Generalized compensation in stock-recruit functions: properties and implications for management

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A general stock-recruit function that explicitly defines density-dependent and -independent components of mortality over multiple stages is derived. By generalizing the stock-recruit function and the timing of density-dependent compensation, the impacts of different sources and magnitudes of mortality during the recruitment phase can be evaluated. Given reasonably comparable stage durations, compensation in early stages of a multistage process dominates density-independent effects; in later stages, density-dependent and -independent factors compete on a more even scale. Ratios of equilibrium statistics associated with the stock-recruit function under alternative compensation timing scenarios can be determined from the ratio of the compensation terms in the models when all scenarios assume the same type of stock-recruit function (Ricker or Beverton–Holt). This analytical result facilitates evaluation of proposed impacts or rehabilitation strategies without the need for a full stock assessment. Exogenous mortality has more impact on the maximum excess recruitment if that rate occurs later in the recruitment interval, especially if it takes place after compensation. Reparameterizing this generalized stock-recruit function in terms of steepness and virgin recruitment, we show that steepness is not influenced by the timing of compensation nor by the length of the recruitment interval; the level of virgin recruitment, however, is affected by both.

Keywords: bycatch fishing mortality, compensation, density-dependence, stock recruitment.

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Introduction

Relating observations of the mature fraction of a population at one time with the subsequent spawned cohort at a later time is a fundamental step in explaining the dynamics of a population. Assuming a linear relationship in both reproduction and survival-at-age implies exponential population growth. Although difficult to detect empirically, most would agree that density-dependent regulation occurs at some stage in the life cycle (Shepherd and Cushing, 1980; Shepherd *et al.*, 1990; Fogarty *et al.*, 1991; Koslow, 1992; Rose *et al.*, 2001). In populations where reproductive output is great and parental investment minimal, density is greatest immediately post-reproduction. Hence, a natural and convenient place to incorporate density-dependence is in the reproductive function, i.e. in the relationship between parental stock at time t, and the resultant cohort that recruits to the population at time $t + \Delta t$. Myers and Cadigan (1993), for example, found evidence of density-dependent mortality during the juvenile stage across a variety of stocks. Here, we are concerned with the timing of density-dependent mortality relative to exogenous mortality (e.g. fishing or pollution) within a defined recruitment interval and the impact on the realized number of recruits at the end of that interval.

A tacit assumption in age-structured stock assessment models is that density-dependence only occurs in the recruitment interval, such that survival decreases as pre-recruit density increases (i.e. compensation). A more realistic view might be that there are many compensatory phases throughout a population's life history, perhaps more subtle to detect or discover, but still potentially contributing to overall population regulation. Paulik (1973) mentions the possibility of multiple compensatory phases, although he relied on graphical methods to assess qualitatively the outcomes of such cases. In magnitude and importance, however, we follow the convention that all density-dependent interaction is in the pre-recruit phase. However, even within the pre-recruit phase, we allow for the possibility of modelling multiple stages of compensation reflecting alternative life history characteristics and possible ontogenic shifts in habitat.

The choice of recruitment interval length effectively defines the point from which all subsequent mortalities are considered to be density-independent. In some cases, this decision may be based on modelling convenience or data availability, rather than expert knowledge of the underlying process. An important implication of that decision is that all post-recruitment exogenous mortality rates would be additive to natural mortality. From a population management perspective, models designed to assess the impact of exogenous mortality (e.g. fishing, pollution, habitat loss or degradation, entrainment) could over- or underestimate the consequences, depending on the magnitude of that mortality and whether it is completely additive. Likewise, if a population is

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already in a vulnerable state and rehabilitation options are being evaluated, then the projected success or failure of rehabilitation would depend on how the proposed action is modelled relative to assumptions about compensation timing.

Another scenario where the timing of compensation matters, and which motivated this study, is the case where more than one user group is exploiting a resource, one group targeting the adult population for harvest and a second group incidentally killing the young of the year as bycatch. In this situation, the management question is twofold: (i) whether the bycatch mortality takes place during a compensatory phase, and therefore is removing fish that likely would have died from density-dependent effects anyway; (ii) to what extent (if any) does bycatch mortality reduce the potential yield to the directed user group.

In what follows, we first derive a general stock-recruit function from first principles. This continuous-time, discrete-stage process includes the Ricker (1954) and Beverton and Holt (1957) models as special cases. The derivation allows for multiple compensatory phases, with explicit notation regarding mortality forces and the time interval during which each force operates. We then analytically evaluate the impacts of compensation timing and exogenous mortality forces on population statistics. We illustrate the methodology with an example of a bycatch and a directed fishery operating on the same fish stock. Finally, we discuss the implications for designing recruitment studies and the estimation of mortality rates during early life history stages. Throughout, our use of the term "recruitment" refers to the process of transforming spawned eggs to recruits, where "recruits" refers to the number of fish at the end of the defined stock-recruit interval. We distinguish our usage from the context where recruitment refers to fish becoming vulnerable to fishing gear.

Recruitment models and their properties

A generalized recruitment process

Assume that the recruitment process can be divided into n discrete stages with duration Δt_i ($i = 1, 2, \ldots, n$). The total duration of the recruitment interval is defined as $T \equiv \sum_{i=1}^{n} \Delta t_i$. Let $R_i(t)$ be the number of fish surviving to time t of stage i ($0 \le t \le \Delta t_i$); the number at time 0 of stage 1 is defined as the number of eggs produced, $E \equiv R_1(0)$. Following this notation, $R_{n+1}(0)$ is the number of fish surviving to the end of the last stage (stage n), i.e. the number of recruits produced from $R_1(0)$. During each stage, there may be both density-independent and -dependent mortalities. Define M_i to be the density-independent component of natural mortality and F_i to be density-independent exogenous mortality, respectively (M_i, $F_i \ge 0$).

Let A_i and B_i be parameters defining density-dependent mortality (A_i, $B_i \ge 0$). A_i defines the *per capita* mortality rate in terms of the number of recruits existing at the beginning of a stage, and it remains constant throughout the stage interval. Ricker (1954) argued that this form of density-dependent mortality might be appropriate when "a prey species is temporarily massed in unusual numbers. . .The main characteristic of such situations is that the number of prey eaten depends on the abundance of predators, but not on the abundance of prey. Hence such situations cannot last long, and the predators cannot make the prey in question their principal yearly food. . .." Assuming that the abundance of predators attracted to the aggregation is proportional to the number of recruits (prey) present at the beginning of a stage, then the mortality rate induced by this factor can be expressed as $A_iR_i(0)$. Alternative mechanisms resulting in Ricker-like processes include cannibalism, habitat limitations, and aggregation (Rose *et al.*, 2001; Powers, 2004).

The second density-dependent parameter, B_i, defines a *per capita* mortality rate that varies continuously with abundance throughout the stage. This form of density-dependence might be appropriate when predator abundance is proportional to the abundance of prey throughout a stage, i.e. proportional to the abundance of the recruits (Beverton and Holt, 1957; Powers, 2004). The mortality rate of this phenomenon is expressed as $B_iR_i(t)$.

The decrease in number of recruits during a given stage, i, can then be modelled by

$$\frac{dR_i(t)}{dt} = -[M_i + F_i + A_iR_i(0) + B_iR_i(t)]R_i(t) \qquad 0 \le t \le \Delta t_i. \tag{1}$$

The solution to Equation (1) for $M_i + F_i + A_iR_i(0) > 0$ is

$$R_i(t) = \frac{R_i(0)\exp[-(M_i + F_i + A_iR_i(0))t]}{1 + B_i/(M_i + F_i + A_iR_i(0))R_i(0) \times\{1 - \exp[-(M_i + F_i + A_iR_i(0))t]\}}. \tag{2}$$

For completeness, we note that if $M_i + F_i + A_iR_i(0) = 0$, then the solution to Equation (1) is

$$R_i(t) = \frac{R_i(0)}{1 + B_itR_i(0)}, \tag{3}$$

which is a special case that will not be considered further.

When $A_i = 0$, $B_i > 0$, and $(M_i + F_i) > 0$, Equation (2) reduces to the Beverton–Holt model

$$R_i(t) = \frac{\beta_iR_i(0)}{1 + \alpha_{\mathrm{BH},i}R_i(0)}, \tag{4}$$

where $\beta_i = \exp[-t(M_i + F_i)]$ and $\alpha_{\mathrm{BH},i} = B_i\{1 - \exp[-t(M_i + F_i)]\}/(M_i + F_i)$. Alternatively, if $A_i > 0$ and $B_i = 0$, then Equation (2) reduces to the standard Ricker form

$$R_i(t) = \beta_iR_i(0)\exp(-\alpha_{\mathrm{R},i}R_i(0)), \tag{5}$$

where $\beta_i = \exp[-t(M_i + F_i)]$ and $\alpha_{\mathrm{R},i} = A_i\,t$. Note that β_i is the same in both cases, and only depends on density-independent mortality forces.

Both the Beverton–Holt and Ricker models may be characterized by a strictly density-independent term (β) and an α term (α_{BH} or α_{R}), which is a function of density-independent and -dependent factors. As α_{R} and α_{BH} include density-dependent mortality terms (A_i or B_i), we refer to them as compensation terms.

Multiple stages

Equation (2) describes the recruitment process within a single stage, during which the parameters are constant. However, Equation (2) can also be used recursively to model multistage recruitment processes. For example, we can describe the number of fish at the beginning of one stage in terms of the number of fish at the beginning of the previous stage. Let $M_i + F_i \equiv Z_i$.

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The equivalent of Equation (2) at the end of stage i (beginning of stage $i+1$) becomes

$$R_{i+1}(0)=\frac{R_i(0)\exp[-(Z_i+A_iR_i(0))\Delta t_i]}{1+(B_i/(Z_i+A_iR_i(0))R_i(0)\{1-\exp[-(Z_i+A_iR_i(0))\Delta t_i]\}}. \quad (6)$$

The number of fish surviving to the end of each stage, and ultimately to the end of the last stage, can be computed recursively using Equation (6).

Multistage Beverton–Holt

Now consider multistage Beverton–Holt processes where $A_i = 0\ \forall\ i$ (each stage is either density-independent or exhibits Beverton–Holt compensation). Beverton and Holt (1957) showed that the outcome of multistage Beverton–Holt processes is, itself, a Beverton–Holt process. The number of recruits after all n stages is given by

$$R_{n+1}(0) = \frac{R_1(0)\beta}{1+R_1(0)\alpha_{\mathrm{BH}}} = \frac{E\beta}{1+E\alpha_{\mathrm{BH}}}, \quad (7)$$

where $\beta = \exp(-\sum_{i=1}^{n} Z_i\Delta t_i)$, and

$$\alpha_{\mathrm{BH}} = \sum_{i=1}^{n} B_i \frac{1-\exp(-Z_i\Delta t_i)}{Z_i}\exp\left(-\sum_{j=1}^{i-1} Z_j\Delta t_j\right) = \sum_{i=1}^{n} B_iG_i. \quad (8)$$

In Equation (8), and in subsequent equations, we follow the convention that $\sum_{j=1}^{0} x_j \equiv 0$. Given stages i and $i+1$,

$$G_i = \frac{1-\exp(-Z_i\Delta t_i)}{Z_i}\exp\left(-\sum_{j=1}^{i-1} Z_j\Delta t_j\right), \text{ and}$$

$$G_{i+1} = \frac{1-\exp(-Z_{i+1}\Delta t_{i+1})}{Z_{i+1}}\exp\left(-\sum_{j=1}^{i-1} Z_j\Delta t_j - Z_i\Delta t_i\right). \quad (9)$$

In Appendix A, we derive conditions where $G_i > G_{i+1}$; in general, this will be true given reasonably comparable Δt_i and Δt_{i+1}, and it will always be true if $\Delta t_{i+1} \le \Delta t_i$.

The variable G_i is solely a function of the density-independent components of mortality; thus, α_{BH} is a weighted sum of stage-specific density-dependent mortality (B_is) in which greater weighting is given to earlier stages in the recruitment process. Therefore, given comparable Δts, the compensatory reduction in the number of recruits will be greater if density-dependence occurs earlier in the process. This is an intuitive result, for the longer the time between spawning and the compensatory interval, the less the density will be due to cumulative mortality up to that point; hence, density-dependence will necessarily be weaker.

Alternatively, consider two scenarios with compensation terms α_{BH} and α_{BH}'. If these two scenarios differ in the timing of compensation, but have the same stage durations and density-independent mortality rates (i.e. the G_is are identical), and if both scenarios produce the same level of recruits, then we must have $\alpha_{\mathrm{BH}} = \alpha_{\mathrm{BH}}'$. This implies that $\sum_i (B_i - B_i')G_i = 0$, i.e. the weighted sum of the stage-specific differences between compensation parameters must also be zero. Therefore, the compensation parameter during at least one of the stages, k, must be larger than the original ($B_k' > B_k$). Note also that introducing exogenous mortality during a multistage Beverton–Holt process reduces the magnitude of the parameter α_{BH} [Equations (8) and (9)], and the degree to which α_{BH} is reduced will depend on the timing of compensation.

Multistage Ricker

If recruitment is defined by multiple density-independent or Ricker stages (i.e. $B_i = 0\ \forall\ i$), then the number of recruits at the end of all n stages is

$$R_{n+1}(0) = R_1(0)\exp\left[-\sum_{i=1}^{n} Z_i\Delta t_i\right]\exp\left[-\sum_{i=1}^{n} R_i(0)A_i\Delta t_i\right] = E\beta\exp[-E\alpha_{\mathrm{R}}(E)], \quad (10)$$

where

$$\alpha_{\mathrm{R}}(E) = \sum_{i=1}^{n} A_iH_i \text{ and } H_i = \Delta t_i \exp\left[-\sum_{j=1}^{i-1} Z_j\Delta t_j - E\sum_{j=1}^{i-1} A_jH_j\right],$$

i.e. $\alpha_{\mathrm{R}}(E)$ is a function of E. Note that $H_i > H_{i+1}$, when $\Delta t_i/\Delta t_{i+1}\exp(Z_i\Delta t_i + EA_iH_i) > 1$. The second term of the inequality is always >1, and the factor by which it exceeds 1 is the magnitude by which Δt_{i+1} should be less than Δt_i. Thus, for reasonably comparable stage intervals, $H_i > H_{i+1}$, and as for the Beverton–Holt model, compensation is stronger when it occurs earlier in the recruitment interval. Akin to the Beverton–Holt result, two different compensation timing scenarios that produce the same level of recruits must have $A_k' > A_k$ at least during one of the stages. Note that if more than one $A_i > 1$, then α_{R} is a complicated function of E, and the resulting recruitment function can be multimodal (Paulik, 1973). Finally, the magnitude of α_{R} decreases when exogenous mortality (F_i) is added to the process, and the magnitude of reduction will depend on the timing of compensation.

Reparameterization for steepness (h) and virgin recruitment (R_0)

An alternate parameterization of the Beverton–Holt relates the number of recruits produced to the level of virgin recruitment and "steepness", which is the proportion of virgin recruits produced by 20% of the virgin spawning stock (Mace and Doonan, 1988). We denote virgin recruitment by R_0, virgin egg production by E_0, and steepness by h. The age at recruitment is given by the length of the recruitment interval, $T = \sum_{i=1}^{n} \Delta t_i$. Define φ_0 to be the virgin level of eggs per recruit, E_0/R_0. Given fecundity-at-age ($\mathrm{fec_a}$) and maturity-at-age ($\mathrm{mat_a}$), age of recruitment (T), age at first maturity (a_{mat}), age-specific post-recruitment natural mortality rate M_a', and maximum age ($A_{\max}$), then

$$\varphi_0 = \left[\sum_{a=T}^{A_{\max}} \mathrm{fec_a}\,\mathrm{mat_a}\exp\left(-\sum_{j=T}^{a-1} M_j'\right)\right] = \exp\left(-\sum_{a=T}^{a_{\mathrm{mat}}-1} M_a'\right)\left[\sum_{a=a_{\mathrm{mat}}}^{A_{\max}} \mathrm{fec_a}\,\mathrm{mat_a}\exp\left(-\sum_{j=a_{\mathrm{mat}}}^{a-1} M_j'\right)\right]. \quad (11)$$

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For the Beverton–Holt model, we can express h and R_0 in terms of φ_0, β, and α_{BH}. By definition,

$$R_0 = \frac{E_0}{\varphi_0} = \frac{\beta E_0}{1 + \alpha_{BH} E_0} \quad \text{and} \quad h = \frac{0.2\beta E_0}{1 + 0.2\alpha_{BH} E_0} \times \frac{\varphi_0}{E_0}, \quad (12)$$

from which we can obtain

$$h = \frac{\beta\varphi_0}{4 + \beta\varphi_0} \quad \text{and} \quad R_0 = \frac{\beta\varphi_0 - 1}{\varphi_0 \alpha_{BH}} = R_{MAX} - \frac{1}{\varphi_0 \alpha_{BH}}, \quad (13)$$

($R_{MAX} \equiv$ asymptotic recruitment $= \beta/\alpha_{BH}$).

From (13), we note several important results. First, steepness will not vary with the timing of compensation, because it is defined entirely by density-independent terms. It will be reduced, however, if exogenous mortality is introduced within the recruitment interval. Also, steepness will remain unchanged regardless of the age of recruitment (i.e. the length of the recruitment interval) provided T is less than the age at maturity, a_{mat}. The reason for this is that β will always encompass survival through T, and from (11), φ_0 will have as a constant multiplier survival from T until the first age at maturity (a_{mat}). In (13), steepness always has the product of β and φ_0, so cumulative survival from spawning through a_{mat} will always pre-multiply non-zero terms in φ_0 (corresponding to mature ages). We also point out that the resulting expression for steepness is in terms of "maximum lifetime reproduction" ($\beta\varphi_0$; Myers *et al.*, 1999, use the notation $\hat{\alpha}$ for this quantity).

On the other hand, R_0 in (13) contains both density-dependent and -independent terms and will therefore vary with compensation timing. Moreover, because the denominator contains only the term φ_0, which will be larger for older T, then assuming a longer recruitment interval will reduce the value of R_0, as one would expect. Additionally, the longer the recruitment interval (T), the smaller will be β (cumulative density-independent survival), so R_{MAX} (asymptotic recruitment $= \beta/\alpha_{BH}$) will be reduced.

The Beverton–Holt function reparameterized with h and R_0 is

$$R = \frac{4hR_0E}{\varphi_0 R_0(1-h) + (5h-1)E}. \quad (14)$$

One customarily thinks of steepness with respect to the Beverton–Holt function, where it is defined on the interval [0.2, 1.0]. In the case of the Ricker function, there is the potential for $h > 1$ as a result of overcompensation at higher stock sizes producing a descending limb of the curve. Nevertheless, a similar derivation can be made for the Ricker function. Given the following two relationships, we can solve for steepness, h, and the level of virgin recruitment, R_0:

$$R_0 = \frac{E_0}{\varphi_0} = \beta E_0 e^{-\alpha_R E_0} \quad \text{and} \quad h = \frac{R(0.2E_0)}{R_0} = \frac{0.2\beta E_0 e^{-0.2\alpha_R E_0}}{E_0/\varphi_0}. \quad (15)$$

Solving (15) for h and R_0 in terms of β and α_R, we obtain

$$h = \frac{1}{5}(\beta\varphi_0)^{4/5} \quad \text{and} \quad R_0 = \frac{\ln(\beta\varphi_0)}{\varphi_0 \alpha_R}. \quad (16)$$

As with the Beverton–Holt case, steepness depends only on density-independent mortality, whereas the expression for R_0 contains both density-independent and -dependent parameters. Conclusions are therefore the same in terms of steepness being invariant to compensation timing and length of recruitment interval, whereas R_0 is affected by both. Note that when $\beta\varphi_0 > 5^{1.25}$, then $h > 1$ (this corresponds to values where the Beverton–Holt $h > 0.65$).

From h and R_0, the Ricker can be reparameterized as

$$R = \frac{E}{\varphi_0}(\beta\varphi_0)^{1-E/E_0}, \quad (17)$$

which is functionally equivalent to the derivation in Porch *et al.* (2006), again noting that $\beta\varphi_0$ is the maximum lifetime reproductive rate as defined in Myers *et al.* (1999).

Effects on population statistics

For a stock-recruit process of given duration, an important question is when does compensation occur within that time interval? A practical reason for asking this is to be able to assess properly the impact of exogenous mortality on a population. One way to evaluate such impacts is to compare statistics associated with maximum excess recruitment (MER) (Goodyear, 1980) under alternative timing scenarios. MER is the maximum of the difference in number of recruits between the stock-recruit function and the replacement line given by $R = E/\varphi_0$ (Figure 1). MER is similar to the concept of surplus production, although the latter is generally in terms of biomass rather than number of recruits. We distinguish MER from maximum sustainable yield (MSY), because they refer to different quantities. MER is the optimal point to which spawning stock should be reduced, because it will produce the maximum number of recruits beyond replacement. Various harvesting strategies can reduce a stock to this level, but the optimal strategy, which involves harvesting at most two age classes (Reed, 1980; Brooks, 2002), would produce MSY. Conditional MSY solutions for suboptimal selectivity can also be found, which are maximal given harvesting limitations attributable to gear constraints.

Formulae giving equilibrium statistics for E_0, R_0, E_{MER}, R_{MER}, spawning potential ratios (SPR_{MER}), and MER for both the multistage Beverton–Holt and multistage Ricker models are given in Appendix B. [Note that the properties are not investigated for multistage recruitment that are mixed Ricker–Beverton–Holt processes.] In the case of the Beverton–Holt model, the formulae are exact. For the Ricker model, an nth order approximation to the exponential compensation term may be used to derive the formulae provided that there is only a single stage of density-dependence (only one $A_i > 0$). MER and associated statistics are shown to be functions of β, α_{BH} (for the multistage Beverton–Holt model), α_R (for the multistage Ricker model), and φ_0. Interestingly, E_0, R_0, E_{MER}, R_{MER}, and MER are all described by $f(\beta, \varphi_0)/\alpha_{BH}$ or $f(\beta, \varphi_0)/\alpha_R$, where the $f(\cdot)$ are solely functions of β and φ_0 (Appendix B). This property provides a convenient mechanism for comparing stock-recruitment scenarios.

Suppose that we wish to compare the MER (E_0, R_0, E_{MER}, R_{MER}) resulting from two alternative scenarios, S1 and S2, which incorporate the same natural and exogenous mortality forces and differ only in their assumption about timing of compensation. Assuming that both scenarios have the same functional form (both Beverton–Holt, or both Ricker), we could look at the ratio of MER

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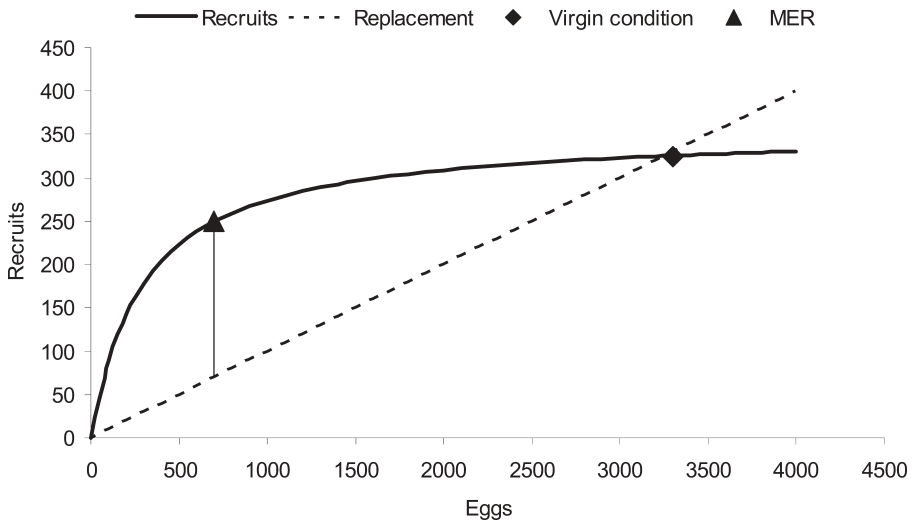

Figure 1. Beverton–Holt stock-recruit function (solid line) and the replacement line (dashed line). The intersection of these two lines defines the virgin condition. MER is the maximum difference between expected recruitment and replacement.

statistics between S1 and S2 to determine if the ratio is greater or less than 1. If the ratio of $\mathrm{MER}^{\mathrm{S1}}$: $\mathrm{MER}^{\mathrm{S2}}$ is >1, then the stock is less impacted under S1. The MER from each scenario is described as a function of $f(\beta, \varphi_0)$ and α. Given that the density-independent factors (β) and the virgin eggs-per-recruit (φ_0) are the same between the two scenarios, then the $f(\cdot)$s cancel out of any ratio of the MER statistics, and the resulting ratio comparisons are simply

$$\frac{E_0^{\mathrm{S1}}}{E_0^{\mathrm{S2}}} = \frac{R_0^{\mathrm{S1}}}{R_0^{\mathrm{S2}}} = \frac{E_{\mathrm{MER}}^{\mathrm{S1}}}{E_{\mathrm{MER}}^{\mathrm{S2}}} = \frac{R_{\mathrm{MER}}^{\mathrm{S1}}}{R_{\mathrm{MER}}^{\mathrm{S2}}} = \frac{\mathrm{MER}^{\mathrm{S1}}}{\mathrm{MER}^{\mathrm{S2}}}$$
$$= \frac{\alpha^{\mathrm{S2}}}{\alpha^{\mathrm{S1}}} = \frac{\sum_i B_i^{\mathrm{S2}} G_i}{\sum_i B_i^{\mathrm{S1}} G_i} \quad \text{or} \quad \frac{\sum_i A_i^{\mathrm{S2}} H_i}{\sum_i A_i^{\mathrm{S1}} H_i},$$

i.e. the inverse ratio of the α terms.

For a given multistage recruitment process, with stage-specific M_i, Δt_i, there are two points for consideration. The first is how the number of maximum excess recruits varies with the timing of compensation. As demonstrated in Appendix A, and above, the values of G_i and H_i are larger in the earlier stages (for reasonably comparable stage intervals), so density-dependence (B_i or A_i) has more impact if it occurs earlier rather than later in the recruitment interval. The second point is how the timing of exogenous mortality (F_i) relative to density-dependent mortality impacts MERs. We prove later that exogenous mortality has more impact on the MER if that rate occurs later in the recruitment interval, especially if it occurs after compensation.

Numerical example with fishing mortality during recruitment stages

We present several comparisons to demonstrate the effects of the timing of fishing mortality relative to compensation on the outcome of the recruitment process. The examples are loosely based on Gulf of Mexico red snapper (*Lutjanus campechanus*), which are impacted by shrimp trawl bycatch mortality during the first 2 y of their life (Schirripa and Legault, 1999). With this stock, debate has ensued over the timing of compensation and, therefore, the impacts of trawl bycatch on yield to the directed fisheries. In the examples, the first $1\frac{1}{2}$ y of red snapper life history were segmented into four stages: the first two stages and the last stage have durations of $\frac{1}{4}$ y each, whereas the third stage has a duration of $\frac{3}{4}$ y. This characterization follows the fish, because they are spawned in July, become vulnerable to trawl bycatch in October (age $\frac{1}{4}$ y), enter a more vulnerable stage in January (at age $\frac{1}{2}$y), then presumably become less vulnerable as they settle out of the water column into benthic habitats at age $1\frac{1}{2}$.

The examples are designed to evaluate the impacts on MER statistics when compensation takes place during stage 1 only (Case E, for "early"), when it occurs throughout stages 1–4 (Case T for "throughout"), or when compensation occurs during stage 4 only (Case L for "late"). Recruitment was assumed to be either a Beverton–Holt process or a Ricker process, but not a combination of the two. Stage-specific natural and fishing mortality rates (M_i and F_i) were the same for all cases (Table 1). The compensation parameters for the Beverton–Holt scenarios (B_i) and for the Ricker (A_i) were defined for each of the three cases, such that virgin recruitment at age $1\frac{1}{2}$ with no pre-recruit fishing was identical. Within a model (Beverton–Holt or Ricker), the three cases produced identical stock-recruitment relationships when there was no pre-recruit exogenous mortality ($F_i = 0$), but the timing of the compensation differed between the three cases.

We note that the "throughout" case for the Ricker example (Table 1) was calculated differently from the Beverton–Holt example. As stated previously, when more than one stage exhibits Ricker-type density-dependence, it is possible that the resulting curve is multimodal. Also, when more than one $A_i > 0$, then parameter α becomes a function of E and the first-order approximation used in Appendix B to derive MER statistics no longer holds. Therefore, we defined the "throughout" case as having a single compensatory parameter A_i for the entire interval of $1\frac{1}{2}$ y.

Results for Beverton–Holt example

Using Equation (6) to calculate the number of recruits at age 1.5, and the parameter values in Table 1, we find that $\beta = \exp\{\sum_{i=1}^{4} (-Z_i \Delta t_i)\} = 0.135$. The value of β is the same for all cases because the density-independent mortalities are the same for

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Table 1. Three cases of alternative timing of compensation using multistage Beverton–Holt (BH) or Ricker (R) models.

Parameter		Stage 1	Stage 2	Stage 3	Stage 4
Δt_i (age interval, y)		$\frac{1}{4}$	$\frac{1}{4}$	$\frac{3}{4}$	$\frac{1}{4}$
M_i		1	1	0.6	0.6
F_i		0	0.6	1	0
BH: Case E: ($A_i = 0$)	B_i	0.441	0	0	0
BH: Case T: ($A_i = 0$)	B_i	0.115	0.115	0.115	0.115
BH: Case L: ($A_i = 0$)	B_i	0	0	0	1.087
R: Case E: ($B_i = 0$)	A_i	0.100	0	0	0
R: Case T: ($B_i = 0$)	A_i	0.01667			
R: Case L: ($B_i = 0$)	A_i	0	0	0	0.259

The cases are distinguished by whether compensation occurs "early", "late", or "throughout" the entire recruitment interval. A_i and B_i are the density-dependent factors for Ricker and Beverton–Holt models, respectively, and their stage-specific values are given for each timing case (α_{BH} and α_R were computed assuming that the value of eggs-per-recruit with no fishing (φ_0) was 30.). When $F_i = 0$, α is the same for Cases E, T, and L within the Beverton–Holt or Ricker scenarios, such that all cases produce the same number of recruits. See text for definition of the Ricker "throughout" case.

all cases. For Case E, we obtain $\alpha_{BH,CaseE} = 0.441/1[1 - \exp(-0.25)]\exp(0) = 0.098$. The remaining α_{BH} values for Case T and Case L are given in Table 2. Taking the inverse ratio of the α_{BH} terms reveals that MER statistics are greatest for Case L and next best for Case T. This can be seen in Figure 2 as well, by comparing the distance between each Beverton–Holt curve and the replacement line.

All three scenarios were calibrated so that they yielded the same recruitment levels in the absence of bycatch mortality ("No F Case"). The proportion of virgin recruits remaining when bycatch mortality is included is 34% for Case E, whereas it is 84% for Case L (Table 3). In all cases, the number of recruits surviving to the end of the recruitment interval was reduced. Similarly, MER is reduced in all scenarios when bycatch is included, ranging from 22% to 54% without bycatch for Cases E and L, respectively (Table 3).

In the context of this bycatch example, the reduction in yield to the directed fishery is greatest if the bycatch mortality occurs after compensation, when that mortality is completely additive to other sources in that interval (i.e. Case E). If, however, compensation occurred throughout the interval, or later in the interval, then the effect of mortality from bycatch would be tempered by compensatory mechanisms operating at the same time. In Appendix C, we evaluate the "throughout" and "early" compensation scenarios, and under what conditions they will tend to be similar.

Table 2. Results of numerical illustration comparing compensation timing on equilibrium statistics.

Case	Beverton–Holt model (α_{BH})	Ricker model (α_R)
Early	0.098	0.025
Throughout	0.074	0.025
Late	0.040	0.01
	Ratio	Ratio
T:E	1.31	1.00
L:E	2.46	2.46
L:T	1.87	2.46

The cases are E, "early", L, "late", and T, "throughout", and refer to the timing of compensation within the recruitment interval. Ratios between scenarios are given by the inverse of the case-specific α terms. Therefore, ratios >1 indicate that there is less impact on the population for the scenario to the left of the ":" symbol.

Results for Ricker example

As in the Beverton–Holt model, $\beta = 0.135$ for all three Ricker cases, because the density-independent mortality rates are the same. For Case E, $\alpha_{R,CaseE} = (0.1)(0.25)\ \exp\ (0) = 0.025$; the remaining α values are given in Table 2. Calculating the inverse α ratios between scenarios, we find that Cases T:E results in a value of 1.0 (Figure 2). This is because Ricker-type compensation assumes that density-dependent mortality is proportional to the number of recruits (or in this example, eggs) at the beginning of the stage. Therefore, the density-dependent factor for Cases E and T is dependent on the initial number of eggs (R_0), whereas for Case L, it depends on the number of recruits that survive from the egg stage to age 1.25 ($R_{1.25}$). This general result of the "early" and "throughout" cases being equal is proved in Appendix C.

The proportion of virgin recruits remaining when bycatch mortality is included is 61% under Cases E and T (Table 3). For Case L, recruitment is actually 50% higher than the virgin level (Figure 2, Table 3), but the fraction that is in excess of replacement (MER) is still less than when there is no bycatch mortality (Table 3). As with the Beverton–Holt process, compensation has more impact if it occurs at earlier stages, and bycatch mortality will cause more substantial reductions in the number of surviving recruits and MER if it occurs after compensation. Therefore, yield would be reduced the least from bycatch if compensation occurred at the end of the interval, after bycatch mortality.

Discussion

We have here developed a multistage generalized stock-recruitment model (6) that explicitly incorporates density-independent mortality factors (including potential exogenous sources), both Beverton–Holt and Ricker density-dependence, and the time intervals where each occurs. Additionally, the multistage Beverton–Holt and Ricker versions [Equations (7) and (10)] exhibit important properties that were discussed by the original authors. In particular, the property that a multistage Beverton–Holt process (7) is mathematically equivalent to a single (long) stage Beverton–Holt model is useful. This means that if one can assume that each stage consists of either density-independent mortality or Beverton–Holt-type compensation and that there is no pre-recruit exogenous mortality, then the entire process can be described by a single-stage Beverton–Holt model without having to know the details of the stage-specific mortality rates, compensation parameters, or stage intervals. Most current usage of Beverton–Holt stock-recruit functions in fishery stock assessment models is implicitly making this assumption, and the terms being estimated (β and α_{BH}) are functions of the stage-specific parameters and stage intervals, with compensation acting throughout the recruitment interval. This will cause no problems in the resulting estimates, provided the rates and timing of mortality sources within the interval have not changed over time, or are not expected to change during the period of forecasting. The drawback of current usage is that one cannot explicitly evaluate impacts occurring within the recruitment interval nor can projections be made that explore actions to reduce those impacts.

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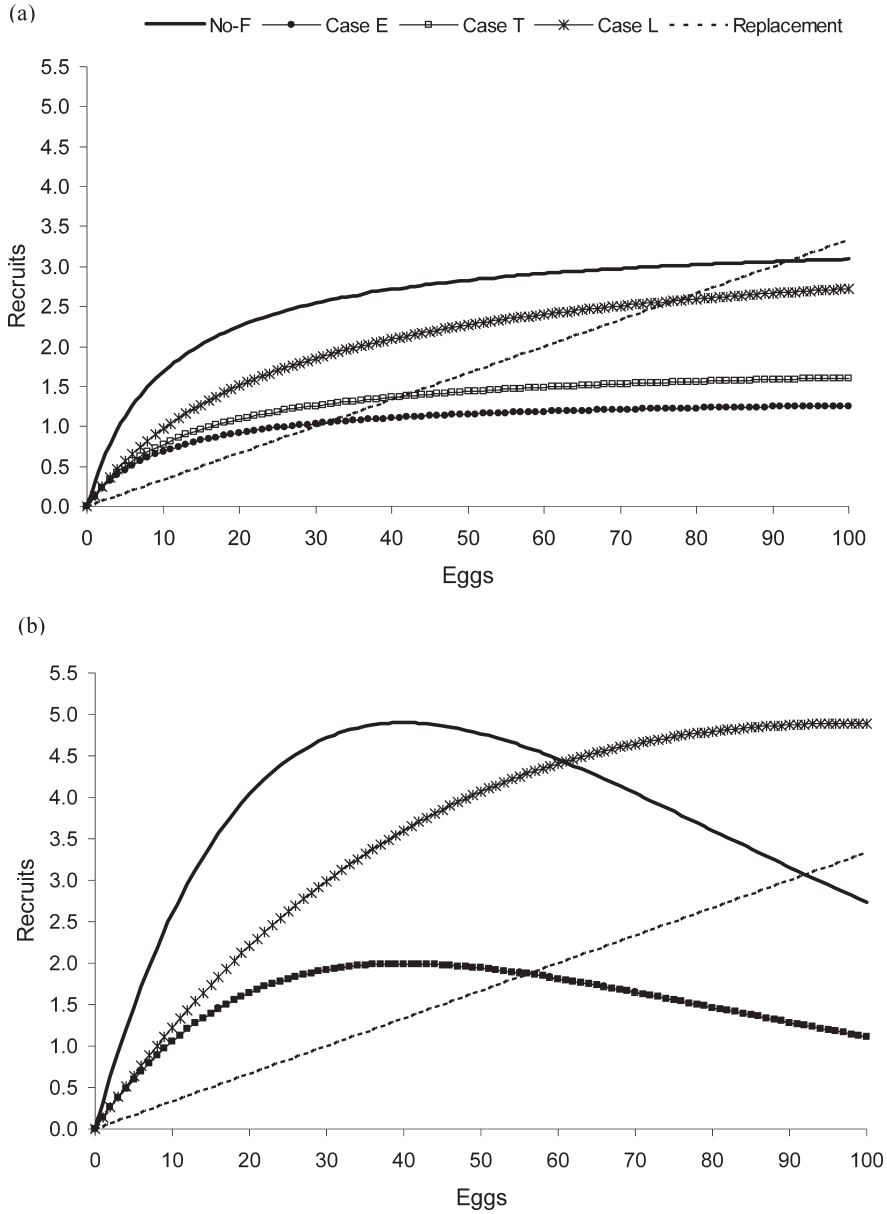

Figure 2. Resulting recruitment functions using the multistage (a) Beverton–Holt or (b) Ricker models with three alternatives for the timing of compensation: Case E, early compensation; Case T, compensation throughout; Case L, late compensation. Results are compared with the situation of no pre-recruit fishing mortality (No *F*). See text and Table 1 for definition of the cases. The diagonal line is the replacement line at no fishing, i.e. eggs/φ_0 with $\varphi_0 = 30$. Note that Cases E and T are indistinguishable in (b).

Table 3. Proportional reduction in virgin recruitment, R_0, or R_{MER}, when bycatch is added to scenarios where compensation occurs "early", "late", or "throughout" the recruitment interval.

Compensation timing	Proportional change in R_0		Proportional change in R_{MER}	
	Beverton–Holt	Ricker	Beverton–Holt	Ricker
Early	0.34	0.61	0.22	0.27
Throughout	0.44	0.61	0.29	0.27
Late	0.84	1.50	0.54	0.65

Values are expressed relative to the "No *F*" scenario (Figure 2). In the absence of bycatch mortality, all scenarios (within either the Beverton–Holt or the Ricker model) produce the same stock–recruit curve.

A property of multistage Ricker processes (as noted graphically by Ricker, 1954; Paulik, 1973) is the possibility of multimodal stock-recruit relationships attributable to the combination of multiple dome-shaped curves. This creates opportunities for population instabilities. Although (10) provides the mathematical mechanism to evaluate this potential, it seems likely that populations would evolve away from conditions that produce multimodality, i.e. multiple Ricker stages.

In general, the "early" vs. "throughout" cases will tend to be more similar for Beverton–Holt functions, as opposed to comparing "early" vs. "late" or "throughout" vs. "late". Given our definition of "throughout" for the Ricker functions, the Ricker "early" vs. "throughout" cases are identical (Appendix C). This is important

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because it focuses the debate about compensation timing, such that we only have to consider if a protracted period of density-independent mortality precedes compensation (as in the "late" scenario). If not, one can model the entire interval as a "throughout" scenario, lasting until an *immature* age to which density-dependence is thought to persist.

This detailed multistage model provides an analytical framework for evaluating the impact of pre-recruit exogenous mortality (such as bycatch, in our example). We have shown that the effects of this mortality on excess recruitment statistics, MER, can be characterized by the inverse ratio of the compensation term (α_{BH} or α_R) between two recruitment scenarios of the same type (Beverton–Holt or Ricker). This convenient property allows analytical comparisons without constructing full-scale population models. Compensatory effects in early stages dominate density-independent effects, given relatively comparable stage intervals (Appendix A). At later stages, density-dependent and -independent factors compete on a more even scale. Finally, the impact of exogenous mortality will be greater if it occurs after rather than before or during a compensatory phase (Appendix D).

We illustrated this generalized framework with bycatch as the exogenous mortality force. This methodology can also be used to evaluate impacts attributable to changes in habitat quality or availability (Moussali and Hilborn, 1986), or to test hypotheses about predation mortality. For example, in some fishing sectors, fisheries can be thought of as competing with marine mammals, and the impact of natural predation could be evaluated in this framework. The influence of environmental effects on perceptions of stock-recruit relationships has been discussed in the literature for several decades (Walters and Ludwig, 1981; Goodyear and Christensen, 1984; Christensen and Goodyear, 1988; Francis, 2006). Environmental factors could be incorporated into this stock-recruit model in a manner similar to bycatch. Finally, the framework provides explicit means for incorporating larval or juvenile abundance surveys and estimates of discards or entrainment for stock assessment analyses.

An important result from the derivation of equilibrium statistics in Appendix B is that SPR_{MER} is solely a function of β and φ_0 [Equations (B4) and (B12)]. For a given population with two competing scenarios of when compensation occurs, if natural mortality and fecundity-at-age are not different between the scenarios, then SPR_{MER} will be the same for both scenarios. In other words, SPR_{MER} will be invariant to assumptions about the timing of compensation.

In general, SPR is a relative measure of the extent to which a population's reproductive potential has been reduced (Goodyear, 1993). SPR_{MER} defines the optimal reduction, in terms of the level where surplus recruits are maximized. Reducing a population below SPR_{MER} can therefore be thought of as overexploitation and suboptimal harvest. Indeed, SPR is sometimes used by fishery managers as a benchmark for evaluating the status of a fish stock. An ideal benchmark would be robust to parameter uncertainty and model misspecification. Our result suggests that SPR_{MER} is a robust management benchmark in situations where one is uncertain about the timing of compensation or the timing of exogenous mortality during the recruitment phase.

In our derivations, F was modelled as density-independent and additive to the density-independent natural mortality component (M). This seems appropriate given our example, trawl bycatch of pre-recruits, because it is standard to assume that catchability is constant, irrespective of density. A more complex form for F could be considered. For example, Nichols *et al.* (1984) for waterfowl, and Allen *et al.* (1998) for sportfish, discuss implications for compensation between M and F. Alternatively, if predation were being modelled, one could evaluate predictions from a simple linear term (density-independent) vs. higher order (density-dependent) predator-response functions. Munch *et al.* (2005) linked predation mortality to the average length of a recruit. Another consideration would be the concurrent density-dependence discussed by Bjorkstedt (2000), where a density-dependent rate at one stage can be affected by a density-dependent process in an earlier stage.

The recruitment models presented use the number of eggs as the independent variable at time 0 of stage 1. However, in many instances, spawning biomass is used, assuming that it is proportional to the number of eggs produced. If spawning biomass or some other proportional index is used, then the models presented here may still be used; however, the values of the density-dependent mortality parameters (A_i and B_i) must be adjusted to the scale of the index. More importantly, we treat the survival of all eggs as equal, though researchers are showing that not all eggs are created equal and that eggs from first-time spawners may be less viable than those of repeat spawners (Trippel, 1998; Vallin and Nissling, 2000; Scott *et al.*, 2006). This could be accounted for by scaling egg production-at-age by a viability ogive related to the age of the female (similar to a maturity ogive), so that instead of total eggs at time 0, we would have total viable eggs.

Although data seldom exist to provide stage-specific recruitment estimates, a multistage model may focus the evaluation of recruitment processes. It could be used to generate hypotheses about time intervals where it would be appropriate to model recruitment as a compensatory process against those time intervals where a simple density-independent survival model would be appropriate. Comparing observed relative abundance indices or catch in number by stage with levels predicted by assuming different compensation scenarios could serve as a diagnostic to reject some hypothesized stock-recruitment relationships. A stage-specific approach for sampling relative abundance as in a scientific survey might be designed to estimate mortality rates and to interpret existing estimates in terms of their density-dependent and -independent components. Similarly, experiments might be designed to test hypotheses of the relevance of various stages in the recruitment cycle and how stock assessments might best be structured to describe the most important features of the recruitment process. A mixed model, perhaps incorporating both Beverton–Holt and Ricker types of density-dependence, might be a useful mechanism to examine the effects of site-specific factors on survival (Rose and Cowan, 2000; Rose *et al.*, 2001). Explicit models such as Equations (6)–(10) provide a framework for these evaluations.

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Appendix A

Conditions where $G_i > G_{i+1}$ for the Beverton–Holt model

Conjecture

$G_i > G_{i+1}$, where

$$G_i = \frac{1-\exp(-Z_i\Delta t_i)}{Z_i}\exp\left(-\sum_{j=1}^{i-1} Z_j\Delta t_j\right)$$

and

$$G_{i+1} = \frac{1-\exp(-Z_{i+1}\Delta t_{i+1})}{Z_{i+1}}\exp\left(-\sum_{j=1}^{i-1} Z_j\Delta t_j - Z_i\Delta t_i\right).$$

If $G_i > G_{i+1}$, then

$$\frac{1-\exp(-Z_i\Delta t_i)}{Z_i}\exp\left(-\sum_{j=1}^{i-1} Z_j\Delta t_j\right) > \frac{1-\exp(-Z_{i+1}\Delta t_{i+1})}{Z_{i+1}}\exp\left(-\sum_{j=1}^{i-1} Z_j\Delta t_j - Z_i\Delta t_i\right)$$

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or

$$\frac{\exp(Z_i\Delta t_i)-1}{Z_i} > \frac{1-\exp(-Z_{i+1}\Delta t_{i+1})}{Z_{i+1}}.$$

Let $X_i = Z_i\Delta t_i$ and $X_{i+1} = Z_{i+1}\Delta t_{i+1}$. Then we have

$$\frac{\exp(X_i)-1}{X_i/\Delta t_i} > \frac{1-\exp(-X_{i+1})}{X_{i+1}/\Delta t_{i+1}} \rightarrow \frac{(\exp(X_i)-1)/X_i}{(1-\exp(-X_{i+1}))/X_{i+1}} > \frac{\Delta t_{i+1}}{\Delta t_i},$$

This inequality will be true $\forall\ X > 0$ and $\Delta t_{i+1}/\Delta t_i < \exp\ (X)$.

Proof

First, $(\exp(X_i)-1)/X_i > 1-\exp\ (-\ X_{i+1})/X_{i+1}$. Recall that if $\lim_{x\to b} f(x)/g(x) = 0/0$, and if both f and g are differentiable on the interval $a \le x < b$, then this is an indeterminate form for which L'Hôpital's rule holds, i.e. $\lim_{x\to b}\ f(x)/g(x) = \lim_{x\to b}\ f'(x)/g'(x)$. We apply L'Hôpital's rule to each side of the inequality and note that both terms approach 1 as X_i and X_{i+1} approach 0. The term on the left-hand side (LHS) approaches 1 from above, whereas the term on the right-hand side (RHS) approaches 1 from below; therefore, $\forall\ X > 0$, this inequality is true.

Next, we prove under what conditions

$$\frac{(\exp(X_i)-1)/X_i}{(1-\exp(-X_{i+1}))/X_{i+1}} > \frac{\Delta t_{i+1}}{\Delta t_i}.$$

There are three cases to consider:

Case (1) $X_i = X_{i+1} = X$. In this case, the LHS reduces to e^X, so the inequality is true when $\Delta t_{i+1}/\Delta t_i < \exp\ (X)$.

Case (2) $X_i > X_{i+1}$. Rewrite $X_i = X+\varepsilon$, $X_{i+1} = X$. Then we have

$$\frac{(\exp(X_i)-1)/X_i}{(1-\exp(-X_{i+1}))/X_{i+1}} = \frac{(\exp(X+\varepsilon)-1)X}{(X+\varepsilon)(1-\exp(-X))}.$$

Application of L'Hôpital's rule as $X \to 0$ results in $(\exp\ (\varepsilon) - 1)/\varepsilon$, which is >1 for $\varepsilon > 0$. Thus, when $X_i > X_{i+1}$,

$$\frac{(\exp(X_i)-1)/X_i}{(1-\exp(-X_{i+1}))/X_{i+1}} > \exp(X),$$

and the conjecture is true when $\Delta t_{i+1}/\Delta t_i < \exp\ (X)$, where $X = \min(X_i, X_{i+1})$.

Case (3) $X_i < X_{i+1}$. Rewrite $X_i = X$, $X_{i+1} = X+\varepsilon$. Then we have

$$\frac{(\exp(X_i)-1)/X_i}{(1-\exp(-X_{i+1}))/X_{i+1}} = \frac{(\exp(X)-1)(X+\varepsilon)}{(X)[1-\exp(-(X+\varepsilon))]}.$$

Application of L'Hôpital's rule as $X \to 0$ results in $\varepsilon\ \exp\ (\varepsilon)/(\exp\ (\varepsilon) - 1)$, which is >1 for $\varepsilon > 0$. Thus, when $X_i < X_{i+1}$,

$$\frac{(\exp(X_i)-1)/X_i}{(1-\exp(-X_{i+1}))/X_{i+1}} > \exp(X),$$

and the conjecture is true when $\Delta t_{i+1}/\Delta t_i < \exp(X)$, where $X = \min(X_i, X_{i+1})$.

Summary

We have shown that $G_i > G_{i+1}$, provided $\Delta t_{i+1}/\Delta t_i < \exp\ (X)$, where $X = \min(X_i, X_{i+1})$, i.e. $X = \min(Z_i\Delta t_i, Z_{i+1}\Delta t_{i+1})$. For very small X, $\exp(X) \to 1$, and we must have $\Delta t_{i+1} \le \Delta t_i$. For larger X, e.g. $X \in [0.4, 1.0]$, then $\exp\ (X) \in [1.5, 2.77]$, and then our conjecture is true when $\Delta t_{i+1}/\Delta t_i < 1.5$. One typically expects relatively high-density independent mortality ($Z_i\Delta t_i$) during the recruitment interval, so it is not unreasonable to conclude that, in general, $G_i > G_{i+1}$ for reasonably comparable stage intervals. Moreover, when all stage durations are equal, then $G_i > G_{i+1}\ \forall\ Z > 0$.

Appendix B

MER statistics for generalized Beverton–Holt and Ricker models

In the body of the paper, we used the notations R_0 and E_0 to refer to virgin recruitment and virgin egg production. We extend that notation to $R_{0,\mathrm{BH}}$, $E_{0,\mathrm{BH}}$, and $R_{0,\mathrm{R}}$, $E_{0,\mathrm{R}}$ to denote the Beverton–Holt and Ricker versions, respectively. Given the stock-recruit relationship $R = E\beta/(1+\alpha_{\mathrm{BH}}\ E)$ or $R = E\beta\ \exp(-\ \alpha_{\mathrm{R}}\ E)$ for the Beverton–Holt and Ricker forms, respectively, then equilibrium statistics are derived as follows (cf. Appendix III of Ricker, 1975). The replacement line for a given number of eggs is $R = E/\varphi_0$, where φ_0 is unfished eggs per recruit. Setting the replacement line equal to the S–R curve and solving for E gives E_0, equilibrium unfished egg production. Equilibrium egg production at MER (E_{MER}) is found by taking the derivative of the S–R curve and solving for E such that $\mathrm{d}R/\mathrm{d}E = 1/\varphi_0$, i.e. the point on the S–R curve where the tangent line is parallel to the replacement line. These and associated statistics for the Beverton–Holt and Ricker models are given below. We note that the derivations hold for both single and multistage recruitment processes. In the Ricker section, the first-order approximation can only be made if we restrict density-dependent mortality (A_i) to one interval. The reason for this is that if more than one $A_i > 0$, then the parameter α becomes a function of E, and a solution would have to be made iteratively.

Beverton–Holt

$$E_{0,\mathrm{BH}} = \frac{\varphi_0\beta - 1}{\alpha_{\mathrm{BH}}}, \qquad R_{0,\mathrm{BH}} = \frac{\varphi_0\beta - 1}{\varphi_0\alpha_{\mathrm{BH}}} \tag{B1}$$

$$E_{\mathrm{MER,BH}} = \frac{\sqrt{\varphi_0\beta}-1}{\alpha_{\mathrm{BH}}}, R_{\mathrm{MER,BH}} = \frac{\beta}{\alpha_{\mathrm{BH}}}\left[1-\frac{1}{\sqrt{\varphi_0\beta}}\right] \tag{B2}$$

$$\mathrm{MER} = R_{\mathrm{MER,BH}} - \frac{E_{\mathrm{MER,BH}}}{\varphi_0} = \frac{E_{\mathrm{MER,BH}}\beta}{1+\alpha_{\mathrm{BH}}E_{\mathrm{MER,BH}}} - \frac{E_{\mathrm{MER,BH}}}{\varphi_0} = \frac{1}{\alpha_{\mathrm{BH}}}\left[\sqrt{\varphi_0\beta}-1\right]^2 \tag{B3}$$

$$\mathrm{SPR}_{\mathrm{MER,BH}} = \frac{E_{\mathrm{MER,BH}}/R_{\mathrm{MER,BH}}}{\varphi_0} = \frac{1}{\sqrt{\varphi_0\beta}} \tag{B4}$$

MER is the maximum number of excess recruits, $R_{0,\mathrm{BH}}$ is the number of equilibrium unfished recruits, $E_{\mathrm{MER,BH}}$ is the equilibrium egg production at MER, and $\mathrm{SPR}_{\mathrm{MER,BH}}$ is the spawning potential ratio at MER. SPR is found by taking the ratio of eggs per recruit with exogenous mortality (φ_F) to virgin eggs per recruit (φ_0). This scaleless quantity is a measure of the extent to which the reproductive capacity of a recruit has been reduced by the exogenous mortality and is sometimes used in fishery

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assessment as a population benchmark that determines whether a fish stock is overfished.

Ricker

$$E_{0,\mathrm{R}} = \frac{1}{\alpha_\mathrm{R}}\ln(\varphi_0\beta), \qquad R_{0,\mathrm{R}} = \frac{1}{\varphi_0\alpha_\mathrm{R}}\ln(\varphi_0\beta) \tag{B5}$$

and

$$E_{\mathrm{MER,R}} = \text{solution to}[\beta\varphi_0 e^{-\alpha_\mathrm{R}E}(1-\alpha_\mathrm{R}E) = 1], \tag{B6}$$

which can be solved numerically. However, if we constrain density-dependent mortality to a single-stage, then α_R does not depend on E, and an approximate solution may be obtained by using an nth-order series approximation to the exponential

$$\exp(-\alpha_\mathrm{R}E) \cong 1 - \alpha_\mathrm{R}E + \frac{(\alpha_\mathrm{R}E)^2}{2!} - \frac{(\alpha_\mathrm{R}E)^3}{3!} + \cdots + \frac{(\alpha_\mathrm{R}E)^n}{n!}(-1)^n. \tag{B7}$$

From (B6) and (B7), we have

$$\left[1 - \alpha_\mathrm{R}E + \frac{(\alpha_\mathrm{R}E)^2}{2!} - \frac{(\alpha_\mathrm{R}E)^3}{3!} + \cdots + \frac{(\alpha_\mathrm{R}E)^n}{n!}(-1)^n\right](1-\alpha_\mathrm{R}E) = \frac{1}{\beta\varphi_0}. \tag{B8}$$

The LHS of (B8) is a polynomial in $\alpha_\mathrm{R}E$, the solution of which is $f_n(\beta\varphi_0)$. Thus, $E_{\mathrm{MER,R}}$ is approximated by $f_n(\beta\varphi_0)/\alpha_\mathrm{R}$.

As an illustration, if $\exp(-\alpha_\mathrm{R}E)$ is approximated using a first-order series, then $\beta\varphi_0\ \exp(-\alpha_\mathrm{R}E)(1-\alpha_\mathrm{R}E) = (1-\alpha_\mathrm{R}\ E)(1-\alpha_\mathrm{R}\ E) = 1/\beta\varphi_0$. Equilibrium statistics are then

$$E_{\mathrm{MER,R}} \cong \frac{1}{\alpha_\mathrm{R}}\left[1 - \sqrt{\frac{1}{\beta\varphi_0}}\right] \tag{B9}$$

and

$$R_{\mathrm{MER,R}} \cong \frac{\beta(1-\sqrt{1/\beta\varphi_0})}{\alpha_\mathrm{R}}\exp\left(\sqrt{\frac{1}{\beta\varphi_0}} - 1\right) \tag{B10}$$

$$\mathrm{MER} = R_{\mathrm{MER,R}} - \frac{E_{\mathrm{MER,R}}}{\varphi_0} \cong \frac{\left(1-\sqrt{1/\beta\varphi_0}\right)}{\alpha_R}\left[\beta\exp\left(\sqrt{\frac{1}{\beta\varphi_0}} - 1\right) - \frac{1}{\varphi_0}\right], \tag{B11}$$

$$\mathrm{SPR}_{\mathrm{MER,R}} \cong \frac{\exp\left(1-\sqrt{1/\beta\varphi_0}\right)}{\beta\varphi_0} \tag{B12}$$

Appendix C

Evaluation of "early" vs. "throughout" compensation scenarios for Beverton–Holt and Ricker models

Here, we demonstrate general results for comparing two scenarios for the timing of compensation, which operates either early in the recruitment interval (Case E) or throughout all stages in the interval (Case T). In the absence of exogenous mortality, both scenarios give the same recruitment. Given n stages in the recruitment interval, we determine how these two scenarios compare if exogenous mortality, F_i, is introduced during interval i, $i \in [1, n]$.

Beverton–Holt

Assume that in Case E, the density-dependent mortality parameter B_i is equal to 0 for all stages except stage 1 ($B_i = B_\mathrm{E} > 0$ when $i = 1$); whereas for Case T, $B_i = B_\mathrm{T} > 0$ for all stages. Using Equation (9), define

$$\Gamma_i = \frac{1-\exp(-M_i\Delta t_i)}{M_i}\exp\left(-\sum_{j=1}^{i-1} M_j\Delta t_j\right).$$

Then given that both cases have the same E_0 and R_0, we have from Equations (7) and (8):

$$\alpha_{\mathrm{BH,CaseE}} = B_\mathrm{E}\Gamma_1 = B_\mathrm{T}\left(\Gamma_1 + \sum_{i=2}^{n}\Gamma_i\right) = \alpha_{\mathrm{BH,CaseT}}. \tag{C1}$$

From (C1), it is clear that $B_\mathrm{E} > B_\mathrm{T}$.

Now, add F_i to any given stage. Recall that $Z_i = (M_i + F_i)$, and Equation (9) is

$$G_i = \frac{1-\exp(-Z_i\Delta t_i)}{Z_i}\exp\left(-\sum_{j=1}^{i-1} Z_j\Delta t_j\right).$$

MER statistics can be evaluated with the inverse ratio of α terms:

$$\frac{\mathrm{MER}^{\mathrm{Throughout}}}{\mathrm{MER}^{\mathrm{Early}}} = \frac{\alpha_{\mathrm{BH,CaseE}}}{\alpha_{\mathrm{BH,CaseT}}} = \frac{B_\mathrm{E}}{B_\mathrm{T}} \times \frac{G_1}{G_1 + \sum_{i=2}^{r} G_i}. \tag{C2}$$

Solving (C1) for $B_\mathrm{E}/B_\mathrm{T}$ and substituting into (C2), we have

$$\frac{\mathrm{MER}^{\mathrm{Throughout}}}{\mathrm{MER}^{\mathrm{Early}}} = \frac{\Gamma_1 + \sum_{i=2}^{n}\Gamma_i}{\Gamma_1} \times \frac{G_1}{G_1 + \sum_{i=2}^{n} G_i} = \frac{1 + \sum_{i=2}^{n}\Gamma_i/\Gamma_1}{1 + \sum_{i=2}^{n} G_i/G_1}. \tag{C3}$$

When $F_i = 0$, then $\Gamma_i \geq G_i$; otherwise when $F_i > 0$, then $\Gamma_i > G_i$. Therefore, if an F_i is included in stage i, then $\sum_{i=2}^{n} G_i/G_1 < \sum_{i=2}^{n}\Gamma_i/\Gamma_1$, and $\mathrm{MER}^{\mathrm{Throughout}} > \mathrm{MER}^{\mathrm{Early}}$. Hence, if fishing is added to two Beverton–Holt processes with equal equilibrium recruitment and egg production (with no post-recruitment fishing), then pre-recruit fishing mortality decreases recruitment less when compensation occurs throughout the stages than with a process where compensation only occurs at an early stage. Note that for $F_j > 0$, $j > 1$, we have

$$\frac{\mathrm{MER}^{\mathrm{Throughout}}}{\mathrm{MER}^{\mathrm{Early}}} = \frac{\sum_{i=1}^{n}\Gamma_i}{\sum_{i=1}^{j-1}\Gamma_j + G_j + e^{-F_j\Delta t_j}\sum_{k=j+1}^{n}\Gamma_k}.$$

The degree to which this ratio is >1 will depend on the magnitude of F_j and how close j is to the end of the interval. As $j \to n$, the "throughout" and "early" compensation cases will be more

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similar than "early" vs. "late" or "throughout" vs. "late". Of course, given reasonably comparable Δt_i, Γ_j terms get smaller as $j \to n$, so the terms in the denominator that are downweighted by $e^{-F_j}\Delta t_j$ do not contribute as much to the summation. Although we have not provided general numerical bounds, we suggest that for finite F_j, the MER ratio will not differ greatly from 1.

Ricker

Recall that the throughout case being tested is simply a single-stage Ricker model in which there is a single compensation parameter acting at the beginning of stage 1. For the "early" and "throughout" scenarios, we have

$$R_{n+1,\text{CaseE}} = E\exp\left[-Z_1 - A_1\Delta t_1 E - \sum_{i=2}^{n} Z_i\right]$$

$$R_{n+1,\text{CaseT}} = E\exp\left[-\sum_{i=1}^{n} Z_i - A_T\sum_{i=1}^{n}\Delta t_i E\right]. \qquad \text{(C4)}$$

Clearly $R_{n+1,\text{ CaseE}}$ and $R_{n+1,\text{ CaseT}}$ have the term $E\exp(-\sum_{i=1}^{n} Z_i)$ in common. Moreover, we assumed that both cases produce the same virgin level of recruitment. Therefore, from Equation (10), we have $\alpha_{\text{R,CaseE}} = A_1\ \Delta t_1 = A_T\ \sum_{i=1}^{r}\ \Delta t_r = \alpha_{\text{R,CaseT}}$. Thus, $R_{n+1,\text{CaseE}} = R_{n+1,\text{CaseT}}$.

Appendix D

Evaluating the timing of exogenous mortality and the impact on MER

Conjecture

Exogenous mortality has more impact on the MER if that rate occurs later in the recruitment interval, especially if it occurs after compensation.

Proof

Lemma 1. Consider Z and Z', where $Z' = Z + \varepsilon$. Then $Z' > Z$, $e^{-Z'} < e^{-Z}$. Next, consider the inequality $(1 - e^{-Z'\Delta t})/Z' < (1 - e^{-Z\Delta t})/Z$. We prove that this is true as follows: first, divide both sides of the inequality by the second term, obtaining $(1 - e^{-Z'\Delta t})/Z'\ Z/(1-e^{-Z\Delta t}) < 1$. Next, consider the term on the LHS of the inequality as $Z \to 0$. After applying L'Hôpital's rule, we have $1/(e^{\varepsilon\Delta t}\ (1 + \varepsilon\Delta t))$, which is clearly <1 for ε, $\Delta t > 0$. As this ratio is a continuous function whose value is <1 $\forall\ Z > 0$, then we have proved that $(1 - e^{-Z'\Delta t})/Z' < (1 - e^{-Z\Delta t})/Z$.

Now, we return to our proof that exogenous mortality has more impact on the MER if that rate occurs later in the recruitment interval, especially if it occurs after compensation. We prove this for both the multistage Beverton–Holt (Case i) and Ricker (Case ii).

(i) Assume a multistage Beverton–Holt stock–recruitment relationship. Suppose that compensation occurs in stage i of the recruitment interval. We consider the impact on MER statistics when adding F_{Early} in stage $j < i$, F_{During} in stage i, and F_{Late} in stage $k > i$. We define the notation for each α term corresponding to these F scenarios as $\alpha_{\text{BH},i(F_{\text{Early}})}$, $\alpha_{\text{BH},i(F_{\text{During}})}$, and $\alpha_{\text{BH},i(F_{\text{Late}})}$, where

$$\alpha_{\text{BH},i(F_{\text{Early}})} = \frac{B_i(1 - e^{-M_i\Delta t_i})}{M_i} e^{-\sum_{p=1}^{i-1} M_p\Delta t_p} e^{-F_j\Delta t_j},$$

$$\alpha_{\text{BH},i(F_{\text{During}})} = \frac{B_i(1 - e^{-(M_i+F_i)\Delta t_i})}{M_i + F_i} e^{-\sum_{p=1}^{i-1} M_p\Delta t_p},$$

and

$$\alpha_{\text{BH},i(F_{\text{Late}})} = \frac{B_i(1 - e^{-M_i\Delta t_i})}{M_i} e^{-\sum_{p=1}^{i-1} M_p\Delta t_p}.$$

Comparing MER statistics between scenarios, we find that

$$\frac{\text{MER}(F_{\text{Late}})}{\text{MER}(F_{\text{Early}})} = \frac{\alpha_{\text{BH},i(F_{\text{Early}})}}{\alpha_{\text{BH},,i(F_{\text{Late}})}} = e^{-F_j\Delta t_j} < 1$$

and

$$\frac{\text{MER}(F_{\text{Late}})}{\text{MER}(F_{\text{During}})} = \frac{\alpha_{\text{BH},i(F_{\text{During}})}}{\alpha_{\text{BH},i(F_{\text{Late}})}} < 1 \quad (\textbf{Lemma 1}).$$

Therefore, in general, adding exogenous mortality later in the recruitment interval will create a greater reduction in MER.

Q.E.D.

(ii) Assume a multistage Ricker stock-recruitment relationship. Suppose that compensation occurs at stage i of the recruitment interval. We consider the impact on MER statistics when adding F_{Early} in stage $j < i$, F_{During} in stage i, and F_{Late} in stage $k > i$. We define the notation for each α term corresponding to these F scenarios as $\alpha_{\text{R},i(F_{\text{Early}})}$, $\alpha_{\text{R},i(F_{\text{During}})}$, and $\alpha_{\text{R},i(F_{\text{Late}})}$, where

$$\alpha_{\text{R},i(F_{\text{Early}})} = A_i\Delta t_i e^{-F_j\Delta t_j} e^{-\sum_{p=1}^{i-1} M_p\Delta t_p},$$

and

$$\alpha_{\text{R},i(F_{\text{During}})} = \alpha_{\text{R},i(F_{\text{Late}})} = A_i\Delta t_i e^{-\sum_{p=1}^{i-1} M_p\Delta t_p}.$$

Comparing MER statistics between scenarios, we find that

$$\frac{\text{MER}(F_{\text{Late}})}{\text{MER}(F_{\text{Early}})} = \frac{\alpha_{\text{R},i(F_{\text{Early}})}}{\alpha_{\text{R},i(F_{\text{Late}})}} = e^{-F_j\Delta t_j} = \frac{\text{MER}(F_{\text{During}})}{\text{MER}(F_{\text{Early}})} < 1.$$

We note that if compensation occurs in interval $i = 1$, then $\alpha_{\text{R},i(F_{\text{Early}})} = A_1\Delta t_1 = \alpha_{\text{R},i(F_{\text{During}})} = \alpha_{\text{R},i(F_{\text{Late}})}$. As F does not enter these α terms, there will be no difference in the resulting MER statistics. Our results therefore apply for compensation occurring at any stage $i > 1$. Given this minor condition for the Ricker recruitment function, adding exogenous mortality later in the recruitment interval will produce a greater reduction in MER statistics.

Q.E.D.

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