

A multivariate stock–recruitment function for cohorts with sympatric subclasses: application to maternal effects in rockfish (genus *Sebastes*)

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Abstract: I present a multivariate stock–recruitment function (MSRF) for calculating recruitment when a cohort comprises sympatric subclasses. Sympatric subclasses emerge when there are closely interacting subgroups occupying a very similar niche, but whose ecology dictates distinct mortality rates. Examples include multispecies complexes of juvenile rockfish (*Sebastes* spp.) in the California current and juvenile salmon (*Oncorhynchus* spp.) in streams following different life history strategies. I derive an MSRF and apply it to the ecology of larval and juvenile rockfish with maternal effects. In several species of rockfish, older mothers produce superior larvae. This is called a maternal effect. For these species, larval and juvenile cohorts comprise several sympatric subclasses, each with a distinct mortality rate related to the age of their mothers. I apply this model to data for black rockfish (*Sebastes melanops*) in California and Oregon and find the recruitment estimates based on data from a declining population may overestimate productivity of a recovering population if maternal effects are neglected. The MSRF proves to be a flexible framework for studying recruitment in the presence of sympatric subclasses.

Résumé : Ce travail présente une fonction multidimensionnelle de stock–recrutement (MSRF) pour calculer le recrutement lorsqu’une cohorte contient des sous-classes sympatriques. Il se produit des sous-classes sympatriques, lorsqu’il y a des sous-groupes en interaction qui occupent des niches très semblables, mais dont l’écologie impose des taux de mortalité différents. Les complexes multispécifiques de jeunes sébastes (*Sebastes* spp.) dans le courant de Californie et les jeunes saumons (*Oncorhynchus* spp.) qui suivent des stratégies différentes de cycle biologique en eau courante constituent de bons exemples. Une MSRF est donc dérivée et appliquée à l’écologie de larves et de jeunes de sébastes possédant des effets maternels. Chez plusieurs espèces de sébastes, les mères plus âgées produisent des larves de meilleure qualité. C’est là un effet maternel. Chez ces espèces, les cohortes de larves et de jeunes comprennent plusieurs sous-classes sympatriques, chacune avec un taux de mortalité distinct relié à l’âge de leurs mères. Le modèle appliqué à des données sur le sébaste noir (*Sebastes melanops*) de Californie et d’Oregon montre que les estimations du recrutement basées sur des données provenant d’une population en déclin peuvent surestimer la productivité d’une population en rétablissement si on ne tient pas compte des effets maternels. La MSRF s’avère être un cadre flexible pour l’étude du recrutement lorsqu’il y a des sous-classes sympatriques.

[Traduit par la Rédaction]

Introduction

Increasingly, fisheries scientists are studying higher levels of complexity in population processes. This is in part due to a mandate for ecosystem-based management, which requires fisheries managers to predict how populations will respond to major ecological change. Processes such as maternal effects or variation in life history strategy introduce complexities relevant to population management but also difficult to quantify. In this paper, I introduce a model for studying complex population processes that lead to the formation of

sympatric subclasses. I apply this model to the example of age-dependent maternal effects in black rockfish (*Sebastes melanops*).

Differential maternal investment, known as maternal effects, creates an offspring cohort composed of subclasses grouped by offspring viability. Traditional stock–recruitment models are not adequate to calculate recruitment for these populations because it requires the ability to assign distinct mortality rates to each subclass of offspring. Additionally, it would not be adequate to separately apply an univariate stock–recruitment model to each subclass because the subclasses co-occur. This sympatry makes it difficult to calculate mortality because the density-dependent mortality experienced by any individual fish depends on the total density across all subclasses, not merely the density within a single subclass. The advantage of a multivariate stock–recruitment function (MSRF) is that it allows us to correctly calculate density-dependent mortality when there are sympatric subclasses. This is particularly important in the case of Beverton–Holt dynamics, where density-dependence depends on continuously changing densities.

Received 11 February 2008. Accepted 27 October 2008.
Published on the NRC Research Press Web site at cjfas.nrc.ca on 20 March 2009.
J20413

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Here, I use an MSRF to examine how recruitment changes as the age structure of the adult population changes. I also show how these changes depend on the assumptions I make about the form of density-dependent mortality (Ricker versus Beverton–Holt) and on assumptions about how the maternal effect changes mortality rates (impact is before versus after settlement).

Maternal effects and rockfish ecology

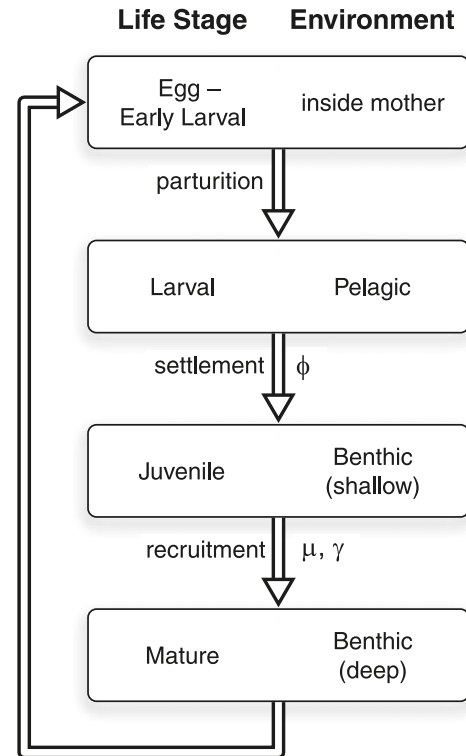
Rockfish are remarkable for their high speciosity and occasionally very long lives coupled with low productivity. There are over 60 species along the west coast of the United States, with maximum ages ranging from 11 to 205 years (Love et al. 2002). Most west coast rockfish are impacted by fishing, either through direct harvest or through bycatch. The low productivity of some rockfish renders them especially vulnerable to overfishing; seven stocks have been formally designated as overfished (PFMC 2008). A fundamental consequence of fishing, and especially intense fishing, is the loss of the older age classes. The discovery of maternal effects in rockfish has raised the following question: Has the loss of older age classes of rockfish significantly reduced the recruitment of rockfish stocks (Birkeland and Dayton 2005; Berkeley 2006; O’Farrell and Botsford 2006)?

In several rockfish species, older and larger mothers produce superior larvae. This characteristic is an example of a maternal effect, a trait that is acquired from the mother, but nongenetic (Lacey 1998). Most notably in black rockfish (*S. melanops*), larvae from older mothers grow three to four times faster and survive starvation two to three times longer than larvae from younger mothers (Berkeley et al. 2004). Additionally, some form of age-dependent maternal effect has been observed in blue (*Sebastes mystinus*), yellowtail (*Sebastes flavidus*), gopher (*Sebastes carnatus*), and kelp rockfish (*Sebastes atrovirens*) (Sogard et al. 2008). Given the similar reproductive physiology among rockfish (Love et al. 2002), coupled with the success of lab studies seeking maternal effects (Sogard et al. 2008), it appears likely that maternal effects are common in rockfish.

Rockfish have a bipartite early life history, and they are live bearers that release larvae fully formed into the pelagic environment. After several months, the larvae transition into juveniles and settle into a benthic habitat (Fig. 1). Maternal effects have been observed in the first few weeks of the pelagic larval stage, but little is known about how the effect will develop over the remaining months of the pelagic larval stage or whether the effect will persist into the benthic juvenile stage. I will present two cases of the maternal effect. In case 1, the maternal effect only impacts survival of the pelagic phase, and in case 2 the maternal effect has lasting impacts into the benthic phase.

Most stock-assessments for rockfish use a Beverton–Holt stock–recruitment model by default, but usually only find moderate to low goodness-of-fit (see Dorn 2002 for several examples). Since the form of the stock–recruitment relationship strongly influences the conclusions drawn, I chose to consider multiple forms of the stock–recruitment curve. I illustrate both cases for a Ricker-type mechanism and for a Beverton–Holt-type mechanism.

Fig. 1. Diagram of a typical rockfish (genus *Sebastes*) life history. Eggs are hatched inside the body of the mother and are released into the pelagic environment as larvae. Larvae develop into juveniles and settle into a benthic nursery habitat. Juveniles move into deep waters as they grow older. Time during the prerecruitment period is indexed by τ ; at the time of settlement, $\tau = 0$, and at the time of recruitment, $\tau = T$. The multivariate stock–recruitment function uses the transition rates ϕ , μ , and γ to calculate the number of recruits.



Solving an MSRF

The traditional way to derive a stock–recruitment model begins with an ordinary differential equation describing per-capita mortality of juveniles. If $n(\tau)$ is numbers of juveniles at time τ , then the differential equation can be written

$$(1) \quad \frac{1}{n} \frac{dn}{d\tau} = -\mu - \Delta(n)$$

where μ is the rate of density-independent mortality, and $\Delta(n)$ is the rate of density-dependent mortality. The solution to eq. 1 requires an initial condition, which is traditionally written

$$(2) \quad n(0) = \phi S$$

where S is the spawning stock biomass and ϕ is the rate of fecundity. For rockfish, I will reinterpret ϕ to be the rate of settlement to create a two-stage model (Fig. 1).

Stock–recruitment models differ in the form of $\Delta(n)$, i.e., the functional form of density dependence. The two most familiar stock–recruitment models are the Beverton–Holt model, where $\Delta(n) = \gamma n$, and the Ricker model, where $\Delta(n) = \gamma S$ (Haddon 2001). Here, γ is the per-capita rate of density-dependent mortality.

I will extend this traditional framework to model populations with multiple co-occurring subpopulations. I begin with the Ricker model, because it is analytically tractable.

To modify the Ricker model, I begin with a differential equation with multiple age classes

$$(3) \quad \text{diag}(\mathbf{n})^{-1} \frac{d\mathbf{n}}{d\tau} = -\boldsymbol{\mu} - \boldsymbol{\gamma}\mathbf{S}$$

where \mathbf{n} , \mathbf{S} , and $\boldsymbol{\mu}$ are vectors of length a_{\max} , and $\boldsymbol{\gamma}$ is a matrix of dimension $a_{\max} \times a_{\max}$. This equation can be solved analytically with the initial condition

$$(4) \quad \mathbf{n}(0) = \boldsymbol{\phi}\mathbf{S}$$

where $\boldsymbol{\phi}$ is a diagonal matrix of dimension $a_{\max} \times a_{\max}$. The values on the diagonal are interpreted as the class-specific settlement rates, i.e., the number of juveniles to settle per unit of spawning stock biomass for juveniles with maternal age a . The solution to the multivariate Ricker model is

$$(5) \quad \mathbf{n}(\tau) = \boldsymbol{\phi}\mathbf{S} e^{(-\boldsymbol{\mu}-\boldsymbol{\gamma}\mathbf{S})\tau}$$

To get recruitment, I evaluate this solution at time T (the length of the prerecruitment period) and sum across the subclasses:

$$(6) \quad R = \sum_a n_a(T)$$

For the Beverton–Holt model, density-dependent mortality is proportional to juvenile density, $\Delta(n) = \gamma n$. The multivariate differential equation for the Beverton–Holt model is

$$(7) \quad \text{diag}(\mathbf{n})^{-1} \frac{d\mathbf{n}}{d\tau} = -\boldsymbol{\mu} - \boldsymbol{\gamma}\mathbf{n}$$

where \mathbf{n} and $\boldsymbol{\mu}$ are vectors of length a_{\max} , and $\boldsymbol{\gamma}$ is a matrix of dimension $a_{\max} \times a_{\max}$. In general, this equation cannot be solved analytically. It is a matrix Riccati equation of a form that lacks an exact solution (Zwillinger 1992). I solve it numerically with the initial condition given in eq. 4.

I found the most standard numerical method, a Runge–Kutta algorithm, to be ineffective. The difficulty is due to the stiffness of the differential equations. Stiffness is usually defined to occur when there are multiple and very disparate time scales of variability; these time scales easily confound algorithms that are classified as explicit, such as the Runge–Kutta algorithm (Burden and Faires 2001).

I use a semi-implicit method: a predictor–corrector method with a second-order Adams–Bashforth algorithm as a predictor step and a second-order Adams–Moulton algorithm as a corrector step (Burden and Faires 2001). This second-order method is initialized with a fourth-order Runge–Kutta with a very small step size. In the special case where $\mu_i = \mu$ and $\gamma_{ij} = \gamma$ for all i and j , eq. 7 reduces to a traditional Beverton–Holt model with a known analytical solution (Quinn and Deriso 1999). I use this special case to quantify the numerical error of the predictor–corrector method. I found that the algorithm converges quickly, but the initial Runge–Kutta steps introduce error to the final solution. However, there is never greater than 1% relative error, an acceptable amount of error for my purpose.

The two age-class case

For heuristic reasons, I will examine the two age-class case in detail. I define class 1 juveniles (n_1) to be from “young” mothers and class 2 juveniles (n_2) to be from “old” mothers. The two age-class multivariate Ricker model can be written

$$(8) \quad \begin{aligned} n_1(\tau) &= \phi_1 S_1 e^{(-\mu_1 - \gamma_{11} S_1 - \gamma_{12} S_2)\tau} \\ n_2(\tau) &= \phi_2 S_2 e^{(-\mu_2 - \gamma_{21} S_1 - \gamma_{22} S_2)\tau} \end{aligned}$$

I now define the total stock size to be $\tilde{S} = S_1 + S_2$ and the variable p to be the proportion of \tilde{S} from old fish

$$(9) \quad p = \frac{S_2}{S_1 + S_2} = \frac{S_2}{\tilde{S}}$$

and I reparameterize so that $\alpha_a = \phi_a e^{-\mu_a T}$ and $\beta_{ak} = \gamma_{ak} T$. This yields the following equation for recruitment in the two age-class Ricker model:

$$(10) \quad R = \alpha_1 (1-p) \tilde{S} e^{-[(1-p)\beta_{11} + p\beta_{12}]\tilde{S}} + \alpha_2 p \tilde{S} e^{-[(1-p)\beta_{21} + p\beta_{22}]\tilde{S}}$$

I can now manipulate the parameters α_a and β_{ak} to give an advantage to class 2 offspring over class 1 offspring — simulating the age-dependent maternal effect — and then look at recruitment (R) as a function of the population age structure (p) and the spawning stock biomass (\tilde{S}). One of the advantages of this parameterization is that I am able to reduce the two density-independent parameters, ϕ and μ , to one parameter, α .

Similarly, I use a numerical solver to calculate the two age-class Beverton–Holt model and then sum across subclasses to find total recruitment.

Case 1: maternal effect in presettlement factors only

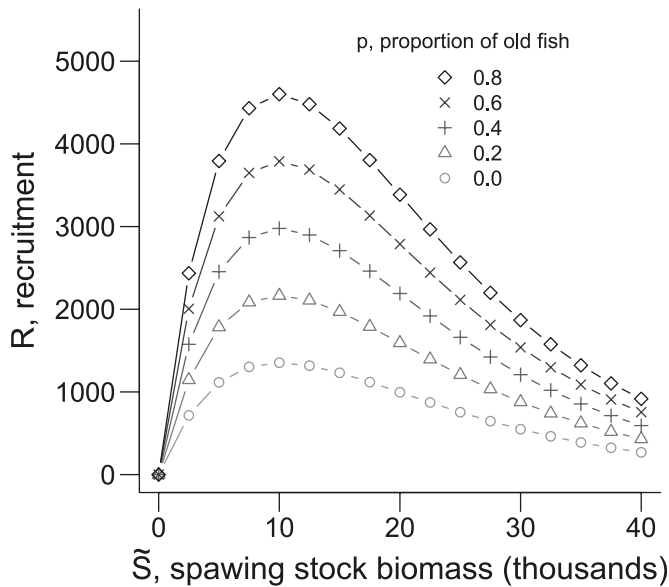
To survive the pelagic stage, larvae need to find food, avoid predators, avoid being swept offshore, and maintain a body temperature that is optimal for growth (Bakun 1996). All of these needs are expected to be facilitated by the improved swimming ability that comes with larger body size; larger larvae can find food faster, avoid predators better, avoid adverse currents, and manage their body temperature by changing their depth in the water column. The maternal effect is expected to reduce larval mortality because it confers a larger larval body size as well as an improved resistance to early starvation. In the model, I represent these kind of advantages by allowing $\phi_2 > \phi_1$.

Alternatively, this case would emerge if fecundity increased with maternal age, a phenomenon ubiquitous in fishes and that has been observed in rockfish (Bobko and Berkeley 2004).

Case 1a: Ricker

Recall that $\alpha_a = \phi_a e^{-\mu_a T}$ and $\beta_{ak} = \gamma_{ak} T$. The first case I consider is $\alpha_2 > \alpha_1$ and $\beta_{11} = \beta_{12} = \beta_{21} = \beta_{22} = \beta$. Here, the maternal effect impacts the density-independent survival, but has no impact on the density-dependent interactions. I find

Fig. 2. A multivariate Ricker stock–recruitment function with the maternal effect only impacting the pelagic stage (case 1a). $\alpha_1 = 0.37$ ($\mu_1 = 0.01, \phi = 1$), $\alpha_2 = 1.47$ ($\mu_1 = 0.01, \phi = 4$), and $\beta = 1 \times 10^{-4}$ ($\gamma = 1 \times 10^{-6}, T = 100$). Note in a standard Ricker model, maximum recruitment occurs when spawning stock biomass is $1/\beta$.



$$(11) \quad R = \alpha_1 \tilde{S} e^{-\beta \tilde{S}} + \tilde{S} e^{-\beta \tilde{S}} (\alpha_2 - \alpha_1) p$$

For a given \tilde{S} , R is a linear function of p , with slope $\tilde{S} e^{-\beta \tilde{S}} (\alpha_2 - \alpha_1)$. If $\beta \tilde{S}$ is very large or \tilde{S} is very small, then the difference in α is no longer important, i.e., the maternal effect is no longer important. This observation is illustrated in Fig. 2. When \tilde{S} is very large or very small, there is very little difference in R for various values of p . But at intermediate population sizes, changes in p matter a great deal. The implication is that when population size is high, density-dependent pressure severely limits the total number of individuals to survive, a standard feature of a Ricker model. This property obscures the impact of even a strong maternal effect when either \tilde{S} or β is large.

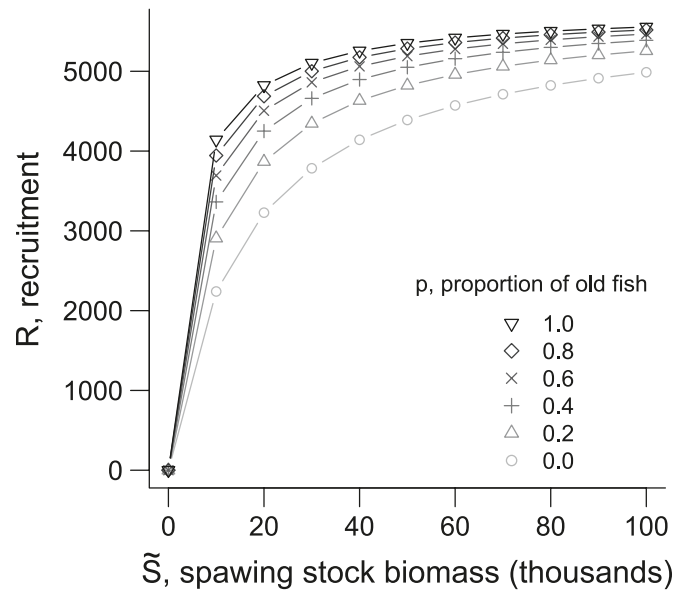
Also, Fig. 2 shows that for any given population size, recruitment increases as p increases. This suggests that management for age structure could be effective.

Case 1b: Beverton–Holt

In Fig. 3, I show the numerical solution of the two age-class Beverton–Holt model when the maternal effect impacts only the survival of the pelagic phase. It is shown that recruitment generally increases as a function of p , but the magnitude of the increase is smaller when \tilde{S} is high.

Raising p from a low value to an intermediate value (0 to 0.2) has a much larger impact on recruitment than raising p from an intermediate value to a high value (0.4 to 0.6). In practice, \tilde{S} and p usually covary. In Figs. 2–5, this means that as you move from left to right on the x axis, you also move from lighter to darker symbols. In Fig. 3, this implies a stock–recruitment curve that ascends more on the right side than might be expected from a univariate model.

Fig. 3. A multivariate Beverton–Holt stock–recruitment function with a maternal effect that impacts only the pelagic stage (case 1b). $\phi_1 = 1, \phi_2 = 4, \mu_1 = \mu_2 = 0.01, \gamma_{11} = \gamma_{12} = \gamma_{21} = \gamma_{22} = 1 \times 10^{-6}$.



Case 2: maternal effect before and after settlement factors

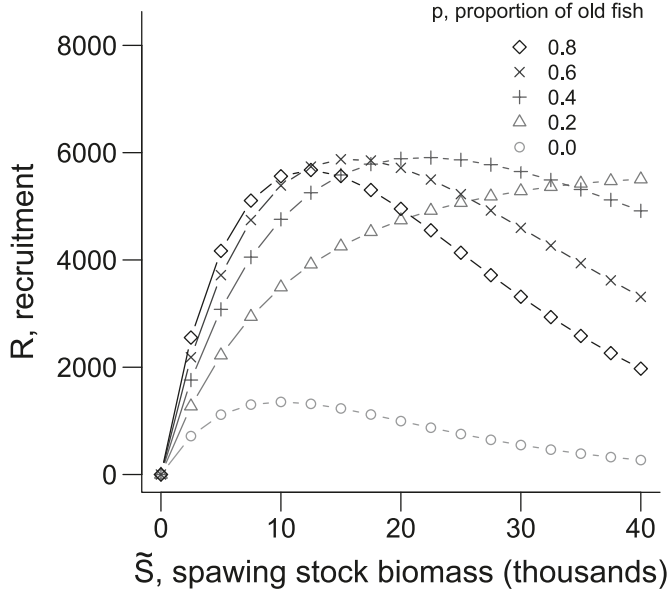
The higher larval growth rate during the pelagic stage is in turn expected to lead to a larger size at settlement (Pechenik et al. 1998; Shima and Findlay 2002). While mortality in the pelagic stage is widely viewed to be density-independent (Ralston and Howard 1995; Hixon and Webster 2002), juveniles in the benthic stage are faced with both density-independent sources of mortality, such as the need to manage body temperature and locate food (Love et al. 1991), and density-dependent sources of mortality, such as competition for shelter space (Johnson 2006a) and density-cued predation (Adams and Howard 1996; Hobson et al. 2001; Hixon and Jones 2005). As with larvae, the ability of juveniles to survive is improved by larger body size. Larger juveniles are better able to manage their body temperature by managing their depth, and they are better able to locate food, compete for shelter space, and avoid predators. The maternal effect is expected to lower juvenile mortality because a faster larval growth rate will cause a larger size at settlement.

There are two important reasons to consider the maternal effect on juvenile survival: (i) Variation in body size has a qualitatively different population impact in the pelagic and benthic stages because the benthic stage includes density-dependent processes. (ii) In the past, much of the variation in pelagic survival has been attributed to environmental variability (Ralston and Howard 1995) and not to variation in individual quality, i.e., it may be that the most important population impact of the maternal effect comes from its delayed impact on the benthic stage.

Case 2a: Ricker

There are many ways to manipulate the values of β_{ak} to model a maternal effect; I chose to model the case where class 1 and class 2 juveniles attract predators in equal num-

Fig. 4. A multivariate Ricker stock–recruitment function with the maternal effect impacting both the pelagic and benthic stages (case 2a). $\alpha_1 = 0.37$ ($\mu_1 = 0.01, \phi = 1$), $\alpha_2 = 1.47$ ($\mu_1 = 0.01, \phi = 4$), and $\beta = 1 \times 10^{-4}$ ($\gamma = 1 \times 10^{-6}, T = 100$). Note in a standard Ricker model, maximum recruitment occurs when spawning stock biomass is $1/\beta$.



bers, but class 1 juveniles are more vulnerable to predation, i.e., class 1 individuals are harder hit by density-dependent mortality. I can represent this by allowing interclass rates to be affected by the maternal effect, $\beta_{21} < \beta_{12}$, but leaving intraclass rates unaffected, $\beta_{22} = \beta_{11}$. Here, I consider a limiting case of this condition: $\beta_{21} = 0$ while $\beta_{22} = \beta_{11} = \beta_{12} = \beta$. The qualitative observations I make for this case are insensitive to this assumption and hold true for any parameterization of β that models a maternal effect. The reader can verify this for themselves by experimenting with eq. 10 in a spreadsheet. I also allow the maternal effect to impact the before settlement stage by setting $\alpha_1 < \alpha_2$.

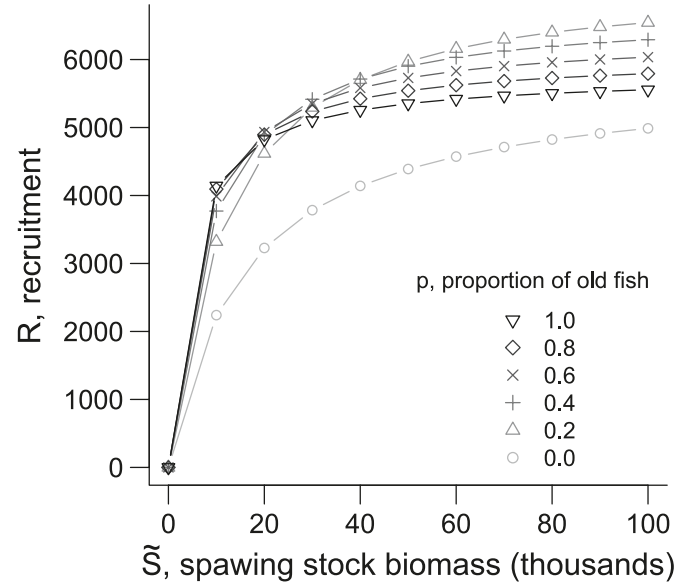
Applying this condition to eq. 10 yields

$$(12) \quad R = \alpha_1 \tilde{S}(1 - p) e^{-\beta \tilde{S}} + \alpha_2 \tilde{S} p e^{-p\beta \tilde{S}}$$

This is not as easy to interpret as eq. 11, so I look to Fig. 4 for interpretation. Figure 4 shows a different pattern than Fig. 2. Here, the maternal effect matters most when \tilde{S} is large. In this case, increasing the proportion of old adults in the population initially increases recruitment, but as the proportion of old adults in the population increases further, recruitment declines. Class 2 juveniles do survive better, but as their numbers increase, their success comes at the expense of class 1 juveniles. It can be seen that the lowest recruitment occurs when $p = 0$, but the highest recruitment occurs at intermediate values of p . Also, the larger the population size, the larger recruitment declines are with higher values of p .

Incidentally, when $p = 0.2$ in Fig. 4, the multivariate Ricker model produces a curve that looks remarkably similar to a traditional Beverton–Holt stock–recruitment relationship.

Fig. 5. A multivariate Beverton–Holt stock–recruitment function with a maternal effect that impacts both the pelagic and benthic stages (case 2b). $\phi_1 = 1, \phi_2 = 4, \mu_1 = \mu_2 = 0.01, \gamma_{11} = \gamma_{12} = \gamma_{22} = 1 \times 10^{-6}, \gamma_{21} = 0$.



Case 2b: Beverton–Holt

In Fig. 5, I show the numerical solution of the two age-class Beverton–Holt model when the maternal effect impacts survival of both the pelagic and benthic phases. There is a substantial increase in recruitment when p increases from 0 to 0.2. However, as p increases further, the change to recruitment is much smaller. When $\tilde{S} > 20,000$ metric tons, then recruitment declines as p increases. The worst declines in recruitment with increasing p occur when \tilde{S} is high. This pattern is similar to the Ricker case illustrated in Fig. 4, but here the changes in recruitment are much smaller than in the Ricker case.

Again, \tilde{S} and p are not independent but covary. In Fig. 5, this could lead to a descending limb. I could generate a curve that resembles a Ricker model even though the curve was generated by a Beverton–Holt process.

Black rockfish and the two age-class Beverton–Holt model

First, let’s consider the age structure of black rockfish. In the two age-class population, p is a natural metric for age structure. It may be instinctive to think of p as a very small proportion; however, its value is a function of the threshold age (a_i) between young and old. If I assume a steady-state age distribution, then

$$(13) \quad p(a_i) = \frac{\int_{a_i}^{a_{\max}} e^{-Ms} ds}{\int_{a_{\text{mat}}}^{a_{\max}} e^{-Ms} ds} = \frac{e^{-Ma_i} - e^{-Ma_{\max}}}{e^{-Ma_{\text{mat}}} - e^{-Ma_{\max}}}$$

where a_{\max} is maximum age, a_{mat} is age of maturity, and M is the rate of natural mortality. For black rockfish, maximum age is about 50 years, age of maturity is about 6 years (Love et al. 2002), $M = 0.115 \text{ year}^{-1}$ (Ralston and Dick

2003), and based on the observed maternal effect, I can guess $a_t = 10$ (Berkeley et al. 2004). In this example, a fully protected black rockfish population with a steady-state age distribution has $p = 0.63$, i.e., 63% of the population is older than 10 years.

In contrast, current rockfish populations are heavily harvested, and only about 15% of the reproductive population is older than 10 years. In Fig. 6a, I show a time series of p_{10} for black rockfish. These values were generated using estimates for numbers-at-age from the most recent stock assessment for California and Oregon rockfish (Sampson 2007). Age structure declined during the heavy harvest period of the 1980s and 1990s, reaching a low of $p_{10} = 0.06$ in 1999. Age structure has since partially recovered, although it is still below the level observed in 1980 and well below my estimate of $p_{10} = 0.63$ for an unfished population.

In Fig. 6b, I show the two age-class Beverton–Holt model calculated using the time series for p_{10} , as well as stock-assessment estimates for spawning stock biomass and the Beverton–Holt rate parameters. I have also added a maternal effect ($\phi_2 = 3\phi_1$) in the rate of fecundity that is comparable with empirically observed values for improved larval viability (Berkeley et al. 2004). This is comparable with case 1b.

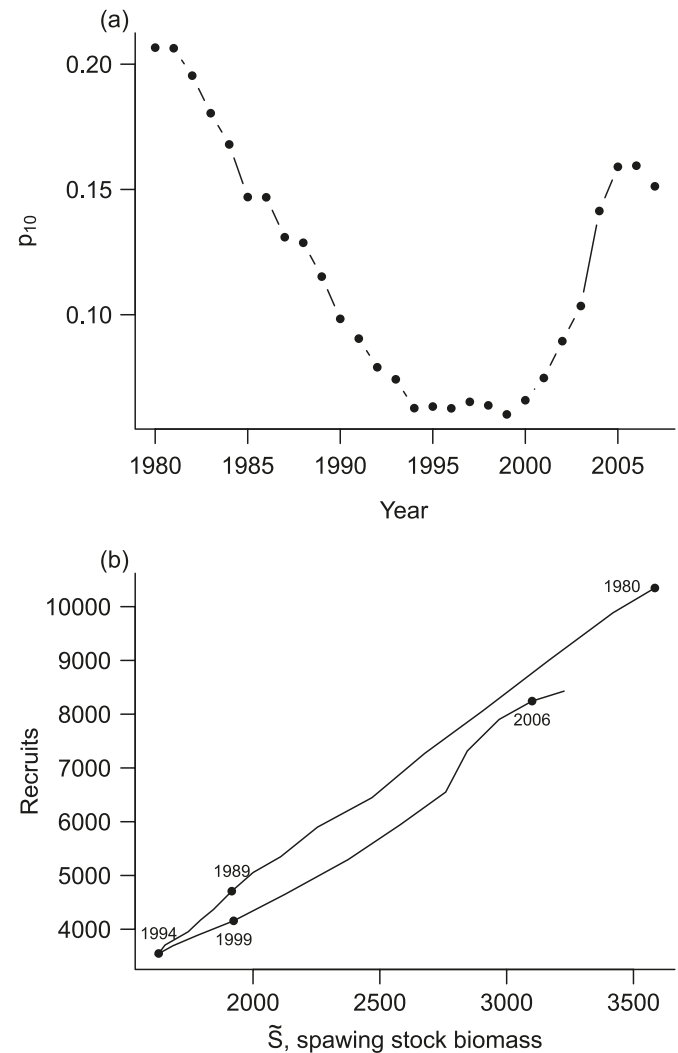
From 1980 to 1995, the population has some residual age structure that helps buoy recruitment while the population is in decline. However, the recovering population (1995–present) lacks this reserve of older fish and has slightly lower productivity as a result. If the true population trajectory follows the lower limb of the time series in Fig. 6b, but the recruitment predictions are based on data from 1980 to 1995, I could overestimate recruitment by as much as 27%. This is despite a relatively modest change in age structure over the time period (p_{10} ranges from 0.06 to 0.21).

Discussion

For rockfish, it is generally impractical to use a stock–recruitment model such as the one presented here as an estimation model. This is because rockfish recruitment is extremely noisy. Much of the variation in recruitment can be attributed to external drivers, such as environmental variation. This environmental noise makes it effectively impossible to acquire a data set with enough information to discern subtle differences in the shape of the underlying stock–recruitment relationship (Dorn 2002). A process such as a maternal effect may have a numerically significant impact, but this impact is almost certainly smaller than the impact due to all other sources of variation and thus cannot usually be teased apart by working backwards from the available recruitment data.

However, by simulating forward I can generate reasonable estimates of the magnitude of change in recruitment that might be attributed to a higher-order process, such as change in age structure. The analysis presented here provides us with a series of qualitative guidelines for when changes in age structure are likely to be important and the ability to place reasonable bounds on the magnitude of impact that might occur. This may not be as desirable as a statistically robust estimate of the exact change to recruitment, but it should be enough to support precautionary management practices.

Fig. 6. Estimates based on the most recent stock assessment for California and Oregon black rockfish (Sampson 2007). (a) A time series of the proportion of individuals 10 years and older. (b) An illustration of the two age-class multivariate Beverton–Holt model with a maternal effect that impacts only the pelagic stage (case 1b). The curve is based on the stock-assessment estimates for spawning stock biomass, the Beverton–Holt parameters ($\alpha = 1.869$ and $\beta = 7.79 \times 10^{-5}$), the above time series for p_{10} , and a maternal effect comparable with the survival advantage observed in empirical studies ($\phi_2 = 3\phi_1$).



I will now discuss some of these qualitative guidelines. When the maternal effect only influences mortality rates in the pelagic stage, then recruitment increases as the the proportion of old mothers increases. This is because only density-independent processes are influenced by the maternal effect. However, the larger the population size, the less the maternal effect matters, unless there is almost no density-dependent mortality in the benthic phase.

In cases where the maternal effect impacts density-dependent mortality rates in the benthic stage, the story is substantially more complex. Here, the maternal effect confers an advantage to some individuals in the population, but also changes the competitive environment for other individuals, so that whole population consequences are not easy to

predict. When part of the advantage conferred by the maternal effect is an escape from density-dependent mortality, a potential trade-off arises between the success of the offspring from older mothers and overall recruitment. It becomes apparent that more old fish will not necessarily increase recruitment and can decrease recruitment.

It appears there is a relatively narrow set of circumstances where managing for age structure would be harmful to recruitment. The circumstances that cause concern are when juvenile densities are very high and there is a large number of juveniles with a strong competitive advantage because of a superior ability to avoid predation. To learn about whether or not this is a concern, researchers should examine data on rockfish settlement for evidence of a size advantage that may be related to maternal age. Researchers should also examine the pelagic stage for evidence that pelagic survival can be increased by improving larval quality.

The MSRF framework can be applied to other systems with sympatric subclasses. For example, juvenile kelp, gopher, and black-and-yellow (*Sebastes chrysomelas*) rockfish together form the KGB complex. During the juvenile stage, these three species share the same habitat, food sources, and predators; they are sufficiently similar that they cannot be reliably distinguished in the field (Carr 1991; Johnson 2006b). Such a closely competing multispecies complex is well suited to the joint treatment of an MSRF. Speciation suggests that the three species have adopted subtly different characteristics, so I expect there to be different juvenile mortality rates. But at the same time, changes in population density of any of the three species are likely to impact members of the other species.

Sympatric subclasses also occur when there are multiple life history strategies present within one juvenile cohort. For example, some juvenile coho salmon (*Oncorhynchus kisutch*) rear in streams before migrating to the ocean. These stream-rearing coho may choose to spend 1 year in the stream before migrating (1+ type) or 2 years in the stream before migrating (2+ type). To be ready to migrate in only 1 year, the 1+ type coho accept higher predation risk to maintain a higher foraging rate and rapid growth. The 2+ type juveniles prefer a more conservative foraging strategy spread across a longer period of time (Reinhardt 1999). An MSRF accounts for density-dependent interactions between these two life history groups while also accounting for their distinct mortality rates.

The discovery of maternal effects in rockfish populations prompted researchers to ask whether the loss of old fish has changed rockfish recruitment; the MSRF makes it possible to address this question directly with a plot of recruitment versus the proportion of old fish in the population. The MSRF framework proved flexible enough to allow me to examine the impact of my assumptions on my conclusions by comparing recruitment for several cases of the model. This model proved to be a valuable tool for learning about the population consequences of maternal effects. I believe the MSRF will prove to be equally valuable for understanding other systems with sympatric subclasses.

Acknowledgements

I am grateful to Marc Mangel and Alec MacCall for careful reading of several drafts of this manuscript. Thanks are

extended to Ian Stewart and Eli Holmes for helpful comments and to John Field for providing the stock assessment numbers-at-age. This work was partially supported by the NMFS – Sea Grant Population Dynamics Fellowship and the Center for Stock Assessment Research, a partnership between UC Santa Cruz and the NMFS–SWFSC Santa Cruz Lab.

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