Compensatory dynamics, functional elasticities, and why the Beverton-Holt Stock Recruitment Relationship cannot exist in nature

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Abstract Models of Stock Recruitment Relationships (SRRs) are used to predict fish population dynamics. Commonly used SRRs include the Ricker, Beverton-Holt, and Cushing functional forms, which differ primarily by the degree of density dependent effects (compensation). The degree of compensation determines whether recruitment respectively decreases, saturates, or increases at high levels of spawning stock biomass. In 1982 J.G. Shepherd united these dynamics into a single model, where the degree of compensation is determined by a single parameter, however the difficulty in relating this parameter to biological data has limited its usefulness. Here we introduce a generalized modeling framework to show that the degree of compensation can be related directly to the functional elasticity of growth, which is a general quantity that measures the change in recruitment relative to a change in biomass, irrespective of the specific SRR that is used. We show that the elasticity of growth can be calculated from short-term fluctuations in fish biomass, is robust to observation error, and can be used to determine general attributes of the SRR in both continuous time production models, as well as discrete time age-structured models. This framework may be particularly useful if fisheries time-series data are limited, and not conducive to determining functional relationships using traditional methods of statistical best-fit. Finally, we show that the Beverton-Holt SRR is qualitatively different than either
Ricker-like or Cushing-like SRRs, and that it is impossible for a Beverton-Holt SRR to exist in nature.

1 Introduction

Recruitment plays a central role in the population dynamics of fish species. Models of fish recruitment include both density-independent and -dependent effects, controlled by the variables $\alpha$ and $\beta$, respectively. That is, when density-dependent effects are negligible, recruitment is generally modeled as $S(B) = \alpha B$, where $B$ is spawning stock biomass, and $\alpha$ is the recruitment rate in the absence of density-dependent effects (e.g., Sissenwine and Shepherd 1987). We note that recruitment functions are often introduced as $R(B)$, but to prevent confusion later on (where we introduce scaled functions denoted by lowercase letters, such that $r$ could be confused as a growth rate), we avoid the use of $R$ to denote recruitment. When density-dependent effects are non-negligible, recruitment is anticipated to deviate from this relationship, such that $S(B) = \alpha BF(\beta, B)$, where the function $F$ controls density-dependent effects on recruitment. Traditional stock recruitment models introduce three general kinds of density-dependent responses to increasing spawning stock biomass: 1) recruitment increases to a maximum and then declines as $B$ increases, 2) recruitment saturates as $B$ increases, 3) as $B$ increases, recruitment continues to increase but at a lower rate than in the absence of density-dependent effects. These alternative scenarios thus differ in the intensity of density dependence (degree of compensation), which determines to what extent recruitment is altered as a function of spawning stock biomass.

Ricker (1954) developed a Stock-Recruitment Relationship (SRR) to introduce declines in recruitment at high levels of spawning stock biomass (Fig. 1a), such that

$$S(B) = \alpha Be^{-\beta B}. \tag{1}$$

As spawning stock biomass increases, recruitment increases to the maximum $S(B) = 1/\beta$ and then declines. The Ricker model is used if there are predatory response lags, when greater stock abundance suppresses juvenile growth, or when cannibalism or nest predation limits recruitment when $B$ is high (Cushing 1988).

Beverton and Holt (1957) introduced a related two parameter model where

$$S(B) = \frac{\alpha B}{1 + \beta B}. \tag{2}$$

Recruitment is thus a saturating function of spawning stock biomass, where saturation occurs at $S(B) = \alpha/\beta$ as $B \to \infty$. Here, it is assumed that density-dependent mortality affects recruitment instantaneously (see Mangel et al. 2006), and that recruitment tends asymptotically towards a finite value as $B$ increases (Cushing 1988). The Beverton-Holt (B-H) relationship is typically used if recruitment is assumed to be limited primarily by food or habitat resources.

In open systems where resources are not locally limiting, Cushing (1973) developed a power-law SRR

$$S(B) = \alpha B (\beta B)^{-1/n_c} = \alpha \beta^{-1/n_c} B^{n_c - 1} \tag{3}$$
Here, the third parameter $n_c$ controls the rate of recruitment increase at high biomass densities, or the degree of compensation. In this case, if $n_c > 1$ recruitment continues to increase with increasing spawning biomass, but at a decreasing rate.

In an attempt to integrate the above relationships into a single function controlled by the degree of compensation, Shepherd (1982) observed that the behaviors exhibited by the Ricker, Cushing, and Beverton-Holt functions can be united into a single framework with three free parameters, where

$$S(B) = \frac{\alpha B}{1 + \beta B^{1/n}}, \text{ for } n > 0. \quad (4)$$

The parameters $\alpha$ and $\beta$ again denote the initial rate of growth and the effects of density-dependence, respectively, while $n$ is the degree of compensation. When $n < 1$, recruitment increases when $B$ is low, and decreases when $B$ is high, similar to the Ricker function. When $n = 1$, Eq. (4) simplifies to the Beverton-Holt (B-H) SRR, where recruitment saturates as $B$ increases. For values of $n > 1$, recruitment behaves similarly to the Cushing function, maintaining a positive slope as $B$ increases. The versatility of the Shepherd function comes at the cost of the additional degree of compensation parameter, which is often difficult to relate to observational data, and this has served to limit its adoption.

Using observational data, we are often unable to distinguish which model is most descriptive of the underlying dynamics. This has been a long-standing problem: in 1982, Gulland noted that “in many cases, the variability of the data makes it difficult to choose between alternative mathematical models” (pg. 17). Such variation may be a product of environmental variability, as well as differences in life-history. For instance, SRRs may be constrained by multiple, rather than a single compensatory event (Brooks and Powers 2007), and these species-specific characteristics can be controlled by many different aspects of fish reproductive biology (Morgan et al 2011). In cases such as these, more complex models may be required, but this is at the cost of additional parameters, limiting the model’s applicability to different systems.

Distinguishing between possible compensatory scenarios without assuming knowledge of the exact form the SRR would thus provide insight into the population dynamics of a fish species, without force-fitting a potentially incorrect recruitment model to observational data. Bayesian Nonparametric techniques provide one way to estimate descriptive characteristics of stock-recruitment functions based only on the data (Munch et al 2005).

Here we present an analytical approach to determine compensatory dynamics, without assuming knowledge of the specific SRR. We use a generalized modeling framework (sensu Gross and Feudel 2006; Gross et al 2009; Stiefs et al 2010; Yeakel et al 2011; Kuehn et al 2012) to derive relationships between the degree of compensation and the functional elasticities (the logarithmic derivative of a function, giving a measure of the change of the function relative to a change in its argument) of a continuous time generalized production model, as well as a discrete time age-structured model.

Our results demonstrate that families of SRRs can be distinguished by these functional elasticities, which can be estimated from the dynamics of perturbations in fish biomass. We also show that some stock-recruitment families can be distinguished
more easily than others, and that these differences are closely related to the stability of populations controlled by different compensatory dynamics. This leads to the observation that the Beverton-Holt function is qualitatively different than either the Ricker or Cushing functions; though the probability of measuring Ricker-like or Cushing-like recruitment dynamics is distinctly non-zero, we show that it is impossible to observe Beverton-Holt recruitment dynamics in nature.

2 Methods and Analysis

Despite the intrinsic simplifications introduced when using production or biomass dynamic models, they can offer direct insight into the mechanisms governing fish recruitment, and thus remain an important and oft-used tool in fisheries management (Mangel et al. 2002, 2013), so we begin with them. We then extend our results and methods to a discrete time age-structured system, and show how functional elasticities can distinguish between stock-recruitment families and provide direct insight into the stability regimes of populations with complex life histories.

2.1 Analysis of a Generalized Stock-Recruitment Model

In a generalized production model, we assume that biomass enlarges according to the function $S(B)$ and shrinks according to the function $D(B)$, such that biomass changes as

$$\frac{dB}{dt} = S(B) - D(B). \tag{5}$$

The enlargement function $S(B)$ may be assumed to have Ricker, B-H, or Cushing recruitment dynamics, whereas $D(B)$ is often assumed to be linear, such that $D(B) = zB$, where $z$ is the rate of biomass loss due to fishing, natural mortality, or a combination thereof. However, in many cases we cannot assign a specific function to either $S(B)$ or $D(B)$. Unfortunately, analysis of such a general model is not straightforward, since the steady state solution ($B^*$, where $S(B^*) = D(B^*)$) cannot be described analytically.

In contrast, specific models present essentially the opposite problem: a steady state solution can often be computed, however the specific mathematical relationships may not accurately represent the dynamics of the population.

The general model presented in Eq. (5) cannot be solved at the steady state because the functions are unknown, however we can identify the unknown steady state(s) with the variable $B^*$. If we assume that $B^* > 0$ and that the signs of the growth and loss functions are biologically meaningful, then we can normalize the system to $B^*$. This allows us to define a set of normalized variables and functions. We set $S^* = S(B^*)$ and $D^* = D(B^*)$ and define

$$b = \frac{B}{B^*}, \quad s(b) = \frac{S(B)}{S^*}, \quad \text{and} \quad d(b) = \frac{D(B)}{D^*}. \tag{6}$$

This normalization procedure enables consideration of all positive steady states in the whole class of systems defined by Eq. (5), with the important property that
at the steady state all generalized functions and variables are equal to unity \((b = 1, s(1) = 1, d(1) = 1)\) By substituting the normalized variables into Eq. (5), we obtain the normalized general production model
\[
\frac{db}{dt} = \frac{S^*}{B^*} s(b) - \frac{D^*}{B^*} d(b),
\] (7)
and under steady state conditions \((b = s(b) = d(b) = 1)\), this simplifies to
\[
0 = \frac{S^*}{B^*} - \frac{D^*}{B^*}.
\] (8)
Thus, at the steady state, the scaled growth and mortality coefficients are equivalent, allowing us to define the timescale of the system
\[
\gamma = \frac{S^*}{B^*} = \frac{D^*}{B^*}.
\] (9)
This parameterization is useful because \(\gamma\) has a biologically relevant interpretation, and represents the biomass turnover rate. That is, for example, \(S^*/B^*\) has units of production per unit time of new biomass per unit of existing biomass. In generalized modeling, coefficients such as \(\gamma\) are referred to as ‘scale parameters’ (Gross and Feudel 2006). Substituting \(\gamma\) into Eq. (7), the generalized equation is thus
\[
\frac{db}{dt} = \gamma (s(b) - d(b)).
\] (10)
Although the normalized functions \(s(b)\) and \(d(b)\) are still unknown, we can assess the dynamics of Eq. (10) by investigating the system under a small perturbation evaluated at the steady state, accomplished by taking the derivative of the normalized system. The derivative of the right hand side of Eq. (10) is
\[
\lambda|_s = \gamma \left( \frac{\partial s(b)}{\partial b} |_s - \frac{\partial d(b)}{\partial b} |_s \right) = \gamma (s_b - d_b),
\] (11)
where \(\lambda\) is the single eigenvalue of the system and \(|_s\) indicates evaluation at the steady state \(B^*\). The system is stable if \(\lambda < 0\), and unstable if \(\lambda > 0\). As \(\lambda\) moves upwards toward 0, the system approaches a saddle-node bifurcation (Mangel 2006; Yeakel et al. 2011), a critical transition associated with the sudden appearance of a stable and unstable fixed point, changing the dynamics rapidly (Kuznetsov et al. 1998).

The linearization of Eq. (10) reveals two additional parameters, \(s_b\) and \(d_b\), which are the partial derivatives of the normalized function \(s(b)\) and \(d(b)\), respectively. Partial derivatives of normalized functions are equivalent to the elasticities of the unnormalized functions (Gross and Feudel 2006; Yeakel et al. 2011), which we show below. In general, elasticities provide a measure of the percent change of a function relative to the percent change in its argument

\[
\text{Elasticity}\{F(a)\} = \frac{a}{F(a)} \frac{\partial F(a)}{\partial a} = \lim_{x \to a} \frac{F(x) - F(a)}{x - a} \frac{a}{F(a)} = \lim_{x \to a} \frac{1 - F(x)/F(a)}{1 - x/a} \approx \frac{\% \Delta F(a)}{\% \Delta a}.
\] (12)
Elasticities are commonly used in metabolic control theory (Fell 1992), economics (Sydsaeter and Hammond 1995) and life history theory (Horvitz et al. 1997).

In generalized modeling, the elasticity of a function $F(X)$ with respect to its steady state $X^*$ is alternatively written as the logarithmic derivative of the function with respect to $X^*$ (Yeakel et al. 2011), and is equivalent to the partial derivative of the normalized function $f(x)$,

$$f_x = \frac{X^* \frac{\partial F}{\partial X}}{F^*} \bigg|_{x=1} = \frac{\partial \log F}{\partial \log X} \bigg|_{x=1} = \frac{\partial f}{\partial x}.$$  \hspace{1cm} (13)

Elasticities offer a number of advantages that are particularly useful for generalized modeling. First, an elasticity of a power-law function of the form $F(X) = aX^p$ is equal to $p$. This can be shown by normalizing $F(X)$ to the equilibrium $X^*$, and taking the derivative at the steady state, such that

$$f_x = \frac{\partial f}{\partial x} \bigg|_{x=1} = \frac{\partial}{\partial x} aX^p \bigg|_{x=1} = \frac{\partial}{\partial x} x^p \bigg|_{x=1} = p.$$  

For instance, if the function $D(B) = zB$ and $z$ is a constant, then the elasticity is equal to unity; if the function is quadratic, the elasticity is equal to 2; for constant functions, the elasticity is equal to 0. For more complex functions, the value of the elasticity may change with the value of the steady state (see below). Importantly, the elasticities of functions governing the time-evolution of an animal population are representative of the environmental conditions present during measurement. Thus elasticities are not defined with respect to unmeasurable biological conditions that serve to bound traditional functional relationships, such as half-maximum values or growth rates at saturation (Fell and Sauro 1985, Fell 1992).

2.2 Relating functional elasticities to the degree of compensation

The degree of compensation in the Shepherd function (Eq. 4) is controlled by the parameter $n$: if $n < 1$ the function is Ricker-like, if $n > 1$ the function is Cushing-like, and if $n = 1$ it is equivalent to the B-H function (Shepherd 1982). In a generalized modeling framework, the degree of compensation is related directly to the functional elasticity. Given that $B^*$ is large enough to experience density-dependent effects, if the elasticity of growth $s_b < 0$ the population grows according to a Ricker-like function, if $s_b > 0$ the population grows according to a Cushing-like function, and if $s_b \to 0$ the population grows according to the B-H function. Thus, $n$ and $s_b$ are closely related, which can be shown by mapping the Shepherd function (Eq. 4) to the generalized model (Eq. 10), where

$$s(b) = \frac{S(B)}{S(B^*)} = \frac{\alpha B}{1 + \beta B^{1/n}} \cdot \frac{1 + \beta B^{1/n}}{\alpha B^*},$$

$$= \frac{1 + \beta B^{1/n}}{1 + \beta B^{1/n} b^{1/n} b}.$$
The elasticity of growth is

$$s_b = 1 - \frac{\beta B^{1/n}}{n(1 + \beta B^{1/n})}.$$  \hspace{1cm} (14)

Eq. (14) shows that the elasticity of growth depends on both the steady state biomass, as well as the degree of compensation, enabling direct comparisons between Ricker-like, Cushing-like, and B-H functions and their corresponding elasticities. For example, as $B^*$ increases, if $n > 1$ (Cushing), then $s_b > 0$; if $n < 1$ (Ricker), then $s_b < 0$; if $n = 1$ (B-H), $s_b \to 0$ (Fig. 1). (This is more readily apparent if the quantity $(1/\beta B^{1/n})(1/\beta B^{1/n})^{-1}$ is factored into the rightmost term of Eq. [14]) Because the value of the elasticity holds for any function $S(B)$, this generalization is not isolated to the Shepherd equation, but extends to any function with degrees of compensation that can be categorized as ‘Ricker-like’, ‘Cushing-like’, or saturating. Thus, when density-dependent effects are present, if the value of the elasticity $s_b$ can be determined, a general functional family can be assigned to the observed recruitment dynamics. This is a key relationship, because assignment of the functional family does not depend on the specific architecture of a given function.

If we assume that recruitment follows a Shepherd function, the degree of compensation can be determined directly if the elasticity $s_b$ is

$$s_b = \frac{\gamma + \alpha(n-1)}{\alpha n}, \text{ or alternatively, } n = \frac{\gamma - \alpha}{\alpha(s_b - 1)},$$  \hspace{1cm} (15)

where as before, $\gamma$ is the biomass turnover rate, and $\alpha$ is the recruitment rate at low biomass. From this relationship, we see that if $s_b < 1$, $\gamma$ is constrained to vary between 0 and $\alpha$ if $n$ is to remain positive. Because $\gamma$ is the biomass loss rate, it is evident that values greater than $\alpha$ (the maximum growth rate independent of density dependent effects) imply extinction of the population.

The discrimination of different governing functional forms (or families of functional forms) from observational data typically requires measures of statistical best fit using multiple years of stock-recruitment data (Munch et al. 2005). Because these data are often highly variable and complicated by changes in birth and death rates over long timespans, distinguishing between functional forms can be problematic (Fig. 1a). However, because the elasticities of alternative functional families have non-overlapping ranges, they may be useful for determining the effects of density dependence on recruitment (Fig. 1b). Moreover, because the sign of the elasticity can differentiate between competing functional families, the determination of functional family from the elasticity of growth may be relatively error-tolerant.

The relationship between the elasticity of growth and the degree of compensation suggests that the Cushing SRR and Ricker SRR are qualitatively different than the B-H SRR. The reasoning for this is straightforward: the elasticity of growth is a continuous variable, and recruitment following the B-H function is defined by the elasticity $s_b = 1$, whereas Cushing-like and Ricker-like functions have elasticities that span a range of values. Mathematically, the elasticities of the Ricker- and Cushing-like functional families can be represented by non-overlapping intervals (Ricker: $s_b \in [-\infty, 0]$; Cushing: $s_b \in (0, \infty]$), whereas the B-H function is a measure zero, or null set
Because the probability that a continuous variable is equal to a single value is always zero, it is evident that recruitment following the B-H functional form cannot exist in nature (Fig. 1b).

2.3 Measuring elasticities from time-series

We have shown that the degree of compensation can be calculated if the elasticity of growth is known. There exists a large body of literature in metabolic control theory for measuring elasticities in nature (which typically consist of experimental manipulations [Fell 1992]), however these tools are not always appropriate for obtaining measurements from animal populations in the wild. We now show that the elasticity of growth can be measured from relatively small perturbations in fish biomass, and we provide a basic example using simulated data.

To begin, we consider single-species dynamics, where \( \frac{dX}{dt} = F(X) \). We define deviation from the steady state, such that the population size at time \( t \) is some distance away from the equilibrium \( X^* \) as \( \xi(t) = X(t) - X^* \). Then to first order

\[
\frac{d}{dt} \xi(t) \approx F'(X^*) \xi.
\]

(16)

For a single-species system, we observe that \( F'(X^*) \) is also the single eigenvalue of the system, \( \lambda_f \), and we use the subscript \( f \) to distinguish the eigenvalue in this example from the eigenvalue \( \lambda \) defined for the production model. Integrating Eq. (16), we find that

\[
\xi(t) = \xi_0 e^{\lambda_f t}.
\]

Thus, the eigenvalue of a single-species system is equivalent to the rate of relaxation to the steady state of the population trajectory after a small perturbation if \( \lambda_f < 0 \).

Our generalized analysis of Eq. (5) shows that \( \lambda = \gamma(s_b - d_b) \). For now, we will assume that \( \lambda \) can be measured. To determine which of the three functional families depicted in Fig. (1a) drive recruitment dynamics, we must determine the elasticity of growth, where \( s_b = \lambda/\gamma + d_b \). If mortality is assumed to be governed by a linear function, such that \( d_b = 1 \), then the criteria are simply defined by comparing the magnitude of the relaxation rate, \( \lambda \), to the timescale of the system, \( \gamma \) (Table 1). If we assume that the steady state is stable (\( \lambda < 0 \)), recruitment is driven by a Ricker-like function if \( \lambda < -\gamma \), recruitment is driven by the B-H function if \( \lambda = -\gamma \), and recruitment is driven by a Cushing-like function if \( \lambda > -\gamma \) (Fig. 1a). Because we do not presume to know the exact architecture of the stock-recruitment function, these relationships are predictive of general families of models. If we assume that growth is governed by the Shepherd function, the general relationship between the degree of compensation and the relaxation rate is (cf. Eqn 15)

\[
n = \gamma \frac{\gamma - \alpha}{\alpha(\lambda + \gamma d_b - \gamma)}.
\]

(17)

which can be simplified further assuming that mortality is governed by a linear function, such that
As the system approaches the saddle-node bifurcation at $\lambda = 0$, small errors in $\lambda$ are likely to generate large errors in the degree of compensation (Eq. 18, Fig. 2), such that Ricker-like SRRs result in measurements that are more error-tolerant than Cushing-like SRRs. Moreover, because an elasticity of growth $s_b < 1$ produces dynamics with a single non-trivial stable steady state (assuming the elasticity of mortality $d_b = 1$), only Cushing-like SRRs can come close to the saddle-node bifurcation at $\lambda = 0$. The rate at which the saddle-node bifurcation is reached as $n$ increases is contingent on the biomass turnover rate $\gamma$, where turnover rates intermediate to 0 and $\alpha$ approach the bifurcation more slowly. If the turnover rate is greater than $\alpha$, $\lambda > 0$ and the system becomes unstable.

2.4 Estimating the degree of compensation from fluctuations in fish biomass

We have derived a relationship between the degree of compensation $n$ and the elasticity of growth $s_b$, and have shown how - in principle - elasticities could be measured from short-term fluctuations in time-series data. To elaborate this idea, we constructed a stochastic dynamic model with growth following the Shepherd function and mortality due to both natural causes $M$ and fishing $F$, coupled with observation error. We perturbed the system at time $t = t_i$ by eliminating the fishing mortality term (the end of a fishing period) until a steady state was reached at the terminal time $t = T$. We included normally distributed observation error $\tilde{P}$ with mean zero and standard deviation $\sigma$. Accordingly, observations of fish biomass $B_{\text{obs}}(t)$ change are then

\[
\frac{dB}{dt} = \frac{\alpha B}{1 + B^{1/n}} - \left( M + \delta F \right) B,
\]

\[
B_{\text{obs}}(t) = B(t) + \sigma \tilde{P},
\]

where $\delta$ controls fishing mortality. During the fishing time interval $t_0 \leq t < t_i$, $\delta = 1$; during the non-fishing time interval $t_i \leq t < T$, $\delta = 0$ (e.g. Fig. 3).

Given the Gaussian assumption about the observation error, we assume that the system trajectory behaves as $B_{\text{obs}}(t) \sim N\{c(1 - e^{-\lambda t}), \sigma\}$ close to the steady state. The stochastic trajectory thus depends on the unknown variables $c$, $\lambda$, and $\sigma$, which we determine using a likelihood approach where $k$ is the number of observations from the end of the fishing period until the trajectory reaches its steady state in the absence of fishing at $t = T$. This problem can be simplified, as the variables $c$ and $\sigma$ can be written in terms of $\lambda$ to obtain the log-likelihood

\[
\log L(\lambda) = -\frac{k}{2} \log(2\pi) - \frac{k}{2} \log \left\{ \frac{1}{k} \left( \sum_{t=t_i}^{T} B(t) - \frac{\sum_{t=t_i}^{T} B(t)(1 - e^{-\lambda t})}{\sum_{t=t_i}^{T}(1 - e^{-\lambda t})} \right)^2 \right\} - \frac{k}{2}
\]

(19)
which we use to find the maximum likelihood estimate for the eigenvalue $\lambda_{\text{MLE}}$.

We aim to discriminate between different families of functional forms using the maximum likelihood estimate for the rate at which a population trajectory returns to its steady state after a perturbation. If the rate of relaxation is known, the degree of compensation can be calculated from Eq. (18). To determine the accuracy of our model estimates across different degrees of observation noise, we calculated $\lambda_{\text{MLE}}$ as a function of the coefficient of variation ($\text{CV} = \sigma/B^*$) for three compensation scenarios: Ricker ($n = 0.5$), Cushing ($n = 1.5$), and B-H ($n = 1$). After estimating $\lambda_{\text{MLE}}$, we calculated the degree of compensation, $n_{\text{MLE}}$ from Eq. (18), and determined the probability that $n$ was correctly distinguished with respect to alternative stock-recruitment functions (Fig. 4a,b), as well as the probability that the functional family was correctly identified (Fig. 4a,c).

3 Results

The analytical relationship between the degree of compensation $n$ and the elasticity of growth $s_b$ (Eq. 18) suggests that populations growing in accordance to Ricker-like functions should be less difficult to measure accurately than those growing in accordance to Cushing-like functions (Fig. 2a). In general, our simulation experiment showed that the rate of relaxation can be estimated from moderately noisy data, and as we predicted, there were large differences in the measurement accuracy for different functional families. The estimated rate of relaxation $\lambda_{\text{MLE}}$, and by transformation $n_{\text{MLE}}$, is estimated more accurately for Ricker-like and B-H functions than for Cushing-like functions (Fig. 4b). We note that the mean value of our estimates always diverged from the set value of $n$ because the rate of return equation is only accurate at values very close to $B^*$ and is therefore a necessarily crude estimate of the solution to $B_{\text{obs}}(t)$.

Despite differences in measurement accuracy, the probability that the correct stock-recruitment function was distinguishable from the other SRRs declined approximately linearly for both Ricker and Cushing models after $\text{CV} = 0.15$, while that for the B-H model declined nonlinearly (Fig. 4b). The B-H model was more difficult to distinguish because estimates of $n$ overlapped values for both neighboring models. However, this comparison is somewhat arbitrary, and the more important question relates to the probability that the functional family is correctly determined with respect to other potential families of functions. Our results showed that the probably of correctly determining the functional family from $\lambda_{\text{MLE}}$ remained relatively high as CV increased (Fig. 4c) for both Ricker-like and Cushing-like functions. The probably that Ricker-like functions were correctly distinguished was generally greater than 0.6 for $\text{CV} \leq 0.30$. The same probability was greater than 0.8 for $\text{CV} \leq 0.5$ for Cushing-like functions, due primarily to the greater range of $n$ for the Cushing functional form. Because the B-H function is a measure zero or null set (see Methods), the probability that it was correctly distinguished was always 0.
4 An Example With Age Structure

Production models effectively summarize the recruitment dynamics of fish populations, and in some cases can provide robust measures of fisheries reference points (MacCall 2002; Mangel et al. 2010, 2013). However, the influence of age-related differences in growth and mortality can have large effects on the dynamics of fish populations (Mangel et al. 2006; Shelton and Mangel 2011). In this section we build upon our prior results and expand the generalized modeling schema to discrete time, age-structured models. The extension of generalized modeling to discrete time systems is useful in its own right, as it provides a method for the dynamical analysis of whole classes of discrete time models (*sensu* Gross and Feudel 2006). First, we briefly illustrate an extension of the generalized modeling approach to an age-structured discrete time system. Second, we show how the degree of compensation in an age-structured system is related to the elasticities of growth and finish by showing how measurements of elasticities in the age-structured model provide important insight into system stability.

We consider an age-structured model where the number of recruits $X(t+1)$ is governed by spawning stock biomass, $B_s(t)$, depending on the degree of compensation $n$. The number of individuals in the mature age class $Y$ is the sum of returning adults and incoming recruits, where adult mortality is given by $M_y$ and recruit mortality is given by $M_x$. It follows that spawning stock biomass is calculated by the number of mature individuals times the average mass of individuals $W_y$. The age-structured model is thus

$$ X(t+1) = F(B_s(t)) = \frac{\alpha B_s(t)}{1 + \beta B_s(t)^{1/n}}, $$

$$ Y(t+1) = G(X, t) + H(Y, t) = X(t)e^{-M_x} + Y(t)e^{-M_y}, $$

$$ B_s(t+1) = K(Y, t) = Y(t)W_y. $$

We can determine the steady state condition $X^*$ (where $X(t+1) = X(t)$) in terms of spawning stock biomass $B_s^*$ because at the steady state $B_s^* = Y^*W_y$, such that

$$ B_s^* = X^*\frac{e^{-M_x}W_y}{1 - e^{-M_y}} = X^*W_y^*. $$

The primary difference between the age-structured and production models is that mortality is not assumed to occur simultaneously with recruitment, and this yields dynamics that diverge strongly from those predicted by the production model. We note that this 3-dimensional model can be slightly modified and collapsed such that $B_s(t) = Y(t)W_y$, and this has little effect on the qualitative dynamics.

The normalization of the age-structured system is analogous to the normalization of the production model (Eq. 7), however because the age-structured system is composed of difference rather than differential equations, the steady state condition requires that the scale parameters are defined differently than before. For example, $y(t+1) = (G^*/Y^*)g(x, t) + (H^*/Y^*)h(y, t)$ is defined at the steady state $1 = G^*/Y^* + H^*/Y^*$, such that we define the ratio of incoming recruits to the abundance...
of the mature age-class $\gamma = G^*/Y^*$ and the ratio of returning adults to the abundance of the mature age-class $(1 - \gamma) = H^*/Y^*$. These coefficients are thus the proportional contributions of recruit and mature age-classes to spawning stock biomass at the steady state. The generalized system is then written

$$
\begin{align*}
x(t + 1) &= \gamma x f(b, t), \\
y(t + 1) &= \gamma y g(x, t) + (1 - \gamma) h(y, t), \\
b(t + 1) &= \gamma b k(y, t).
\end{align*}
$$

We can immediately simplify the problem by observing that the scale parameters for recruits and biomass can be reduced to

$$
\gamma_x = F^* X^* = \frac{\alpha W^*}{1 + \beta (W^* X^*)^{1/n}} = 1,
$$

$$
\gamma_b = K^* B^* s = 1.
$$

For the production model, elasticities were defined with respect to the linearized system (Eq. 11). Because the age-structured system is multi-dimensional, the linearization is defined by the Jacobian matrix evaluated at the steady state $J|*$, where each element is defined by the partial derivative of each differential equation with respect to each variable. The elasticities of the generalized system can then be calculated, such that

$$
J|* = \begin{pmatrix}
\frac{\partial F}{\partial X} |* & \frac{\partial F}{\partial Y} |* & \frac{\partial F}{\partial B} |* \\
\frac{\partial G + H}{\partial X} |* & \frac{\partial G + H}{\partial Y} |* & \frac{\partial G + H}{\partial B} |* \\
\frac{\partial K}{\partial X} |* & \frac{\partial K}{\partial Y} |* & \frac{\partial K}{\partial B} |*
\end{pmatrix} = \begin{pmatrix}
0 & 0 & f_b \\
\gamma & (1 - \gamma) & 0 \\
0 & 1 & 0
\end{pmatrix},
$$

and for the specific age-structured model, $\gamma_i = 1 - e^{-M_i}$, and

$$
f_b = \frac{\alpha W_i^* (n - 1) + 1}{\alpha W_i^* n}.
$$

The Jacobian matrix determines the stability of the system; we solve for the eigenvalues that satisfy the characteristic equation $\text{Det}(J|* - \lambda I) = 0$, where $I$ is the identity matrix. From Eq. (24), the characteristic equation is $f_b \gamma + \lambda^2 - \gamma Y - \lambda^3 = 0$, which yields three distinct eigenvalues, and though the solutions for these eigenvalues are large and unwieldy, they can be easily derived with algebraic computing languages such as Maple or Mathematica.

Simulation of the age-structured system (where $\alpha = 8$, $\beta = 1/80$, $M_x = 0.2$, $M_y = 0.7$, and $W_y = 2$) across a range of values for the degree of compensation reveals a single steady state for $n > 0.376$. For $n < 0.376$, stable cycles emerge, which in turn give rise to five-period cycles for lower values of $n$ (Fig. 5a,b). In discrete time systems, the emergence of cyclic conditions can result from crossing a Neimark-Sacker
bifurcation (cf. [Guill et al. 2011a;b]), which occurs when a pair of complex conjugate eigenvalues cross the unit circle on the complex plane. If \( \lambda_1 \) and \( \lambda_2 \) are the complex conjugate eigenvalue pair, the test-function for this condition is \( \lambda_1 \lambda_2 = 1 \) (Kuznetsov et al. 1998). Using solutions for \( \lambda_1 \) and \( \lambda_2 \) from the characteristic equation, we numerically determined that a supercritical Neimark-Sacker bifurcation is crossed at \( n = 0.376 \) (Fig. 5a,c). Supercritical Neimark-Sacker bifurcations yield stable closed invariant curves, such that local trajectories initiated interior and exterior to the cycle are attracted to the curve (cf. Fig. 5b; Kuznetsov et al. 1998). Predictions of population dynamics are thus possible, but only if the degree of compensation, in addition to the other parameters, is known. As before, the specific age-structured model introduces strong assumptions regarding functional forms, and these assumptions may not hold (or be conducive to measurement) in many situations.

Because the degree of compensation is related directly to the elasticity of growth (Eq. 25), we can use the generalized age-structured system to gather direct insight into the potential dynamics applicable to any class of models substituted into the general functions \( F(B) \), \( G(X) \), \( H(Y) \), and \( K(Y) \). Although the test-function for the Neimark-Sacker bifurcation is not analytically tractable (even for the generalized system), we can numerically simulate the relationship between the elasticity of growth \( f_b \), the proportion of maturing recruits to the mature age class \( \gamma_y \) (which has a value of 0.50 in the simulated age-structured model), and the test-function \( \lambda_1 \lambda_2 \). Our numerical results show that only Ricker-like SRRs can result in cyclic dynamics \( (\lambda_1 \lambda_2 \geq 1; \text{Fig. 5d}) \). Moreover, we observe that cyclic dynamics can only emerge if \( f_b \leq -1 \) for any potential value of \( \gamma_y \), and this result applies to all potential SRRs. Accordingly, as the ratio of maturing recruits declines (low \( \gamma_y \); realized as the mortality of the mature age-class \( M_y \) decreases), cyclic dynamics are less likely to occur unless the elasticity of growth is extremely low, which is biologically unreasonable. As the ratio of maturing recruits increases (higher mature age-class mortality), the opposite occurs, and cyclic dynamics are more likely for a broader range of Ricker-like SRRs. We have thus obtained a very powerful result: independent of the particular functions introduced into the general age-structured system, cyclic dynamics require 1) that spawning stock biomass includes a relatively large proportion of incoming recruits, and 2) that compensatory dynamics are driven by a Ricker-like function, where the elasticity of growth has a value \( \geq -1 \). By relating the elasticity of growth to stability regimes, knowledge of general aspects of the system - without assuming specific functional relationships - provides direct insights into the compensatory dynamics of age-structured populations.

5 Discussion

We have shown that the elasticity of growth in a generalized production model can be related directly to the degree of compensation parameter that determines Ricker-like, Cushing-like, or Beverton-Holt behaviors. The elasticity of growth is useful because it is defined with respect to the biological and environmental conditions present during measurement, and thus can be estimated from limited time-series data. Moreover, because large ranges of the elasticity of growth, and by extension the rate of re-
laxation, characterize families of functional forms, these measures are error tolerant (Fig 4c), particularly if the goal is to distinguish between SRRs with Ricker-like or Cushing-like recruitment dynamics.

The functional elasticities of both production and age-structured models can be used to determine directly the compensatory dynamics driving SRRs. This method may be of most use to recent fisheries, where long-term time-series data do not yet exist. Because we have employed elasticities in a generalized modeling framework, they are well-suited to inform knowledge of the general nature of compensation, and thus may be particularly useful for developing priors for parameters in flexible SRRs, such as the degree of compensation in the Shepherd model. Determining SRRs from elasticities may also be useful if populations have highly variable recruitment dynamics, or dynamics that are strongly sensitive to changing environmental conditions, and it may be instructive to consider alternative approaches for measuring elasticities across a broader range of management scenarios.

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Fig. 1  a. Recruitment $S(B)$ as a function of spawning stock biomass $B$. b. The elasticity of growth $s_b$ as a function of the steady state spawning stock biomass $B^\ast$. The distributions to the right represent potential measurements of recruitment (A.) and the elasticity of growth (B.) for Ricker, B-H, and Cushing recruitment functions. Although measurements for SRRs overlap in (A.), the elasticities of the Ricker- and Cushing-like functional families can be represented by non-overlapping intervals. Ricker: $s_b \in [-\infty, 0)$; Cushing: $s_b \in (0, \infty]$), whereas the B-H function is a measure zero, or null set, B-H: $s_b \in \emptyset$. 

Fig. 2  a. The rate of relaxation to the steady state $\lambda$ vs. the degree of compensation $n$ for a biomass turnover rate $\gamma = 1$. The red line at $\lambda = 0$ denotes a saddle-node bifurcation below which the system is stable, and above which the system is unstable. b. The biomass turnover rate $\gamma$ as a function of the degree of compensation $n$ and the rate of relaxation $\lambda$ (contour lines). The trajectory shown in (A.) is denoted by the blue line. Values of $0 < \gamma < (\alpha = 3)$ result in stable dynamics, and only Cushing-like functions, where $n > 1$ can result in values of $\lambda$ close to the saddle-node bifurcation.
Fig. 3 An example of the transition from a fishing to a non-fishing interval used to measure the rate of relaxation $\lambda$ from time-series data. The non-fishing interval is initiated at $t = t_i$, and biomass values immediately after $t_i$ can be used to find the maximum likelihood estimate for $\lambda$. The best-fit trajectory using the likelihood technique is shown in orange.
Fig. 4  a. Estimation of the degree of compensation as a function of the coefficient of variation for 6300 simulated population trajectories (300 for each of 21 different values of CV). Shaded areas show the standard deviation of estimated $n$ values, while colored lines show the means (blue: Ricker; red: Cushing; yellow: B-H). b. The probability of correctly identifying the specific model from the others (Ricker: $n = 0.5$; Cushing: $n = 1.5$, and B-H: $n = 1$). c. The probability of correctly identifying the SRR family (Ricker: $n < 1$; Cushing: $n > 1$; B-H: $n = 1$). The probability of measuring the B-H SRR is always zero.
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Fig. 5  a. Bifurcation diagram showing the onset of cycles followed by multi-period oscillations for the age-structured model as the degree of compensation lowers beyond $n = 0.376$. b. Examples of the corresponding dynamics where $n = 0.70$, $n = 0.376$, $n = 0.30$, and $n = 0.10$. c. Values of the test-function $\lambda_1 \lambda_2$ across different values of $n$ for the specific model. A Neimark-Sacker bifurcation exists at $\lambda_1 \lambda_2 = 1$, which is crossed at $n = 0.376$. This condition exists when two complex conjugate eigenvalues cross the unit circle on the complex plane (inset). d. Numerically estimated values for the test-function $\lambda_1 \lambda_2$, given the elasticity of growth $f_b$ and the ratio of incoming recruits to the mature age-class $\gamma$. The red contour denotes the Neimark-Sacker bifurcation condition; systems below this contour have cyclic dynamics.

Table 1  Criteria for determining the elasticity of growth $s_b$ from the rate of return to the steady state after a perturbation, $\lambda$, for the production model. The non-overlapping intervals for the elasticity of growth uniquely identify of Ricker-like, Beverton-Holt, and Cushing-like recruitment dynamics.

| Model          | Elasticity ($B^* > 0$) | Criterion                      |
|----------------|------------------------|--------------------------------|
| Ricker-like    | $s_b < 0$ s.t. $\frac{\lambda}{2} + d_b < 0$ | $\lambda < -pd_b$            |
| Beverton-Holt  | $s_b = 0$ s.t. $\frac{\lambda}{2} + d_b = 0$ | $\lambda = -pd_b$            |
| Cushing-like   | $s_b > 0$ s.t. $\frac{\lambda}{2} + d_b > 0$ | $\lambda > -pd_b$            |
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