biomass per recruit. Since $\overline{N}(a) = S(a)R_0$ and $B_0 = (1 - r)R_0\overline{W}_f$ we have

$$R_0 = \frac{\alpha_s \times (1 - r)R_0\overline{W}_f}{1 + \beta \times R_0\overline{W}_f} \qquad (21)$$

which is an equation for R_0. In particular, we have

$$\beta(1 - r)R_0\overline{W}_f = \alpha_s(1 - r)\overline{W}_f - 1. \qquad (22)$$

When spawning stock biomass is 20% of B_0 the recruitment is

$$R = \frac{\alpha_s(1 - r) \times 0.2R_0\overline{W}_f}{1 + \beta(1 - r) \times 0.2R_0\overline{W}_f} \qquad (23)$$

and in analogy to Equations (12 and 13) steepness is

$$h = \frac{\dfrac{\alpha_s \times 0.2(1 - r)R_0\overline{W}_f}{1 + \beta \times 0.2(1 - r)R_0\overline{W}_f}}{R_0} \qquad (24)$$

so that

$$h = \frac{0.2\alpha_s(1 - r)\overline{W}_f}{1 + 0.2\beta(1 - r)R_0\overline{W}_f} \qquad (25)$$

and in light of Equation (22)

$$h = \frac{0.2\alpha_s(1 - r)\overline{W}_f}{1 + 0.2[\alpha_s(1 - r)\overline{W}_f - 1]} = \frac{\alpha_s(1 - r)\overline{W}_f}{4 + \alpha_s(1 - r)\overline{W}_f} \qquad (26)$$

Note that Equations (20 and 25) can be used to give a point estimate for steepness in which the age structure of the population has been perturbed from a stable age distribution, by computing $\overline{W}_f$ for the perturbed age structure (cf. Wiedenmann *et al.* in press). To connect Equations (13 and 26) note that the production model requires that $M(a)$ is a constant (M). Then

$$S(a) = e^{-Ma} \qquad (27)$$

In addition, the production model cannot have age structure; let us assume that we can replace $W_f(a)p_{f,m}(a)$ in Equation (20) by a constant, say $\overline{W}_{f,m}$, interpreted as the average biomass of a spawning female. With this assumption we can rewrite Equation (20) as

$$\overline{W}_f = \sum_{a=1}^{a_{\max}} e^{-Ma}\overline{W}_{f,m} = \overline{W}_{f,m}\frac{1 - e^{-Ma_{\max}}}{1 - e^{-M}} \qquad (28)$$

If $a_{\max}$ is sufficiently large then the numerator in the last expression in Equation (28) is approximately 1. If M is not too large, then we can Taylor expand the denominator as $1 - e^{-M} \approx M$. Thus $\overline{W}_f \approx \frac{\overline{W}_{f,m}}{M}$ and Equation (26) becomes

$$h = \frac{\alpha_s(1 - r)\frac{\overline{W}_{f,m}}{M}}{4 + \alpha_s(1 - r)\frac{\overline{W}_{f,m}}{M}} \qquad (29)$$

By defining $\alpha_p = \alpha_s\overline{W}_{f,m}$ Equations (13 and 29) are the same.

In summary we have shown (1) how to compute steepness for a production model (Equation 13) and that steepness depends only upon maximum per capita productivity and mortality rates; (2) how to compute steepness for an age-structured model (Equation 26) and that steepness depends only upon the schedule of survival and fecundity at age and maximum per capita productivity; and (3) the conditions under which the production model is recovered from the fully age structured model (Equations 28 and 29). For completeness, in Appendix 1 we derive the analogue of Equation (26) for the case of an over-compensatory recruitment function.

Accounting for uncertainty and stochasticity

Equations (13 and 26) involve the quantities α_p, M, r, α_s and $\overline{W}_f$. We assume that $W(a)$ is allometrically related to length so that $W(a) = c_1 \cdot L(a)^{c_2}$ where c_1 and c_2 are constants and where

$$L(a) = L_\infty(1 - e^{-k(a-a_0)}) \qquad (30)$$

where L_∞ is asymptotic size, k is the growth rate, and a_0 is the (theoretical) age at which size is 0 or is a parameter that allows us to account for the initial condition $L(0) = l_0$. It is possible to associate probability distributions with both asymptotic size and von Bertalanffy growth rate (e.g. Siegfried and Sansó 2006) from single set of data or to conduct a meta-analysis on published growth curves.

If natural mortality were constant over time and age, the probability of surviving a single year is e^{-M}. However, as noted by McAllister *et al.* (2001), individual fish will experience different survival trajectories, determined by this annual probability. Adding uncertainty in natural mortality broadens the variation in survival trajectories. We focus first on fish that have recruited to the population, and in the next section discuss fluctuations in the survival of eggs and larvae.

To begin, consider the production model. To characterize variation in the rate of natural mortality, we use the gamma density (Mangel 2006) so that the probability density function for M is

$$f(m) = \frac{\lambda^v}{\Gamma(v)}e^{-\lambda m}m^{v-1}\,\mathrm{d}m \qquad (31)$$

where v and λ are parameters. In this formulation the expected value of M is $E(M) = \overline{M} = \frac{v}{\lambda}$ and the coefficient of variation is $CV(M) = \frac{1}{\sqrt{v}}$.

Given that M has a probability distribution, imagine drawing a sequence $m_0, m_1, m_2, m_3, \ldots, m_{a-1}$ from the gamma density given by Equation (31). From those, we can construct a random variable $\tilde{S}(a)$ for survival to age a according to

$$\tilde{S}(a) = \prod_{i=0}^{a-1} e^{-m_i} \qquad (32)$$

and thus generate a family of survival trajectories that account for the uncertainty in natural mortality, and also allow for individuals experiencing differences in natural mortality at age.

Although the assumption of a constant rate of natural mortality is commonly used in stock assessments, it cannot apply across the range of a fish's life – where individuals, for example, may be prey when young and predators when older. When such data are available, they should be used. For example, for yellowfin tuna and bigeye tuna (*Thunnus obesus*, Scombridae) Hampton (2000) shows classical trajectories of mortality as a function of age: a rapid decline from the youngest age class, a leveling out of mortality, and then an increase of mortality with increasing age (also see Chen and Watanabe 1989). This suggests that we replace constant natural mortality by a function of size and age, as in

$$M(l, a) = m_0 + \frac{m_1}{l} + m_2 \times a \qquad (33)$$

where $L(a) = l$ is length at age a and m_0, m_1 and m_2 are parameters. Such data, in which age and length are treated separately, rarely exist. However, if length is treated as a function of age, then $M(l,a) = M(l(a),a) = M(a)$ only. We use empirically reported values of $M(a)$ (see below for details) as the means for the probability density in Equation (31) and assume the same value of v for all ages, determined as explained below.

Given the distribution of age-dependent mortality, we follow a prescription similar to the one leading to Equation (32) to develop survival to age functions that take size dependent natural mortality into account and are used in the age structured model.

The early life history

In almost all fishery population dynamics models, the early life history of the fish is treated separately from the later ages (the notion being that the von Bertalanffy parameter a_0 captures the early life history). However, a biological interpretation of steepness requires that we consider the early life history in more detail.

Suppose that a fish is recruited to the population dynamics model at mass $W(0)$ after a juvenile period of d_l days. We let $w_l(d)$ denote the wet mass of the larvae on day d. Assuming exponential growth during this phase (Kaji *et al.* 1996, Shoji *et al.* 2005) we have

$$w_l(d) = w_l(0) \times \exp(k_l \times d) \qquad (34)$$

where k_l is determined so that the individual grows from $w_l(0)$ to $W(0)$ in d_l days. In this paper, as a first approximation we ignore individual variation in larval growth rates.

To compute the expected mass that an egg contributes to future biomass, we need to find the survival during the period before being recruited to the population dynamics model. We use McGurk (1986) to characterize mortality during the early life history phase rather than modeling the density dependent mortality explicitly. McGurk showed that eggs and larvae have a steeper size-dependent mortality than juveniles and proposes that two different equations be used. In particular, we let $M_l(w_d)$ denote the daily mortality rate of an individual of dry mass w_d. McGurk (1986, Equation 7) concluded that if If w_d is less than $w_c = 0.00504g$ then

$$M_l(w_d) = 2.2 \times 10^{-4} \times w_d^{-0.85} \qquad (35)$$

and otherwise (McGurk 1986, Equation 2)

$$M_l(w_d) = 5.26 \times 10^{-3} \times w_d^{-0.25} \qquad (36)$$

Equation (35) applies to fish eggs and larvae and Equation (36) to juvenile fish (McGurk 1986, Fig. 1). Fish eggs and larvae typically have a different hydration factor than juveniles. We use the general values reported by Kamler (1992) of a 65% hydration factor for eggs and larvae and 85%

for juveniles and convert the crossing value of dry weight, w_c, to a wet weight value by assuming the weight wet crossing is $4.76 \cdot w_c$ (obtained by averaging the wet weights based on 65% or 85% hydration). Equations (35 and 36) are the regression lines reported by McGurk (1986), from log–log plots. In order to estimate the variance in mortality rate, we digitized the data and fit either of these equations to $\log(M) = m_0 + m_1 \log(w_d) + Z_\sigma$, where Z_σ is a normally distributed random variable with mean 0 and standard deviation σ. Larval survival to day d, $S_l(d)$ (with $S_l(0) = 1$) is

$$S_l(d) = S_l(d-1) \times \exp(-M_l(w_d)) \qquad (37)$$

Because survival may be a very small number, it is also useful to consider the accumulated mortality $M_a(d)$ to day d. We have $M_a(0) = 0$ and

$$M_a(d) = M_a(d-1) + M_l(w_d) \qquad (38)$$

To implement these equations, we first compute dry weight from $w_l(d-1)$ and then use Equation (35 or 36) as appropriate, incorporating the random component to early life history survival.

Interpreting α_p and α_s

We will now provide an interpretation of α_p and α_s. First consider α_p. Note that

$$\frac{\alpha_p(1-r)B}{1 + \beta(1-r)B} = \alpha_p(1-r)B \times \frac{1}{1 + \beta(1-r)B} \qquad (39)$$

Thus $\alpha_p B$ is the maximum rate at which all biomass is added (female biomass being a fraction $1 - r$ of the total biomass) before density dependence acts and $\frac{1}{1+\beta(1-r)B}$ is the fraction of that biomass which survives to increase the population.

To find α_p, consider a female fish of age a, with mass $W(a)$, length $L(a)$, and probability of being mature $p_{f,m}(a)$. Suppose that $\mathscr{E}(W(a))$ is the fecundity of this individual in a single spawning event and s_f is the spawning frequency. Each egg contributes $W(0) \times S_l(d_l)$ to new biomass so that

$$\alpha_p = \frac{\mathscr{E}(W(a)) \times W(0) \times S_l(d_l) \times s_f}{W(a)} \qquad (40)$$

In practice, since $\mathscr{E}(w)$ will be a typically large number and $S_l(d_l)$ a small number, it is wiser to compute their product as

$$\mathscr{E}(w) \times S_l(d_l) = \exp(\log(\mathscr{E}(w) - M_a(d_l)))$$

We employ a simulation algorithm to implement Equation (40). Imagine that we sub-sample K

populations of simulated fish, with N female fish in each of the samples. Our goal to create the age for each of the N fish in the sub-sample of the kth population. To do this, we denote the age of the nth fish in the kth population by $a_{n,k}$, which is found by choosing a uniformly distributed random variable $\tilde{U}_{nk}$ and then setting $\tilde{S}(a_{n,k}) = \tilde{U}_{nk}$, where $\tilde{S}(a)$ is determined by Equation (32) for the production model or its extension for the age structured model. For the case of constant mortality M, this equation is easily solved and we find $a_{n,k} = -\frac{1}{M}\log(\tilde{U}_{nk})$. For the case of age-dependent natural mortality we first find the age j satisfying $\sum_{a=0}^{j} M(a) < \log(\tilde{U}_{nk}) < \sum_{a=0}^{j+1} M(a)$; $a_{n,k}$ is then this age plus a linearly interpolated increment between the two years. When employing these algorithms, for the case of constant natural mortality, each population k experiences a different value of m, drawn from the gamma density in Equation (31); for the case of age dependent mortality, each population experiences a series of values of $m_0, m_1, \ldots m_{a-1}$, drawn from age-specific gamma densities. In this manner, we randomly generate the age structure of a subsample the spawning population; at no point do we estimate the total size of the population, but that is not necessary.

Once we know the age of the fish, we know its length, weight, and probability of being mature. It is then possible to compute $\alpha_p(n,k)$ from Equation (40). The total biomass in population k is $\sum_{n=1}^{N} W(a_{n,k})$ and the total reproduction is $W(0) \times S_l(d_l) \times s_f \sum_{n=1}^{N} \mathscr{E}(W(a_{n,k}))$. Thus the estimate for α_p in this population is

$$\tilde{\alpha}_p(k) = W(0) \times S_l(d_l) \times s_f \frac{\sum_{n=1}^{N} \mathscr{E}(W(a_{n,k}))}{\sum_{n=1}^{N} W(a_{n,k})} \quad (41)$$

which is a random variable because $a_{n,k}$ is a random variable. Note that the units of α_p are *new biomass per spawning biomass* while those of α_s are *new individuals per spawning biomass*. Thus with $W(0)$ removed, Equation (40) gives us an estimate α_s and with $W(0)$ removed, Equation (41) provides an estimate of $\tilde{\alpha}_s(k)$. Note that the sex ratio would appear in both numerator and denominator of Equation (41), thus cancelling, so that we can think of the simulation as drawing only female fish and measuring only the female offspring produced.

Equations (13 and 41) (or Equation (26) and the modification of Equation (41) for the age structured model) allow us to generate a frequency distribution for steepness based on the K populations (we use

$K = 200$ for computation) of N fish (we also use $N = 200$ for computations). To create the frequency distribution, we discretized values of steepness between 0.2 and 1.0 in increments of 0.013. Repeating the process summarized in Equations (13 or 26), and 41 allows us to obtain multiple versions of the frequency distribution for steepness. This allows us to generate an ''empirical'' distribution for steepness. We can fit that distribution to one of the classical frequency distributions of probability theory, the beta density (Mangel 2006). To do this, we introduce the variable $y = 1.25 \cdot h - 0.25$ which ranges from 0 to 1 as steepness ranges from 0.2 to 1.0. Thinking of steepness now as a random variable, $\tilde{h}$, the transformed variable also becomes one $\tilde{y}$ and

$$E[\tilde{y}] = 1.25 \times E[\tilde{h}] - 0.25 \quad (42)$$

$$Var[\tilde{y}] = 1.5625 \times Var[\tilde{h}] \quad (43)$$

If $\tilde{y}$ follows a beta density with parameters a_β, b_β, so that its probability density is

$$f_\beta(y) = \frac{\Gamma(a_\beta + b_\beta)}{\Gamma(a_\beta)\Gamma(b_\beta)} y^{a_\beta - 1}(1 - y)^{b_\beta - 1}$$

and if we introduce the parametrizations (Dorazio and Royle 2003) $\mu_\beta = \frac{a_\beta}{a_\beta + b_\beta}$ and $\tau_\beta = a_\beta + b_\beta$ then

$$E[\tilde{y}] = \mu_\beta \quad (44)$$

$$Var[\tilde{y}] = \frac{\mu_\beta \times (1 - \mu_\beta)}{\tau_\beta + 1} \quad (45)$$

We thus obtain numerical values for μ_β and τ_β from Equations (42–45) and then determine the values of the beta density from $a_\beta = \tau_\beta \times \mu_\beta$ and $b_\beta = \tau_\beta \times (1 - \mu_\beta)$. We implemented the simulation using C.

An example with bluefin tuna

To illustrate our ideas, we use the parameters reported in Bayliff (1994) for northern bluefin tuna. Bayliff (1994) estimates natural mortality to have mean value $\overline{M} = 0.276 \text{ yr}^{-1}$ and that the 90% confidence interval for mortality is $[0.16, 0.471] \text{ yr}^{-1}$. Anonymous (2008) give age dependent mortality $M(a)$ for bluefin tuna: $M(0) = 1.6 \text{ yr}^{-1}$, $M(1) = 0.46 \text{ yr}^{-1}$, $M(2) = 0.27 \text{ yr}^{-1}$, $M(3) = 0.2 \text{ yr}^{-1}$ and $M(a) = 0.12 \text{ yr}^{-1}$ for $a \geq 4 \text{ yr}$.

We use von Bertalanffy growth (Equation 30) with the parameters from Bayliff (1994): $L_\infty = 320.5 \text{ cm}$, $k = 0.1035 \text{ yr}^{-1}$, and $a_0 = -0.7034 \text{ yr}$. We assume
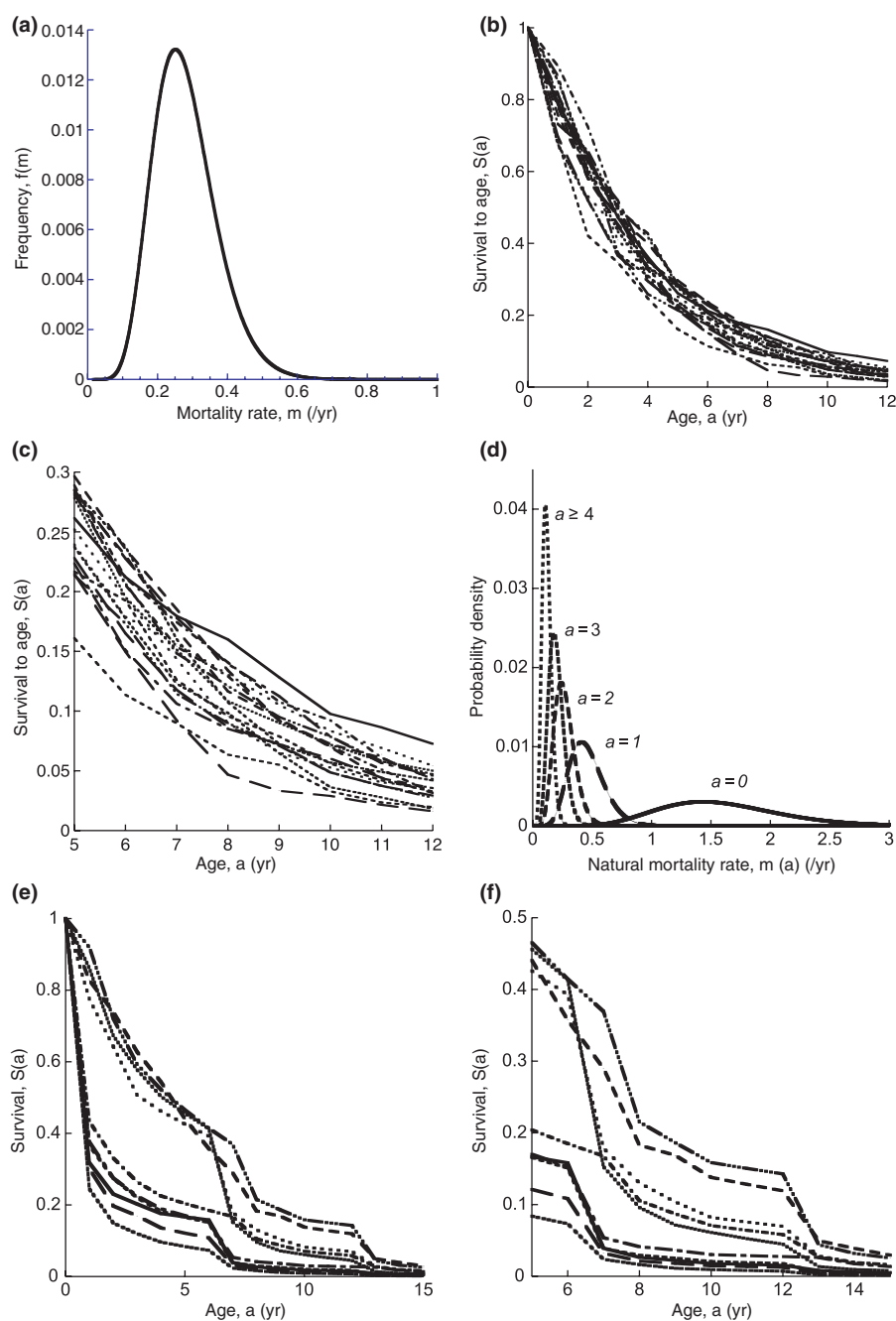
Figure 1 (a) The gamma frequency distribution *f(m)* for constant natural mortality estimated used for the example of our method with bluefin tuna. (b,c) Sample survival trajectories created by assuming annual mortality is drawn from the distribution shown in panel (a) on a yearly basis. (d) If we assume age dependent mortality with the same coefficient of variation as that used in panel (a), then there is a family of probability distributions for the rate of mortality, depending upon age *a* and this introduces more variability in survival to age (panels e,f), particularly at older ages, when we expect individuals to be more fecund. Regardless of whether we use constant or age dependent mortalities, the consequence of variation in survival is to create variation in steepness.

the length weight allometry $W(a) = 0.001L(a)^{2.4}$. These values produce a fish that is about 215 cm and 400 kg at age 10. We assume that the probability that a fish is mature at age a is

$$p_m(a) = \frac{e^{\frac{a-a_{50}}{\sigma_m}}}{1 + e^{\frac{a-a_{50}}{\sigma_m}}} \quad (46)$$

where a_{50} is the age at which 50% of a cohort is mature. We choose $a_{50} = 5$ yr.

For the early life history, we use an initial egg wet mass of 0.00035 g, which corresponds to an egg radius of about 0.5 mm and neutral buoyancy at 25 °C and assume 256 days [corresponding to the value of a_0] to $W(0) = 1.76$ kg. For spawning information, we use Chen *et al.* (2006). Batch fecundity at length L is

$$\mathscr{E}(L(a)) = 3.24 \times 10^5 \times L(a) - 5.21 \times 10^7 \quad (47)$$

Spawning frequency is every 3.3 days during the spawning season, which is 6 weeks from late April to mid-June.

Results

Bayliff's (1994) data, we find that $v = 9.7$ for the probability density in Equation (31). The resulting probability density (Fig. 1a) is peaked close to the mean and relatively symmetric, although there is a somewhat wider right hand tail. There is noticeable variation in survival determined by Equation (32) (Fig. 1b) and especially at the oldest ages, when we expect fish to be the biggest and most productive (Fig. 1c). When we do the same assuming age dependent mortality, we generate a series of probability densities for mortality rate (Fig. 1d) which then show more variation in survival (Fig. 1e,f). For the von Bertalanffy growth parameters given above, length at age is nearly a linear function (as Bayliff (1994) noted, and the inflection point in mass at age occurs very early in the life of a tuna. The probability that an individual is mature ranges from about 20% at age 4 to nearly 100% at age 8.

In Fig. 2, we show the probability distributions obtained for 200 replicate runs of our method using the production model (panel a) or the age structured model (panel b). The production model shows a relatively tight distribution and an excellent fit to the beta probability density, with a peak around $h = 0.9$ and all of the probability in about $0.8 \le h \le 0.95$. The situation changes noticeably
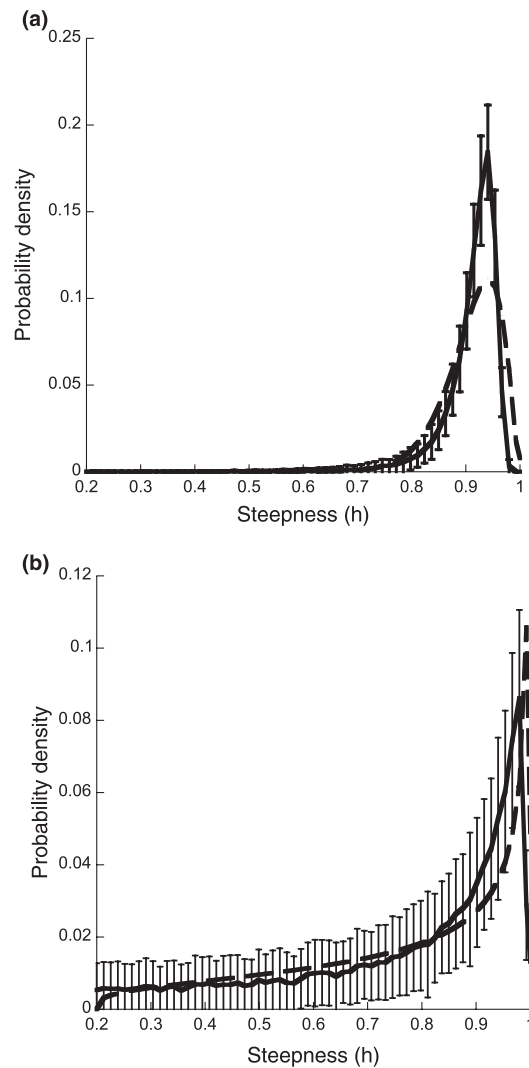

Figure 2 We simulated subsamples of 200 fish from 200 populations, using bluefin tuna life history parameters, and constructed an empirical frequency distribution for steepness, for which we show the mean (solid line) and standard deviation (error bars) and then estimate the parameters for a beta density. In panel (a) we show the results for the production model and in panel (b) the results for the age-structured model.

when the age-structured model is used. Now, nearly the entire range of steepness is possible and the fitted beta density, while generally doing well, misses the peak by a little bit.

Discussion

In this paper, we have shown how to formulate steepness for a production model (Equation 13)

such as might be used in the management of data-poor fisheries and for an age-structured model (Equation 26) for a fishery that is richer in data. Our approach is based on the reproductive biology of the species and thus complements previous work that has developed priors for steepness from a more statistical viewpoint (Punt and Hilborn 1997; Dorn 2002; Myers *et al.* 2002; Schnute and Kronlund 2002; Punt *et al.* 2005). We have also shown (Equations 27–29) how the two formulations are connected by making simplifying assumptions about the age structure. For data poor fisheries, in the absence of an empirical estimate of the natural mortality rate, the mean value of natural mortality rate could be estimated from basic life history information such as the age of maturity (a_m) and the growth coefficient (k) assuming Beverton–Holt life history invariants (Beverton 1992; Jensen 1996; Mangel 2006; Mangel *et al.* 2007). By assuming that annual survival varies among recruited individuals, we have been able to derive our main result – a prior for steepness that can be fit with a transformed beta density (Fig. 2). Clearly fluctuations in annual mortality is only one source of variation. For example, our results are conditioned on asymptotic size L_∞ and growth rate k and one may hypothesize that variation in these will broaden the distribution of steepness. He *et al.* (2006) used an evolutionary persistence principle for a production model as a means of constructing a prior for steepness and showed that low values of steepness are unlikely because of the low probability that a population with such low values can persist in the face of recruitment fluctuations. Our result for the production model could be combined with that of He *et al.* (2006), which requires an assumption about the rate of natural mortality, but only in a qualitative way since He *et al.* (2006) did not assume fluctuations in the rate of natural mortality.

Thus, our work continues a tradition of attempting to provide biological interpretation to the parameters of the Beverton–Holt stock–recruitment relationship and interpretation of those parameters in terms of maximum sustainable harvest rate and catch (Schnute and Richards 1998) or in the context of persistence under fishing pressure and recovery from over-exploitation (e.g. Jennings *et al.* 1998) or sustainability (Reynolds *et al.* 2001). In particular, Walters *et al.* (2006) recommend the use of the Compensation Ratio (CR; Goodyear (1977, 1980, 1993)) in the formulation of the recruitment function [although in a later paper (Forrest *et al.* 2008) they revert to Equation (1) here]. The CR was introduced by Goodyear to provide a measure of the relationship of survival, fecundity, and fishing mortality under which populations can persist. A number of formulations of the Beverton–Holt stock recruitment relationship using the CR can be found in the literature (e.g. Goodwin *et al.* 2006; Walters *et al.* 2006). For example, Walters *et al.* (2006) assume that recruitment $R(E)$ when E eggs are produced by the spawning population is $R(E) = \frac{K(R_0/E_0)E}{1+[(K-1)/E_0]E}$, where K is the compensation ratio, R_0 is the recruitment in the unfished population, and E_0 is the egg production in the unfished population. It is a straight-forward repetition of the analysis in Equations (9–13) to show that $\frac{R(0.2E_0)}{R(E_0)} = \frac{0.2K}{0.8+0.2K}$ so that the Goodyear Compensation Ratio is exactly the Beverton number $\frac{\alpha_p(1-r)}{M}$. This Beverton number has can be interpreted as the rate at which new biomass is added to the stock per unit biomass ($\alpha_p(1-r)$) multiplied by the mean lifespan of biomass added to the stock ($1/M$). A similar interpretation holds for the age-structured model, as noted by Goodwin *et al.* (2006).

Perhaps most importantly, Equations (20 and 26) show that as soon as we are able to develop a demographic model for the survival of a cohort (Equation 20) we are close to being able to obtain a point estimate for steepness (Equation 26 or 53 in Appendix 1). That is, steepness is endogenous to the demography of the stock; it cannot be chosen arbitrarily. This point is buried in other work on steepness, but needs to be made explicit: demographic information about the fate of a cohort also tells us about the reproductive resilience of the population. It also means that one cannot arbitrarily modify steepness while holding all of the other biological parameters constant (cf. Rose and Cowan 2003) and is another example of the importance of incorporating life history characteristics into assessments.

This is of more than academic or theoretical interest. Many fish stocks are managed on the basis of reduction in Spawning Potential Ratio (*SPR*), which measures the reduction in lifetime spawning output at a fixed fishing mortality F relative to the unfished stock. That is, if we define Lifetime Egg Production when fishing mortality is F as *LPR(F)* then

$$SPR(F) = \frac{LEP(F)}{LEP(0)} = \frac{\sum_{a=0}^{a_{\max}} e^{-\sum_{a'=0}^{a-1}(M(a)+F(a))} W_f(a) p_{f,m}(a)}{\sum_{a=0}^{a_{\max}} e^{-\sum_{a'=0}^{a-1} M(a)} W_f(a) p_{f,m}(a)} \tag{48}$$

where $F(a)$ is the product of F and a measure of selectivity of the fishery for individuals of age a. The typical management strategy is to choose $F_{x\%}$ so that $SPR(F_{x\%}) = x/100$ is a proxy for $SPR(F_{MSY})$. For example, most US West Coast groundfish stocks were managed to achieve $F_{35\%}$ as a proxy for F_{MSY} during the 1990s (Brodziak 2002). However, for many of these stocks, the SPR target has subsequently been adjusted upwards to reflect lower estimates of stock resilience and to be more conservative (*i.e.* to increase x because of declines of the stock). Note that Equation (48) includes nearly all of the information needed to obtain a point estimate for steepness; only maximum productivity is missing. However, as most clearly illustrated in Equation (8), assuming a value for mortality implies a minimum value for maximum productivity. Thus, we are thus able to ask if the SPR chosen for management is consistent with the reproductive resilience implied by the steepness. Most importantly, assuming steepness $h=1$ to assess intensively exploited resources is not a good idea and cannot be consistent with the demographic information. Using yield-based biological reference points that implicitly assume a steepness of $h = 1$, e.g., F_{MAX} or $F_{0.1}$ is also a bad idea.

The structured model can clearly be extended to species that change sex by adjustment of the population dynamics and maturity schedule (Alonzo and Mangel 2004, 2005; Alonzo *et al.* 2008). Both the production and structured models can be extended to account for changes in steepness due to fluctuating environmental regimes, such as the California Current System – and Equations (13 and 26) provide direction on what variables should be measured. As described in Appendix 1, our approach immediately extends to species that may exhibit overcompensatory stock–recruitment dynamics, such as Dungeness crab (*Cancer magister*, Cancridae).

For the example of bluefin tuna that we considered, the results are consistent with the expectation that steepness is relatively high for this stock and that environmental forcing is an important determinant of recruitment strength. Such environmental forcing can be built into the early life history through fluctuations in mortality rate and into productivity through fluctuations in egg production.

To conclude we return to the question of the choice of an appropriate value of steepness when one assumes that recruitment is environmentally driven. Jeffreys (1931) would consider steepness to be a derived magnitude, even though it is measured in terms of a number, and pointed out that the structure of derived magnitudes is more complicated than the ones used to compute them because they are less immediately connected to the actual data (which Jeffreys called *sensations*, see pages 98–101). Even so, steepness is surely real – since it relates spawning biomass and associated recruitment. Setting $h = 1$ is equivalent to assigning 100% probability to the event of unfished recruitment when spawning biomass is 20% of its steady state value. This is biologically inconsistent and also inconsistent with a precautionary approach. More importantly, it is the wrong scientific inference and this would apply to any single value of h specified. The correct inference is that if there is no relationship between spawning biomass and recruitment then nearly any value of steepness is possible – so that the prior for steepness in such a case should be close to uniform, but small at both $h = 0.2$ (for reasons explained in He *et al.* (2006) and $h = 1$ for the reasons illustrated in this paper. There is much more to be learned by taking a biological rather than statistical view of steepness.

Acknowledgements

References

Aires-da-Silva, A. and Maunder, M.N. (2007) Status of Bigeye tuna in the Eastern Pacific Ocean in 2006 and utlook. Inter-Amer. Tropical Tuna Commission Stock

Assessment Report, 7, pp. 117–248. Available at: http://www.iattc.org/PDFFiles2/SARM-9-06b-BET-assessment-2007.pdf (accessed 28 November 2008).

Alonzo, S.H. and Mangel, M. (2004) The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. *Fishery Bulletin* **102**, 1–23.

Alonzo, S.H. and Mangel, M. (2005) Sex-change rules, stock dynamics, and the performance of spawning-per-recruit measures in protogynous stocks. *Fishery Bulletin* **103**, 229–245.

Alonzo, S.H., Ish, T., Key, M., MacCall, A.D. and Mangel, M. (2008) The importance of incorporating protogynous sex change into stock assessments. *Bulletin of Marine Science* **83**, 163–179.

Anonymous. (2008) Report of the Pacific Bluefin Tuna Working Group Workshop. International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean.

Bayliff, W.H. (1994) A review of the biology and fisheries for northern bluefin tuna, *Thunnus thynnus*, in the Pacific Ocean. *FAO Fisheries Technical Paper* **336**, 244–295.

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

Beverton, R.J.H. and Holt, S.J. (1957/1993) *The Dynamics of Exploited Fish Populations*. Chapman and Hall, London.

Brodziak, J. (2002) In search of optimal harvest rates for West Coast groundfish. *North American Journal of Fisheries Management* **22**, 258–271.

Chen, S. and Watanabe, S. (1989) Age dependence in the natural mortality coefficient in fish population dynamics. *Nippon Suisan Gakkaishi* **55**, 205–208.

Chen, K., Crone, P. and Hsu, C-C. (2006) Reproductive biology of female Pacific bluefin tuna *Thunnus orientalis* from south-western North Pacific Ocean. *Fisheries Science* **72**, 985–994.

Dorazio, R.M. and Royle, J.A. (2003) Mixture models for estimating the size of a closed population when capture rates vary among individuals. *Biometrics* **59**, 351–364.

Dorn, M.W. (2002) Advice on west coast rockfish harvest rates from Bayesian meta-analysis of stock–recruit relationships. *North American Journal of Fisheries Management* **22**, 280–300.

Forrest, R.E., Martell, S.J.D., Melnychuk, M.C. and Walters, C.J. (2008) An age-structured model with leading management parameters, incorporating age-specific selectivity and maturity. *Canadian Journal of Fisheries and Aquatic Sciences* **65**, 286–296.

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 Sciences* **63**, 494–509.

Goodyear, C.P. (1977) Assessing the impact of power plant mortality on the compensatory reserve of fish popula-tions. In: *Proceedings of the Conference on Assessing the Effects of Power Plant induced Mortality on Fish Popula-tions* (ed. W. Van Winkle). Permagon Press, New York, pp. 186–195.

Goodyear, C.P. (1980) Compensation in fish populations. In: *Biological Monitoring of Fish* (eds C. Hocutt and C.J. Stauffer). D.C. Heath Co., Lexington, MA, pp. 252–280.

Goodyear, C.P. (1993) Spawning stock biomass per recruit in fisheries management: foundation and current use. In: *Risk Evaluation and Biological Reference Points for Fisheries Management* (eds S.J. Smith, J.J. Hunt and D. Rivard), Canadian Special Publications in Fisheries and Aquatic Sciences 120, Ottawa, Ontario, Canada, pp. 67–81.

Hampton, J. (2000) Natural mortality rates in tropical tunas: size really does matter. *Canadian Journal of Fisheries and Aquatic Sciences* **57**, 1002–1010.

He, X., Mangel, M. and MacCall, A. (2006) A prior for steepness in stock–recruitment relationships, based on an evolutionary persistence principle. *Fishery Bulletin* **104**, 428–433.

Jeffreys, H. (1931) *Scientific Inference*. Cambridge University Press, Cambridge, UK.

Jennings, S., Reynolds, J.D. and Mills, S.C. (1998) Life history correlates of responses to fisheries exploitation. *Proceedings of the Royal Society of London B* **265**, 333–339.

Jensen, A. (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.

Kaji, T., Tanaka, M., Takahashi, Y., Oka, M. and Ishibashi, N. (1996) Preliminary observations on development of Pacific bluefin tuna *Thunnus thynnus* (Scombridae) larvae reared in the laboratory, with special reference to the digestive system. *Marine and Freshwater Research* **47**, 261–269.

Kamler, E. (1992) *Early Life History of Fish. An Energetics Approach*. Chapman and Hall, London and New York.

Kimura, D.K. (1988) Stock–recruitment curves as used in the stock-reduction analysis model. *Journal du Conseil Internationale Exploration de la Mer* **44**, 253–258.

MacCall, A.D. (2002) Use of known-biomass production models to determine productivity of west coast ground-fish stocks. *North American Journal of Fisheries Management* **22**, 272–279.

Mace, P.M. and Doonan, I.J. (1988) A generalised bioeco-nomic simulation model for fish population dynamics. *New Zealand Fishery Assessment Research Document 88/4*. Fisheries Research Centre, MAFFish, POB 297, Wellington, NZ.

Mangel, M. (2005) Invariant ratios vs. dimensional ratios. *Science* **310**, 1426–1427.

Mangel, M. (2006) *The Theoretical Biologist's Toolbox*. Cambridge University Press, Cambridge and New York.

Mangel, M., Levin, P. and Patil, A. (2006) Using life history and persistence criteria to prioritize habitats for management and conservartion. *Ecological Applications* **16**, 797–806.

Mangel, M., Kindsvater, H.K. and Bonsall, M.B. (2007) Evolutionary analysis of life span, competition, and adaptive radiation, motivated by the Pacific rockfishes (*Sebastes*). *Evolution* **61**, 1208–1224.

Maunder, M.N. (2007) Status of yellowfin tuna in the Eastern Pacific Ocean in 2006 and outlook. *Inter-Amer. Tropical Tuna Commission Stock Assessment Report* **8**, 3–103. Available at: http://www.iattc.org/PDFFiles2/SAR8-YFT-ENG.pdf (accessed 11 May 2009).

McAllister, M.K., Pikitich, E.K. and Babcock, E.A. (2001) Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. *Canadian Journal of Fisheries and Aquatic Sciences* **58L**, 1871–1890.

McGurk, M.D. (1986) Natural mortality of marine pelagic fish eggs and larvae: the role of spatial patchiness. *Marine Ecology Progress Series* **34**, 227–242.

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

Munch, S.B., Kottas, A. and Mangel, M. (2005) Bayesian nonparametric analysis of stock–recruitment relationships. *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 1808–1821.

Myers, R.A., Bowen, K.G. and Barrowman, N.J. (1999) Maximum reproductive rate of fish at low population sizes. *Canadian Journal of Fisheries and Aquatic Sciences* **56**, 2404–2419.

Myers, R.A., Barrowman, N.J., Hilborn, R. and Kehler, D. (2002) Inferring Bayesian priors with limited direct data: applications to risk analysis. *North American Journal of Fisheries Management* **22**, 351–364.

Osenberg, C.W., Sarnelle, O., Cooper, S.D. and Holt, R.D. (1999) Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology* **80**, 1105–1117.

Punt, A.E. and Hilborn, R. (1997) Fisheries stock assessment and decision analysis: the Bayesian approach. *Reviews in Fish Biology and Fisheries* **7**, 35–63.

Punt, A.E, Smith, D.C and Koopman, M.T. (2005) Using information for 'data-rich' species to inform assessments of 'data-poor' species through Bayesian stock assessment methods. Final Report to Fisheries Research and Development Corporation Project No. 2002/094. Primary Industries Research Victoria, Queenscliff.

Reynolds, J.D., Jennings, S. and Dulvy, N.K. (2001) Life histories of fishes and population responses to exploitation. In: *Conservation of Exploited Species* (eds J.D. Reynolds, G.M. Mace, K.H. Redford and J.G. Robinson). Cambridge University Press, Cambridge, pp. 148–168.

Rose, K.A. and Cowan, J.H. (2003) Data, models, and decisions in US marine fisheries management: lessons for ecologists. *Annual Review on Ecology and Systematics* **34**, 127–151.

Schnute, J.T. and Richards, L.J. (1998) Analytical models for fishery reference points. *Canadian Journal of Fisheries and Aquatic Sciences* **55**, 515–528.

Schnute, J.T. and Kronlund, A.R. (2002) Estimating salmon stock–recruitment relationships from catch and escapement data. *Canadian Journal of Fisheries and Aquatic Sciences* **59**, 433–449.

Shoji, J., Machara, T. and Tanaka, M. (2005) Larval growth and mortality of Japanese Spanish mackerel (*Scomberomorus niphonius*) in the central Seto Inland Sea, Japan. *Journal of the Marine Biological Association of the United Kingdom.* **85**, 1255–1261.

Siegfried, K. I. and Sansó, B. (2006). Two Bayesian methods for estimating parameters of the von Bertalanffy growth equation. *Environmental Biology of Fishes* **77**, 301–308.

Walters, C.J., Martell, S.J.D. and Korman, J. (2006) A stochastic approach to stock reduction analysis. *Canadian Journal of Fisheries and Aquatic Sciences* **63**, 212–223.

Wiedenmann, J., Fujiwara, M. and Mangel, M. (in press) Transient population dynamics and viable stage or age distributions for effective conservation and recovery. doi:10.1016/j.biocon.2009.07.031.

Winemiller, K.O. and Rose, K.A. (1992) Patterns of life-history diversification in North American fishes: implications for population regulation. *Canadian Journal of Fisheries and Aquatic Sciences* **49**, 2196–2218.

Appendix 1: The over-compensatory recruitment function

In this Appendix, we derive the analogue of Equation (26) for the case of an over-compensatory recruitment function. That is, we replace Equation (14) by

$$N(0, t) = \alpha_s B_s(t) e^{-\beta B_s(t)} \tag{49}$$

where $B_s(t)$ is given by Equation (15) and the age dependent dynamics in Equation (16) apply. Note that we could generalize even further (but will not do so) by writing

$$N(0, t) = \alpha_s B_s(t) f_d(B_s(t), \beta) \tag{50}$$

where $f_d(z, \beta)$ characterizes the nature of the density dependence and is a decreasing function of z and β.

In the steady state, we have

$$R_0 = \alpha_s B_0 e^{-\beta B_0} \tag{51}$$

and where B_0 is given by Equation (19). We solve Equation (51) for βB_0; noting that $B_0 = $

$(1 - r)R_0\overline{W}_f$ allows us to cancel R_0 from both sides and obtain

$$\beta B_0 = \log(\alpha_s(1 - r)\overline{W}_f) \qquad (52)$$

Steepness is now

$$h = \frac{\alpha_s(1 - r)0.2B_0^{-0.2\beta B_0}}{\alpha_s(1 - r)B_0e^{-\beta B_0}} = 0.2e^{0.8\beta B_0} \qquad (53)$$

Substituting Equation (52) into the final term on the right hand side of Equation (53) we obtain

$$h = 0.2(\alpha_s(1 - r)\overline{W}_f)^{0.8} \qquad (54)$$

Note that now steepness no longer ranges from 0.2 to 1, but rather from 0.2 to ∞. This can be understood as follows. The function $be^{-\beta b}$ is maximized at $b^* = \frac{1}{\beta}$, so that for values of $B_0 > b^*$, R_0 declines. A large value of B_0 may thus imply a small value of recruitment, and reducing the stock to 20% of that value may increase recruitment by many multiples of the value at B_0. This is a small, but perhaps under-appreciated, point about the range of values that steepness can take.

For the more theoretically inclined reader, we note that if we use Equation (50), then steepness is

$$h = 0.2\alpha_s(1 - r)\overline{W}_f f\left(0.2f^{-1}\left(\frac{1}{\alpha_s(1 - r)\overline{W}_f}\right)\right) \qquad (55)$$

where f^{-1} is the inverse function of the density dependent term on the right hand side of Equation (50), i.e. $f(f^{-1}(x)) = f^{-1}(f(x)) = x$.

Appendix 2: Adding process uncertainty to the stock–recruitment relationship

In this Appendix, we show that although adding process uncertainty to the stock recruitment relationship seems to produce a distribution for steepness, it does not mitigate the issues raised in the body of the paper. For simplicity, we use the production model, for which recruitment at spawning stock size B is $R(B) = \frac{\alpha_p(1-r)B}{1+\beta(1-r)B}$. The more common way of adding process uncertainty to the stock recruitment relationship is to multiply by a log-normal random variable (e.g. He $et\ al.$ 2006) so that we obtain

$$\tilde{R}(B) = \frac{\alpha_p(1 - r)B}{1 + \beta(1 - r)B}\exp\left(Z_{\sigma_r} - \frac{1}{2}\sigma_r^2\right) \qquad (56)$$

where Z_{σ_r} is a normally distributed random variable with mean 0 and standard deviation σ_r intended to capture the fluctuations in recruitment. Note that if one does this recruitment is no longer bounded by $\frac{\alpha_p}{\beta}$ when B is very large. Thus, Equation (56) allows for steepnesses larger than 1. An alternative (Mangel 2006), which avoids this problem, is to replace Equation (56) by (Mangel $et\ al.$ (2006))

$$\tilde{R}(B) = \frac{\alpha_p(1 - r)B \times \exp(Z_{\sigma_r} - \frac{1}{2}\sigma_r^2)}{1 + \beta(1 - r)B \times \exp(Z_{\sigma_r} - \frac{1}{2}\sigma_r^2)} \qquad (57)$$

in which case the upper limit of recruitment remains and the parameters retain their original interpretation.

Because Equation (56) is more commonly used, we use it here to illustrate the idea. Steepness is defined by the condition $R(0.2B_0) = hR_0$. We now

Figure A1 The probability of obtaining a recruitment deviation, when process uncertainty is added to the stock–recruitment relationship, large enough to conclude that steepness is 1, given the true value of steepness (x-axis) and the standard deviation of the log-normal variable characterizing recruitment variation (y-axis).
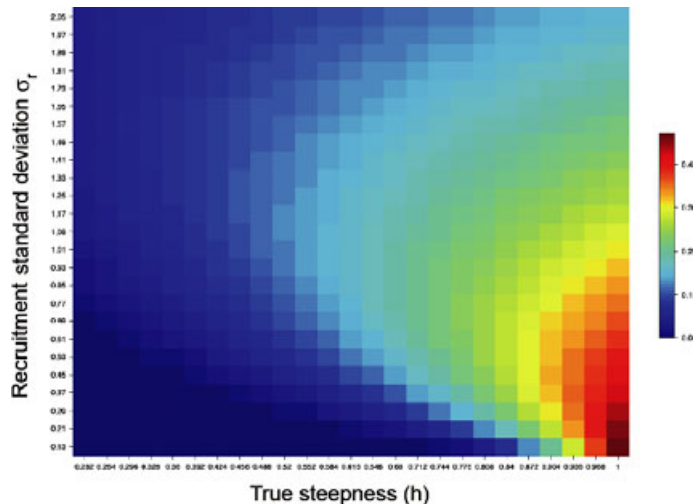
ask: what is the size of the recruitment deviation that will lead us to conclude that $h = 1$? (Actually, as noted above, $h \geq 1$.) That is, to conclude that steepness is 1, we need a recruitment deviation 20% of spawning biomass that produces a recruitment R_0. This will be true if

$$1 = h \times \exp\left(Z_{\sigma_r} - \frac{1}{2}\sigma_r^2\right) \qquad (58)$$

Thus, a recruitment deviation leading to the conclusion that steepness is 1 or more requires that $exp(Z_{\sigma_r} - \frac{1}{2}\sigma_r^2) > \frac{1}{h}$ or that $Z_{\sigma_r} - \frac{\sigma_r^2}{2} > -\log(h)$. We computed this quantity using the R program-

ming language (http://cran.r-project.org/) and show the result in Fig. A1. Here we show the true value of steepness on the *x*-axis, the intensity of the recruitment variation, measured by σ_r on the *y*-axis and the probability of obtaining a deviation large enough to conclude that steepness is $h = 1$, given the true value of steepness of σ_r. We conclude that adding process uncertainty to the stock–recruitment relationship, while effectively creating an *ad-hoc* log-normal distribution for steepness, does not lead us to the conclusion that steepness is close to 1 unless it really is.