DR. RAY HILBORN (Orcid ID : 0000-0003-2326-2305)

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Title: Modeling the impacts of two age–related portfolio effects on recruitment variability with and without a marine reserve

Authors: Carey R. McGilliard[1,2], André E. Punt[2], Ray Hilborn[2], and Tim Essington[2]

[1]Corresponding Author Current Address: National Oceanic and Atmospheric Administration, Alaska Fisheries Science Center, 7600 Sand Point Way NE, Seattle, WA 98115

[1]Corresponding Author Current Email Address: carey.mcgilliard@noaa.gov

[2]School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195, USA.

Abstract

Many rockfish species are long-lived and thought to be susceptible to being overfished. Hypotheses about the importance of older female rockfish to population persistence have led to arguments that marine reserves are needed to ensure the sustainability of rockfish populations. However, the implications of these hypotheses for rockfish population dynamics are still unclear. We modeled two mechanisms by which reducing the proportion of older fish in a population has been hypothesized to influence sustainability, and explored whether these mechanisms influenced mean population dynamics and recruitment variability. We explored whether populations with these mechanisms could be managed more sustainably with a marine reserve in addition to a constant fishing mortality rate (*F*) than with a constant *F* alone. Both hypotheses can be seen as portfolio effects whereby risk of recruitment failure is spread over a "portfolio" of maternal ages. First, we modeled a spawning window effect whereby mothers of different ages spawned in different times or locations (windows) with local environmental conditions. Second, we modeled an offspring size effect whereby older mothers produced larger offspring than younger mothers, where length of a starvation period over which offspring could survive increased with maternal age. Recruitment variability resulting from both models was 55-65% lower than for models without maternal age-related portfolio effects in the absence of fishing and increased with increases in *F*s for both models. An offspring size effect caused lower output reproductive rates such that the specified reproductive rate input as a model parameter was no longer the realized rate measured as the reproductive rate observed in model results; this quirk is not addressed in previous analyses of offspring size effects. We conducted a standardization such that offspring size effect and control models had the same observed reproductive rates.

A comparison of long-term catch, the probability of falling below a biomass threshold, and recruitment variability over a range of exploitation rates for models with an age–related portfolio effect showed no benefit of a marine reserve implemented in addition to a constant *F* (as compared to a constant *F* alone) for populations with sedentary adults and sedentary or mobile larvae.

Keywords: marine reserve, maternal age effects, recruitment variability, fish population dynamics models, fisheries management, marine protected areas, density-dependent mortality, larval dispersal, spatial models, rockfish, life history

Introduction

Many rockfish species are long-lived and are thought to be susceptible to overfishing (Love et al. 2002, Patrick et al. 2010). Berkeley et al. (2004b) argue that rockfish may utilize longevity in several ways which may be important for persistence in a variable environment; thus reducing the extended age structure of rockfish may not be sustainable. Many authors (e.g. Pauly et al. 2002, Berkeley et al. 2004b, Birkeland and Dayton 2005) have argued that perhaps the only way to protect age structure and ensure sustainability is through marine reserves. Berkeley et al. (2004b) suggest that maintenance of older rockfish in a population is essential for sustainability because older fish may spawn in a different time or place than younger fish. Environmental conditions may change over time or space and therefore it is likely that even though environmental conditions may be poor for some offspring, conditions will be favorable for other offspring within the same spawning season or year. This can be thought of as a potential portfolio effect whereby spawners utilize the diversity of available spawning time or space over which environmental conditions may vary, and this is hypothesized to reduce the risk of no offspring survival and to lower the inter-annual variance of offspring survival (Hilborn et al. 2003, Figge 2004, Hooper et al. 2005, Schindler et al. 2010). A second hypothesis put forth by Berkeley et al. (2004a, 2004b) is that older mothers may produce larger offspring that are able to survive starvation longer than offspring from younger mothers (a maternal age effect). Berkeley et al. (2004a) conducted laboratory experiments, which showed that older black rockfish produced larvae with larger oil globules than those of younger mothers and that the larvae from older mothers survived longer starvation periods than larvae from younger mothers. Laboratory experiments presented in Sogard et al. (2008) showed similar results for several other rockfish species.

The potential for a spawning window effect to influence population dynamics has not been fully explored. Le Bris et al. (2015) investigated relative effects of batch spawning, an exponential increase in fecundity with increased weight, and the influence of maternal age on hatching probability for stocks that were well below B_{MSY}, where the influence of density dependent mortality is minimal. They found that the influence of the fecundity-weight relationship was the most influence on population resistance to and recovery from fishing pressure of the three effects; however, the density dependent mortality that occurs by way of the stock-recruit curve would likely dampen the influence of increased fecundity at higher stock sizes.

The potential influence of a maternal age effect on population dynamics has been the subject of several studies and much debate (e.g. O'Farrell and Botsford 2006, Spencer et al. 2007, Venturelli et al. 2009, Trippel 1997). Previously explored hypotheses of the potential influence of a maternal age effect on fish population dynamics have modeled the effect deterministically as a mean or average effect on fecundity or survival of recruits. O'Farrell and Botsford (2006) explored how a maternal age effect in which older individuals produce more larvae than younger individuals (beyond weight-specific increases in fecundity) would affect lifetime egg production (LEP), analogous to spawning biomass per recruit (SBPR), and found that a maternal-age effect acting on larvae prior to density-dependent mortality had only small effects on LEP. One reason that increases in the number of larvae produced by older individuals has limited influence on population dynamics is that density-dependent mortality occurs after accounting for the maternal age effect and this means that while older individuals may produce more larvae, this doesn't necessarily translate into the survival of more larvae than in models with no maternal age effect. Lucero (2008) explored how a maternal age effect influencing density-dependent mortality via the Beverton-Holt stock-recruit curve would affect time to recovery of overexploited stocks, concluding that a maternal age effect acting on the stock-recruit curve would cause small increases in the amount of time for recovery for only a few stocks. In addition, Spencer et al. (2013) modeled a maternal age effect acting on density-independent and -dependent mortality via a Beverton-Holt stock-recruit curve for Pacific Ocean perch and Pacific cod, showing that a maternal age effect leads to small changes in optimal fishing mortality rates. These studies suggest that maternal age effects may have a small influence on population productivity, population recovery time, and reference points relative to equivalently parameterized models that do not include a maternal age effect. Notably, previous studies of maternal age effects have each assumed that the effect influences deterministic population dynamics; no previous work has been conducted to explore the potential for a maternal age effect to influence characteristics of recruitment variability.

Marshall et al. (2010) questioned the ecological underpinnings of a maternal age effect by asking why younger mothers would produce smaller offspring if larger offspring were more viable in the ocean environment. We hypothesize that in a highly variable environment, such as the ocean, selection for an optimal offspring size may be inconsistent. It is possible that only larger offspring survive when environmental conditions are poor and resources are scarce. However, both small and large offspring may survive when resources are plentiful. Therefore, while large offspring may have higher survival rates when environmental conditions are poor, they may not have the same survival advantage over smaller offspring when resources are not limited and therefore selection for larger offspring may be inconsistent. The resulting effect is that having many small offspring allows the population to take advantage of favorable environmental conditions, while having some large offspring that can survive longer periods of starvation increases the probability that some offspring survive to recruit to the population even when environmental conditions are poor. These larger offspring may serve as a buffer against environmental uncertainty. We hypothesize that a maternal age effect would influence recruitment variability and that its primary influence on population dynamics may be a portfolio effect over offspring size which acts to limit recruitment variability in the absence of fishing. Such a portfolio effect may be eroded by fishing due to the reduction of the contribution of larger offspring from older mothers. There are variety of mechanisms by which fishing and age-truncation could influence population variability (see Hsieh et al. 2006, Anderson et al. 2008, and Botsford et al. 2014); in this study, we model the two mechanisms described above, which may be important to long-lived iteroparous fish. The two mechanisms are: (1) changes in the timing or location of spawning (spawning window) as a function of maternal age (a spawning window model) and (2) changes in offspring size as a function of maternal age, where larger offspring are able to withstand longer periods of starvation (an offspring size model). We explore the extent to which these two mechanisms act as portfolio effects, lowering recruitment variability in a stochastic environment in the absence of fishing. We also explore the implications of fishing and (and thus reducing the proportion of older fish) on population dynamics and the characteristics of recruitment variability. Finally, we investigate the impact of marine reserves on population dynamics and population response to exploitation.

Methods

Spawning and recruitment for both models is described below and additional population dynamics are described in Appendix S1. The dynamics of larval dispersal are the same for both the offspring size and spawning window models and are described in Appendix S1. We parameterized both models to represent black rockfish using parameters from Sampson (2007), with a steepness parameter of h= 0.6, natural mortality of M = 0.12yr^{-1}, and ages at which 50% and 95% of fish were selected in the fishery of a_{50} =3yr and a_{95} =6yr, respectively. Growth parameters were L_{∞} =442mm, κ =0.33yr^{-1}, and t_0 =0.75yr, length-weight relationship parameters were α =0.00000168, β =3, ages at 50% and 95% maturity were a_{50}^{mat} = 7.5yr and a_{95}^{mat} = 14yr, respectively, and the plus group started at $a_{\max}$ =50yr.

The spawning window model

The spawning window model was an age-structured population dynamics model with ten spawning windows, which can be interpreted as spawning grounds or spawning times. Fish of different ages spawned at different spawning windows, where each window experienced independent environmental conditions within a year. Spawning windows were ephemeral structuring of the population that existed only at the time of spawning and not year-round. When not spawning, the population occurred in one or two spatial areas with population dynamics occurring within each area. Adult fish within each area were sedentary with sedentary larvae, or were linked by larval movement between areas. The convention "spawning windows" refers to the ephemeral structure in the distribution of maternal ages over time or space at the time of spawning, while "area" refers to permanent spatial structure in the population. Areas are included in the model to explore scenarios with a marine reserve (where one area is open to fishing and the other is a marine reserve). Spawning and recruitment for the spawning window model is described below with equations in Table 1; additional equations are specified in Appendix S1.

Spawning and Recruitment for the "spawning windows" model

Several hypotheses about recruitment dynamics and the distribution of spawning stock biomass over time or space were modeled.

<u>Distribution of spawning biomass across spawning windows</u>

Two biological scenarios were modeled to represent potential ways that spawners could be distributed across spawning windows. First, spawners progress across spawning windows as they age, shifting spawning windows by the same increment each year (age-specific distribution of spawners over spawning windows; Figure 1a). Figure 1b shows that most of the offspring were from younger mothers and therefore came from only a few of the spawning windows (windows 2-4 especially) when the age-specific distribution of spawners was applied. Alternatively, spawners may shift to a new spawning window when reaching a new developmental stage (stage-specific distribution of spawners over spawning windows; Figure 1c). The stage-specific alternative was developed to create a scenario that would maximize a spawning window portfolio effect by resulting in a distribution of offspring over spawning windows that was as uniform as possible (Figure 1d). The two alternatives can be seen as two opposite extremes for the configuration of spawning windows, where the age-specific distribution of spawners models distinct spawning windows for each age group and the stage-specific distribution models a large amount of overlap in spawning windows among ages such that the spawning window effect is maximized. Both alternatives are described in more detail below.

<u>Age-specific distribution of spawners over spawning windows</u>

We modeled the process by which spawners distribute among spawning windows using a discrete Beta function (Equation 1). This parameterization allows flexibility in the overlap of different ages in each spawning window, which impacts survival of recruits owing to stochastic events or density-dependent mortality.

(1) $$\mathrm{P}_{a,i} = \frac{i^{\alpha_a - 1}(n-i+1)^{\beta_a - 1}}{\sum_i i^{\alpha_a - 1}(n-i+1)^{\beta_a - 1}},$$

where $\mathrm{P}_{a,i}$ is the proportion of age *a* spawners that spawn at spawning window *i* and *n* represents the total number of spawning windows. The means, μ_a, of the Beta functions for each fish age are evenly spaced values between 0.1 and 0.999 (Figure 1a). This model creates a gradual change in spawning window use with maternal age. The variance of the age-specific Beta functions was 0.001 for all ages so that the distribution of spawning biomass over spawning windows was distinct for each age; a large value for the variance would dampen the influence of spawner age on resulting variation in recruitment. Likewise, holding the CV (rather than the variance) of each Beta function constant across ages would result in an overlap of multiple older ages within a spawning window; this effect is modeled using the stage-specific scenario (described below), where ages (especially older ages) are grouped together such that the spawning window effect is approximately maximized. The parameters α_a and β_a are calculated from the mean and variance of the Beta function.

<u>Stage-specific distribution of spawners across spawning windows</u>

Here we represent a similar ontogeny of spawning windows, but instead presume that spawning window selection is similar for distinct life history stages, each corresponding to multiple age-classes. We consider eight of these stages, G_k, where *k* is an index for group number. The means, μ_k, of the Beta functions for fish group were evenly spaced values between 0.1 and 0.9 and the variance for each group-specific beta function was 0.001. As for the age-specific distribution of spawners, α_k and β_k were calculated from the mean and variance for group *k*.

$$\begin{aligned}
G_1 &= 1 \le a < 8 \\
G_2 &= 8 \le a < 11 \\
G_3 &= 11 \le a < 13 \\
G_4 &= 13 \le a < 15 \\
G_5 &= 15 \le a < 17 \\
G_6 &= 17 \le a < 21 \\
G_7 &= 21 \le a < 28 \\
G_8 &= a \ge 28
\end{aligned}$$

These groupings and the number of groups were not based on black rockfish life history, but were chosen because they resulted in an approximately uniform distribution of offspring across spawning windows (Figure 1d) and therefore would maximize the portfolio effect across spawning windows in the absence of fishing. An exponential increase in fecundity-at-age as a function of weight-at-age is an alternative example of an effect that would result in a more even spread of eggs across spawning windows (Le Bris et al. 2015). The standardized Beta function for each group, *G*, was:

(2) $$P_{k,i}^{G} = \frac{i^{\alpha_k - 1}(n - i + 1)^{\beta_k - 1}}{\sum_i i^{\alpha_k - 1}(n - i + 1)^{\beta_k - 1}}$$

The standardized Beta function for each age was

(3) $$P_{a,i} = P_{k,i}^{G} \quad \text{for } a \in G_k .$$

Recruitment

The equations for recruitment and environmental variation are given in Table 1. Throughout the manuscript the term “environmental variation” will refer to a model input and “recruitment variability” will refer to a model output. For the spawning window model, environmental variation influences density-independent survival at each spawning window. Recruitment variability is the amount of variability in the number of recruits from year to year that results from the specifications of environmental variability.

Density-dependent mortality occurs by way of the Beverton-Holt stock-recruitment curve and can occur within spawning window (local) or globally. Environmental variation can occur before or after density-dependent mortality. Reproductive rate, h, is measured as the proportion of the unfished number of recruits, $R_{i,j,0}$, in spawning window i and area j produced when the number of eggs in spawning window i and area j is 20% of the number of eggs in spawning window i and area j when the population is in an unfished state, $B^{E}_{i,j,0}$; this definition of reproductive rate is often referred to as "steepness." Egg production is assumed to be proportional to mature female spawning biomass. Environmental variation (process error) influences recruitment in each annual time-step and for each spawning window, i, with correlation, ρ, among spawning windows where $\varepsilon_{i,t} \sim N(0,\sigma^2_{\mathrm{R}})$ and $\eta_{i,t} = \rho\eta_{i-1,t} + \varepsilon_{i,t}\sqrt{1-\rho^2}$.

Biological scenarios

Scenarios where environmental conditions in all spawning windows were perfectly correlated ($\rho = 1$) were compared to scenarios where environmental conditions at each spawning window were uncorrelated ($\rho = 0$). A set of simulations for each biological and management scenario with and without a spawning window effect were conducted. Scenarios with age- and stage-specific distributions of spawning biomass over spawning windows were performed. For both of these scenarios, we conducted simulations where environmental variation occurred before and after density-dependent mortality. Density-dependent mortality was assumed to be global among spawning windows, but local to spatial area (Table 1). Several biologically feasible scenarios could be imagined where density-dependent mortality would be a global effect, including that spawners could experience global density-dependent mortality prior to occupying spawning windows and completing parturition. Alternatively, density-independent mortality could occur within spawning windows prior to global density-dependent mortality at the time of settlement. An exploratory simulation was conducted assuming that density dependence was local to spawning window and spatial area (Table 1, Equations T.2 and T.9) and results did not differ from simulations conducted with global density dependence (Table 1, Equations

T.3 and T.8); therefore, simulations with density dependence as local to spawning window were not explored further.

Model setup and standardization

Two main approaches were used to evaluate the spawning window model. Environmental variability, though confounded with observation error, is often assumed to be in the vicinity of CV = 0.5 or 0.6 (e.g. Sampson 2007). Therefore, first we specified a moderate level of environmental variability (σ_R =0.5) and calculated the resulting magnitude of recruitment variability (the coefficient of variation (CV) of recruitment over years and simulations) for models with ($\rho = 0$) and without ($\rho = 1$) a spawning window effect. We used this approach to evaluate whether the spawning window effect resulted in lower recruitment variability for a population in an unfished state. Second, we standardized the magnitude of recruitment variability (CV of recruits) for a population in an unfished state by finding the level of environmental variability (value of σ_R) in each scenario that resulted in recruitment variability of CV = 0.5 for an unfished population. We used this approach to compare the relative influence of fishing on recruitment variability among models (the offspring size and spawning window models) and corresponding “control” scenarios.

Methods for the offspring size model

The offspring size model assumes that older mothers produce larger offspring that are able to survive a longer starvation period than smaller offspring from younger mothers. Accounting for an offspring size effect is conducted in five steps. First, environmental conditions for each year are defined by a distribution of the number of days of starvation that offspring may experience. The number of days of starvation at time t, d_t, is chosen from a lognormal distribution, where $\varepsilon_{d,t} \sim N(\mu_d, \sigma_d^2)$ such that $d_t = \exp(\varepsilon_{d,t} - \sigma_d^2/2)$. For example, if d_t = 0 food is readily available at the time of birth at time t and all larvae will survive starvation. If d_t = 10, only larvae that are equipped to survive for 10 days with no food will survive. Second, a relationship between maternal age and the number of days at which 50% of offspring from maternal age *a* die of starvation, $D_{50,a}$, is defined based on data from laboratory experiments (Berkeley et al. 2004a). Third, logistic functions for each maternal age are defined that map the relationship between the number of days of starvation in a particular year, d_t, to the survival of offspring from each maternal age; these logistic functions use the number of days to 50% starvation, $D_{50,a}$, as a parameter. Fourth, the survival of offspring from each maternal age is combined with information about the current age distribution and unfished age distribution of the population to calculate a single survival term that is applied to eggs or recruits. Steps 2-5 are described in more detail below.

Relating maternal age to number of days of starvation at which 50% of offspring die

Berkeley et al. (2004a) reported the number of days to 50% mortality for offspring from mothers aged 4 to 18 years, and fit a nonlinear model to these data. There are no data beyond age 18, even though black rockfish are long-lived and the maximum age in the population dynamics model is $a_{max} = 50$; by fitting a model to these data we are making assumptions about the relationship between maternal age and time to 50% mortality for mothers whose ages are outside the range of the data. Therefore, we develop biological scenarios using the model from Berkeley et al. (2004a), as well as exponential and linear models fit to the data published in Berkeley et al. (2004a). . Based on the data available, Berkeley's model appears to be the most reasonable model fit, but the other two scenarios were included to capture the uncertainty in this relationship for offspring of mothers above age 18 (Figure 2a). Berkeley's model is:

(4) $$D_{50,a} = 15.23 \quad 28.79(1 \quad e^{-0.23a}),$$

where $D_{50,a}$ is days to 50% mortality of offspring from maternal age *a*. The exponential model is:

(5) $$D_{50,a} = 4.557e^{0.0717a}.$$

The linear model is:

(6) $$D_{50,a} = 0.6534a + 3.1395\ .$$

Mapping number of days of starvation to survival of offspring of each maternal age

The number of days of starvation to 50% mortality for each maternal age, $D_{50,a}$, and δ, the difference between the number of days to 95% mortality and $D_{50,a}$, define a descending logistic model for each maternal age relating the number of days of starvation to offspring survival, $\gamma_{a,t}$ (Figure 2b-d).

(7) $$\gamma_{a,t} = \left[1 + \exp\left(\frac{-\ln(19)(d_t - D_{50,a})}{-\delta}\right)\right]^{-1}.$$

The proportion of larvae surviving d_t days of starvation, λ_t, is a function of numbers-at-age in area j at time t (the subscript i is omitted because there is only one spawning window in the offspring size model), maturity at age, O_a, weight at age, w_a, survival of offspring of maternal age a at time t, and offspring survival for offspring of maternal age a in year t, $\gamma_{a,t}$.

(8) $$\lambda_t = \frac{\sum_a \left(\gamma_{a,t} O_a w_a \sum_j N_{a,j,t}\right)}{\sum_a \left(O_a w_a \sum_j N_{a,j,t}\right)}.$$

Spawning and recruitment for the offspring size model

As for the spawning window model, density-dependent mortality can occur before or after environmental variation. The subscript i is omitted from the description of recruitment dynamics for the offspring size model for simplicity because there is only one spawning window. Egg production is assumed to be proportional to mature female spawning biomass.

<u>Density-dependent mortality followed by environmental variation</u>

Recruitment prior to larval dispersal, $R'_{j,t+1}$, follows the Beverton-Holt stock-recruitment function where $B_{j,t}$ is the spawning stock biomass in area *j* at time *t*. A survival scalar, ϕ, is necessary; λ_t represents environmental variation, but will never have a value greater than 1 and hence will lower the mean number of recruits from its pre-defined value when the population is in an unfished state. The value of the survival scalar, ϕ, is found numerically for each scenario such that mean recruitment when the population is in an unfished state remains equal to $R_{j,0}$.

(9) $$R'_{j,t+1} = R_{j,0}\frac{4h\left(B_{j,t}/B_{j,0}\right)}{(1-h)+(5h-1)\left(B_{j,t}/B_{j,0}\right)}\lambda_t\phi \,.$$

<u>Environmental variation followed by density-dependent mortality</u>

The number of eggs in area *j* at time *t* is a function of the spawning stock biomass, $B^E_{j,t}$, the proportion of eggs that survive environmental variation at time *t*, λ_t, and the survival scalar, ϕ. The number of recruits prior to larval dispersal, $R'_{j,t+1}$, is:

(10) $$R'_{j,t+1} = R_{j,0}\frac{4h\left(B^E_{j,t}\lambda_t\phi/B_{j,0}\right)}{(1-h)+(5h-1)\left(B^E_{j,t}\lambda_t\phi/B_{j,0}\right)}\,.$$

Biological scenarios

All simulations were conducted for (1) the offspring size model and (2) a control model, which assumed that all offspring had the size and characteristics that would be associated with an offspring from an age 15 mother produced from the offspring size model; almost

100% of age 15 individuals are mature and so offspring are large enough to survive a few days of starvation in most model parameterizations.

An offspring size model and a control model were based on the three assumptions (Berkeley, linear, and exponential models; Equations 4-6) relating maternal age to the time to 50% mortality of offspring. In addition, all of the above scenarios were conducted when density-dependent mortality occurred prior to environmental variation.

Model setup and standardization

Three main approaches were used to evaluate the offspring size model. First, the true distribution of the number of days of starvation experienced by larvae of any given fish population is unknown, but recruitment variability is often assumed to be in the vicinity of CV = 0.5 (e.g. Sampson et al. 2007). To evaluate the role of an offspring size effect in determining recruitment variability in the absence of fishing we found a value for the mean number of days of starvation, μ_d, that resulted in recruitment variability of CV = 0.5 for an offspring size model. The same mean number of days of starvation, μ_d, was applied to the control model for a population in an unfished state to assess the magnitude of additional recruitment variability that would occur in the absence of the offspring size effect.

Second, as for the spawning window model, to evaluate the influence of fishing on the magnitude of recruitment variability and to allow for comparison of results between the offspring size and spawning window models, we standardized both offspring size and control models such that recruitment variability was CV = 0.5 in the absence of fishing by changing the mean number of days of starvation, μ_d.

Third, initial runs of the offspring size model showed that reproductive rate (steepness) is reduced by an offspring size effect. In a typical age-structured model, the reproductive rate that is specified as a model input is also the average reproductive rate that results from model runs. The input parameter for reproductive rate, *h*, is not steepness by definition in the offspring size model; when spawning stock biomass is 20% of unfished spawning stock biomass, the proportion of recruits that occur is less than *h* of the unfished number of recruits. That is (omitting the subscript *j* for simplicity),

$\frac{R}{R_0} \neq h$ when $\frac{B}{B_0} = 0.2$. Hence, a comparison of an offspring size model and a corresponding control model with the same values specified for reproductive rate parameter *h* is a comparison of stocks with different reproductive rates. Although this is an interesting theoretical feature of this model (an offspring size effect may be a factor that contributes to the reproductive rate that we observe for a stock), we are interested in comparing stocks with the same reproductive rates, with and without an offspring size effect. Therefore, in the third approach we introduce the parameter *z*, which is the reproductive rate (steepness) in the offspring size model and we find the value of *h* (which determines the reproductive rate, but is not the reproductive rate itself) for which *z*, the actual reproductive rate (steepness), is equal to 0.6. Mathematically, for typical age structured models and in the spawning window model $\frac{R}{R_0} = z = h$ when $\frac{B}{B_0} = 0.2$. For the offspring size model, we numerically found the value of *h* such that $\frac{R}{R_0} = z$ when $\frac{B}{B_0} = 0.2$ for a given mean number of days of starvation, μ_d. The process of standardizing the reproductive rate was nested within the aforementioned standardization of the mean number of days of starvation (such that recruitment variability was equal to CV = 0.5) because the mean number of days of starvation influences the extent to which the input measure for reproductive rate, *h*, differs from the resulting reproductive rate. For each trial combination of the mean number of days of starvation and the input measure for reproductive rate, (μ_d & *h*), we found the survival multiplier (ϕ), as mentioned previously, so that the average recruitment for an unfished population was equal to the value for the number of recruits in an unfished population that was specified as a model input, R_0.

Management Scenarios (both models)

Two management scenarios were evaluated for each biological scenario: a constant *F* strategy with logistic selectivity and a constant *F* strategy with a no-take marine reserve covering 20% of the area with logistic selectivity in the fished area and where the *F* was applied to biomass in the fished area. Choice of spawning window was based only on fish age or stage and was independent of whether a fish occurred within a marine reserve or fished area. Values for fishing mortality (*F*) ranging from 0 to 0.2yr^{-1} were simulated for each management scenario. For each management scenario, the population was initialized at an equilibrium corresponding to that scenario and a value for *F*. Outcomes of a no-take marine reserve are expected to change with fish movement dynamics. Therefore, the management scenario that included a marine reserve was always conducted for a sedentary population with no larval and adult movement as well as for a population with extensive larval movement. Larval movement occurred after density-dependent mortality (Appendix S1). The outcome of the management scenarios without no-take marine reserves does not depend on larval movement patterns and therefore were only simulated for a sedentary population.

Performance Measures (both models)

The following metrics were used to measure differences in performance of models with and without a spawning window or offspring size effect and to compare the offspring size model to the spawning window model for scenarios with constant F policies: (1) average inter-annual variability in recruitment (referred to as “recruitment variability” throughout the manuscript). Average inter-annual variation was calculated by measuring the inter-annual CV (standard deviation/mean) over 100 years beginning after a 100 year burn-in period and averaged over 500 simulations for each fishing mortality rate and (2) the distribution of catches at each fishing mortality rate, including catches from the 100 years after the burn-in period and over the 500 simulations.

To compare the efficacy of constant F policies with and without a marine reserve covering 20% of the area we evaluated the following metrics over a range of exploitation rates (catch/total biomass where total biomass includes biomass within marine reserves): (1) average inter-annual variability in recruitment (as described above), (2) the probability of the spawning stock biomass falling below 20% of unfished spawning stock biomass, and (3) the long-term (cumulative) catch averaged over simulations.

Results

The structure of the results section is as follows. First, we show that a portfolio effect exists for both the spawning window and offspring size models in the absence of fishing whereby recruitment variability is lower with an offspring size or spawning window effect than without such an effect. Next, we discuss the effects of fishing on recruitment and catch variability for the spawning window model and then for the offspring size model and show the effect of the offspring size model on reproductive rate. Lastly, we show the performance metrics for constant *F* policies with and without a marine reserve for a sedentary population and a population with high larval movement rates.

Existence of a portfolio effect for populations in an unfished state

As expected, both of the potential mechanisms (age-specific spawning windows and variation in offspring size by age) lead to a portfolio effect, exhibiting lower recruitment variability than for control models without these mechanisms for populations in an unfished state (Figure 3). More specifically, Figure 3a shows that the spawning window model ($\rho = 0$) results in inter-annual recruitment variability in the absence of fishing mortality that is 55% lower than a model with only one spawning window ($\rho = 1$) when both models simulate the same level of environmental variability (σ_R). Likewise, Figure 3b shows that the offspring size model exhibits recruitment variability that is 65% lower than for a control model in the absence of fishing mortality when both the offspring size and control models simulate the same mean number of days of starvation (μ_d).The magnitude of variability shown in Figure 3a is not comparable to that in Figure 3b; the total amount of recruiment variation for the offspring size effect model originates from the mean number of days of starvation (μ_d), as well as σ_R, while the magnitude of recruitment variation for the offspring size model originates from a combination of ρ and σ_R.

Effects of fishing on the spawning window portfolio effect

Figure 4 shows the influence of fishing mortality on recruitment variability where the recruitment variability was standardized to be CV = 0.5 for the spawning window and corresponding control models for populations in an unfished state. Recruitment variability increases as a function of increasing fishing mortality for the spawning window model, while it remains constant for all fishing mortality and spawning stock biomass levels in the control models for both the age- and stage-specific spawning window models when environmental variation occurs after density-dependent mortality (Figure 4a & b). Recruitment variability also increases as a function of increasing fishing mortality and decreasing spawning stock size when environmental variation occurs before density-dependent mortality (Figure 4c & d), but the increase in the recruitment variability due to the declining influence of density-dependent mortality on offspring at lower spawning stock sizes (which applies to the spawning window and control models alike) is much greater in magnitude than the influence of age- or stage-specific spawning windows (Figure 4c & d).

Effects of fishing on the offspring size portfolio effect

Variation in offspring size by maternal age results in lower reproductive rates at intermediate spawning stock sizes (steepness is approximately 16% lower) than for a corresponding control model for all offspring size model scenarios (a “mean effect;” e.g. Figure 5a). This means that the input parameter for the reproductive rate, which is measured as steepness in a typical age-structured model (e.g. Figure 5a, black line), is no longer the reproductive rate for the fish stock (Figure 5a, solid red line). Figure 5b shows that the stock-recruit relationship is nearly identical in shape and magnitude at each stock size to a typical, deterministic Beverton-Holt stock-recruit curve with no offspring size effect when the reproductive rate (steepness) is standardized. Therefore, the mean effect caused by the offspring size model can be completely removed by standardizing the reproductive rate such that it is the same as for a control model. With the mean effect removed, other performance metrics can be compared between offspring size and control models.

Recruitment variability increases as a function of increasing fishing mortality rates for scenarios with Berkeley, linear, and exponential relationships between maternal age and time to 50% mortality and when the offspring size effect occurred after density-dependent mortality (Figure 6a-c). The increases in recruitment variability with increases in fishing mortality are least pronounced when the Berkeley relationship is applied (Figure 6a) and largest when the exponential relationship is used (Figure 6c). Figure 6d-6f confirm that the mean stock recruit curves for each of the offspring size model scenarios is nearly identical to the deterministic Beverton-Holt stock recruit curve after the reproductive rates are standardized to match that of the deterministic Beverton-Holt curve.

Simulations where environmental variation occurred prior to density-dependent mortality for the offspring size models required the mean number of days of starvation to be greater than or equal to 119 days to achieve recruitment variability of CV = 0.5 for an unfished stock. These scenarios were not explored further because it is unrealistic to assume that the mean number of days of starvation endured by larvae is 119 or more days (Berkeley et al. 2004a, Sogard et al. 2008).

How do portfolio effects influence variation in catch?

Variability in catch is higher for the stage-specific spawning window and offspring size models than for the corresponding control models (Figure 7). However, the increase in variability is mostly due to spikes in catches, rather than extremely low catches, as indicated by the long upper tails of the distributions of catch at each fishing mortality level for the spawning window and offspring size model in Figure 7 (relative to the control models). In contrast, the lower tails of the distributions are similar for spawning window and offspring size effect and control models (Figure 7). The largest catches for the spawning window model (Figure 7a) are approximately double the size of the largest catches for the offspring size model (7b) for intermediate fishing mortality rates (e.g. $F = 0.1\text{yr}^{-1}$).

Comparing the constant F policy with no marine reserve to the constant F policy with a marine reserve

Recruitment variability increases with increasing fishing mortality rates up to an F of 0.15yr^{-1} and then decreases for higher Fs for a population with sedentary larvae and adults influenced by a spawning window or offspring size effect (Figure 8b & e). This result occurs because, as the population outside the marine reserve is fished to extinction, the total population resides within the marine reserve and has the age structure of an unfished population. Therefore the recruitment variability returns to a CV of 0.5, the magnitude of the recruitment variability for an unfished population.

A similar effect occurs for populations with highly mobile larvae, but extinction in the fished area occurs at a higher fishing mortality rate than for the scenario with a marine reserve and sedentary larvae (Figure 8c & f); likewise a flow of larvae from the marine reserve means that the fishing mortality associated with maximum sustainable yield in the fished area is slightly higher (by 0.02yr^{-1}) than for the scenario with a marine reserve and sedentary larvae (Figure 8b & c). Increases in recruitment variability at very low fishing mortality rates are similar for both marine reserve and non-marine reserve management scenarios for both the spawning window and offspring size models (Figure 8c & f), while recruitment variability continues to increase at high *F*s in the absence of a marine reserve for both the spawning window and offspring size models.

Results for the spawning window model were very similar to those for the offspring size model in comparisons of the constant *F* policy with no marine reserve to that with a marine reserve. The constant *F* policy with no marine reserve produced the highest cumulative catch; the marine reserve policy applied to a population with highly mobile larvae could produce up to 90% of the highest cumulative catch, while a marine reserve policy applied to a population with sedentary larvae could produce 80% of the highest cumulative catch (Figure 9a & d). In the case of the population with sedentary larvae managed with a marine reserve, cumulative catch and exploitation rate become very low as *F* becomes high because the biomass in the fished area (and thus available to the fishery) is very low when *F* is high and is not supplemented by fish moving from the marine reserve to the fished area; total biomass remains stable due to the biomass within the marine reserve (Figures 9a & d, black dashed line).

The probability of spawning stock biomass falling below 20% of unfished spawning stock biomass increases at lower exploitation rates for the marine reserve policy applied to both populations with sedentary and highly mobile larvae than for the constant *F* policy with no marine reserve. Recruitment variability increases as a function of exploitation rate as is nearly identical for the marine reserve and constant *F* with no marine reserve policies (Figure 9c & f); one exception is that recruitment variability is higher when *F* is very high and exploitation rates are low (a signal that population is nearly extinct outside of the marine reserve) when a marine reserve is applied to a population with sedentary larvae for the offspring size model (Figure 9f, black dashed line).

Discussion

General main points applying to both models

Both the spawning window and offspring size mechanisms acted as portfolio effects for all biological scenarios (the age-specific, stage-specific spawning window models and the Berkeley, linear, and exponential relationships for the offspring size model), reducing recruitment variability relative to control models substantially (by 55-65%) for populations that were unfished (Figure 3). In the case of the spawning window models, offspring from mothers of different ages spawn in different windows (times or sites) such that a year with poor environmental conditions (or particularly good environmental conditions) for all offspring is rare. In the case of the offspring size model, older mothers produce offspring that are able to survive more days of starvation and therefore environmental conditions must be poor for longer time periods to result in a recruitment failure than if all offspring had equal abilities to survive starvation. Fishing eroded the portfolio effects for both mechanisms that were modeled such that recruitment variability increased with increased fishing mortality levels by 20-40% at F_{MSY} and recruitment followed the environmental signal more closely at low stock sizes for all biological scenarios (e.g. Figures 4 & 6). As fishing mortality rates increased, fewer older mothers remained in the population and therefore the spawning window and offspring size effect were less pronounced, increasing both recruitment variability and subsequently increasing variability in catch.

While the spawning window portfolio effect was large relative to larval survival, the effect was small as compared to the influence of density-dependent mortality when density-dependent mortality occurred during post-larval stages (after environmental variation). This finding corroborates results from Minto et al. (2008) showing that increases in recruitment variability at low stock sizes can be explained by a release from density-dependent mortality. However, Minto et al. (2008) did not consider alternative mechanisms that could contribute to increased recruitment variability at low stock sizes, such as the portfolio effects investigated in this paper. The influence of a spawning window or offspring size effect on recruitment variability would be confounded with effects of density-dependent mortality in data. Whether density-dependent mortality occurs primarily at an early larval stage, or early or late in the juvenile stage (such as time of settlement) and how much environmental variation occurs before versus after density-dependent mortality is an open area of research (e.g. Myers and Cadigan 1993a, b, Wiedenmann and Essington 2006). For the offspring size model, parameterization of the mean number of days of starvation for a scenario with environmental variation occurring before density-dependent mortality was unrealistic ($\mu_d = 119$ days or more). When environmental variation occurs prior to density-dependent mortality, density-dependent mortality acts on the larvae that survive starvation in a given year, rather than spawning stock biomass. The number of larvae that survive environmental variation in a year with favorable environmental conditions can be much greater than the deterministic number of larvae produced at unfished biomass. However, at this magnitude of larvae, there is an asymptote in the Beverton-Holt stock-recruit curve such that a very high number of larvae still translate into the survival of R_0 recruits (the deterministic number of recruits in the absence of fishing). This means that all of the recruitment variation comes from negative deviations in environmental conditions and the average number of days of starvation (which determines the amount of recruitment variability in the offspring size model) required to maintain negative deviations such that recruitment variability is equal to CV = 0.5 is very high. Therefore, it is either unrealistic that all of the environmental variation comes from the number of days of starvation endured by offspring and/or it is unrealistic that all of the environmental variation occurs before density-dependent mortality.

General conclusions about marine reserve policies vs a constant F policy with no marine reserve for populations with spawning window or offspring size effects

A marine reserve policy was found to perform worse than or equal to a constant *F* policy with no marine reserve for both portfolio effects (populations with an offspring size or spawning window effect) for all of the sustainability metrics that were explored. The constant *F* policy with no marine reserve produced cumulative catches that were larger than or equal to those for the marine reserve policy (for populations with sedentary and highly mobile larvae) at all exploitation rates. In addition, the probability of spawning stock biomass falling below 20% of unfished spawning stock biomass is equivalent among policies or lowest for the constant F policy with no marine reserve at all. Lastly, recruitment variability was a monotonically increasing function of exploitation rate without a marine reserve and with a marine reserve recruitment variability increased with increasing fishing mortality rates except in the case of fishing mortality rates that were well above F_{MSY}. For both the spawning window and offspring size models, the population outside the marine reserve was at very low biomass at high values of F and the recruitment variability began to return to levels for an unfished population, reflecting the unfished state inside the marine reserve. In the most extreme case a marine reserve was applied to a population with sedentary larvae where the sub-population in the fished area was almost extinct.

The results for cumulative catch are not new; previous studies have also found that potential long-term catches are higher with conventional regulations than with a marine reserve when adults are sedentary and with or without larval movement (Gerber et al. 2005, Hilborn et al. 2006, McGilliard and Hilborn 2008). An exception to this conclusion is when larval dispersal occurs before density dependent mortality and density dependent mortality occurs locally (Ralston and O'Farrell 2008, McGilliard and Hilborn 2008). A wealth of previous marine reserve modeling efforts explore a variety of assumptions about fishing fleet behavior, economics, marine reserve size, number, and spacing, and the details of larval or adult movement, among other topics, and some of these assumptions impact the influence of marine reserves on cumulative catch (e.g. Botsford et al. 2001, Hart 2006, Hart and Sissenwine 2009, Moffitt et al. 2009). This manuscript addresses only whether there is a particular benefit of marine reserves for sustainability due to age-related portfolio effects.

Spawning window model conclusions

Results for the age-specific spawning window model show that the magnitude of increase in recruitment variability at fishing mortality rates at or below F_{MSY} is small (approximately 0.1 or less; Figure 4) and never increases more than 0.15, even at very high *F*s. Figure 1b shows that although spawners are spread evenly over the spawning windows, offspring are aggregated in windows 2-5, a minority of the spawning windows. Although the older fish spawn in different windows than younger fish and have higher fecundity than younger fish, there are not many of them and most of the offspring still come from younger spawners. The stage-specific spawning window model maximizes the portfolio effect by spreading offspring evenly among spawning windows and shows a substantial increase in recruitment variability at high fishing mortality rates when density-dependent mortality occurs before environmental variation.

Offspring size model conclusions

The offspring size model displayed a small decrease in the population reproductive rate as was reported in several previous studies on maternal age effects (Spencer et al. 2007, 2013, Lucero 2008). However, this study shows that for a density-independent offspring size effect the change in reproductive rate can be taken into account by changing the input parameter for reproductive rate (*h*, which is not steepness in the offspring size model) so as to compare the offspring size model to a control model with the same resulting mean stock-recruit curve and the same reproductive rate (steepness; Figure 4). Without standardizing the reproductive rate it would not be possible to compare the results of the offspring size model to a control model – this would be a comparison to two stocks or species with fundamentally different mean reproductive rates. Observations of fish stocks and estimates of reproductive rates inherently account for any mean effect caused by an offspring size effect –fish stocks are never observed prior to the occurrence of a mean offspring size effect and hence the mean effect of the offspring size model is already taken into account when estimating the reproductive rate within a stock assessment with typical assumptions about recruitment. Spencer and Dorn (2013) and Shelton et al. (2012) fit models with and without a maternal age effect to data (Spencer et al. 2013b) or time-series of recruits and spawners estimated by a stock assessment (Shelton et al. 2012). Spencer et al. (2013b) estimated a slightly different stock-recruit curve in models with maternal age effects than without maternal age effects. Some models from Shelton et al. (2012) with maternal age effects better explained the time series of recruits and spawners than models without maternal age effects. However, both studies included models with a density-dependent maternal age effect, which was not explored in our study.

The offspring size effect influences recruitment variability even after the reproductive rate has been standardized (Figure 6, a-c). Typical assessments for U.S. West Coast rockfish species are age-structured models with a specified (or occasionally estimated) value for recruitment variation which is not assumed to vary as a function of stock size. Mis-specifying the recruitment variation can lead to substantial bias in biomass and steepness estimates (Methot and Taylor 2011). Future studies could explore the impacts of specifying or estimating a constant value for recruitment variability for a stock where recruitment variability varies as a function of stock size.

Assumptions and potential future studies

As with any modeling effort, the offspring size and spawning window models were based on some assumptions that may not be realistic. The offspring size model that uses an exponential relationship between maternal age and offspring size is an extreme scenario because offspring from the oldest mothers can survive unrealistically long starvation periods (Figure 2d). This case must be interpreted as an extreme upper bound on the potential influence of an offspring size effect. There is a large age range (age 18+ that is outside of the range of the data. The three relationships between maternal age and time to 50% mortality that were modeled were intended to explore the upper and lower bounds of the potential influence of an offspring size effect; the exponential relationship provides an effective upper bound. Likewise, the Berkeley relationship can be interpreted as a lower bound on the potential influence of an offspring size effect. The Berkeley relationship assumes that offspring size (and hence time to 50% mortality) stops increasing for offspring born to mothers older than approximately age 18.

Future studies could explore the magnitude of age-related portfolio effects when environmental conditions are temporally autocorrelated. Additionally, inter-annual temporal autocorrelation in recruitment is observed for many marine fish species; future analyses could explore the interplay between age-related portfolio effects and inter-annual temporal autocorrelation.

The possibility that older spawners may utilize a larger range of spawning windows than younger individuals could be explored as an extension to the spawning window model. The offspring size model assumed an arbitrary value for the slope of the logistic curve relating the number of days of starvation to the proportion of offspring that survive. In the offspring size model, the mean number of days of starvation was changed to standardize the CV of recruits for an unfished population. Alternatively, the mean could be held constant and the variation of the number of days of starvation could be adjusted to standardize the CV of recruits. Future analyses could explore the potential importance of these factors.

Other portfolio effects that are not age-related could be occurring. For instance, evidence exists that rockfish populations may utilize multiple habitats or spawning windows, but this may be genetic and unrelated to age (Hauser and Carvalho 2008, Palof et al. 2011). Heterogeneity in reproductive success could, in part, be driven by the length distribution (rather than the age distribution) of the population. Several studies have found evidence of multiple genetic sub–populations of rockfish over their geographic range (Withler et al. 2001, Buonaccorsi et al. 2002). Future modeling studies could evaluate the relative influence of these portfolio effects on overall recruitment variability and associated implications for management.

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Supporting Information

Additional supporting information may be found in the online version of this article at http://onlinelibrary.wiley.com/doi/10.1002/eap.xxxx/suppinfo

Data Availability

Data available from the GitHub Data Repository: https://zenodo.org/badge/latestdoi/94338492

Tables

Table 1. Recruitment equations for the spawning window model

Type of recruitment	Equations
Local density-dependent mortality followed by	T.1 $B^{\mathrm{E}}_{i,j,t} = 0.5\sum_{a} N_{a,j,t}P_{a,i}O_{a}w_{a}$

environmental variation	T.2 $R'_{i,j,t+1} = R_{i,j,0} \frac{4h\left(B^{E}_{i,j,t} \middle/ B^{E}_{i,j,0}\right)}{(1-h)+(5h-1)\left(B^{E}_{i,j,t} \middle/ B^{E}_{i,j,0}\right)} \exp(\eta_{i,t} - \sigma^2_R/2)$
Global density-dependent mortality followed by environmental variation	T.3 $R''_{j,t+1} = R_{j,0} \frac{4h\left(B^{E}_{j,t} \middle/ B^{E}_{j,0}\right)}{(1-h)+(5h-1)\left(B^{E}_{j,t} \middle/ B^{E}_{j,0}\right)}$ T.4 $\Omega_{i,j,t} = \frac{\sum_{a=1}^{a_{\max}} N_{a,j,t} P_{a,i} O_a w_a}{\sum_{a=1}^{a_{\max}} N_{a,j,t} O_a w_a}$ T.5 $R'_{i,j,t+1} = \Omega_{i,j,t} R''_{j,t+1} \exp(\eta_{i,t} - \sigma^2_R/2)$
Environmental variation followed by global density-dependent mortality	T.6 $E_{i,j,t} = 0.5 \sum_a N_{a,j,t} P_{a,i} O_a w_a \exp(\eta_{i,t} - \sigma^2_R/2)$ T.7 $E_{j,t} = \sum_i E_{i,j,t}$ T.8 $R'_{j,t} = R_{j,0} \frac{4h(E_{j,t} / B^{E}_{j,0})}{(1-h)+(5h-1)(E_{j,t} / B^{E}_{j,0})}$
Environmental variation then local density-dependent mortality	T.9 $R'_{i,j,t} = \frac{4h(E_{i,j,t} / B^{E}_{i,j,0})}{(1-h)+(5h-1)(E_{i,j,t} / B^{E}_{i,j,0})}$

Figure legends

Figure 1. Distribution of spawners over spawning windows by age (a & c) and the resulting distribution of offspring over spawning windows (b & d) for the spawning window models. Graphs a & b show age-specific distribution of spawners over spawning windows and graphs c & d show stage-specific distribution of spawners over spawning windows.

Figure 2. Panel (a) shows time to 50% mortality ($D_{50,a}$) for maternal age *a* in the offspring-size model. Dots are data from Berkeley et al. (2004a) and lines are three models fit to the data used as hypotheses about the relationship between maternal age and $D_{50,a}$: a model fit by Berkeley et al. (2004a; black line), a linear model (blue line), and an exponential model (red line). Panels b – d show survival over a range of number of days of starvation resulting from use of the Berkeley (b), the linear (c), and the exponential (d) relationship for a range of maternal ages (lines).

Figure 3. Recruitment relative to R_0 for a sample simulation for (a) the age-specific spawning window model with simulated environmental variability of $\sigma_R = 0.5$ and (b) the offspring size model with an exponential relationship between maternal age and time to 50% mortality of offspring; mean number of days of starvation, μ_d, is that which results in output recruitment variability of CV = 0.5 for a scenario with an offspring size effect. Control scenarios are shown in grey and offspring size and spawning window effects (the portfolio effects) are shown in black.

Figure 4. Recruitment variability (CV; y-axis) as a function of fishing mortality (x-axis) for the spawning window model with density-dependent mortality occurring before environmental variation (a & b) and after environmental variation (c & d); (a & c) show an age-specific distribution of offspring across spawning windows, (b & d) show a stage-specific distribution of offspring across spawning windows. Control scenarios ($\rho = 1$) are solid black lines and spawning window models are grey dotted lines ($\rho = 0$).

Figure 5. The relationship between spawning stock biomass relative to unfished spawning stock biomass and recruits for the offspring size model with a linear relationship between maternal age and time to 50% mortality for (a) an input reproductive rate of $h = 0.6$ and (b) an input reproductive rate (h) standardized such that output reproductive rate (steepness) is equal to $z = 0.6$. Data points are indicated with grey dots, mean stock-recruit relationship (red solid line), and 90% intervals (red dashed lines). The black line

shows a deterministic Beverton-holt stock-recruit curve with steepness equal to 0.6 and the number of recruits corresponding to unfished biomass (R_0) equal to that used for the offspring size model.

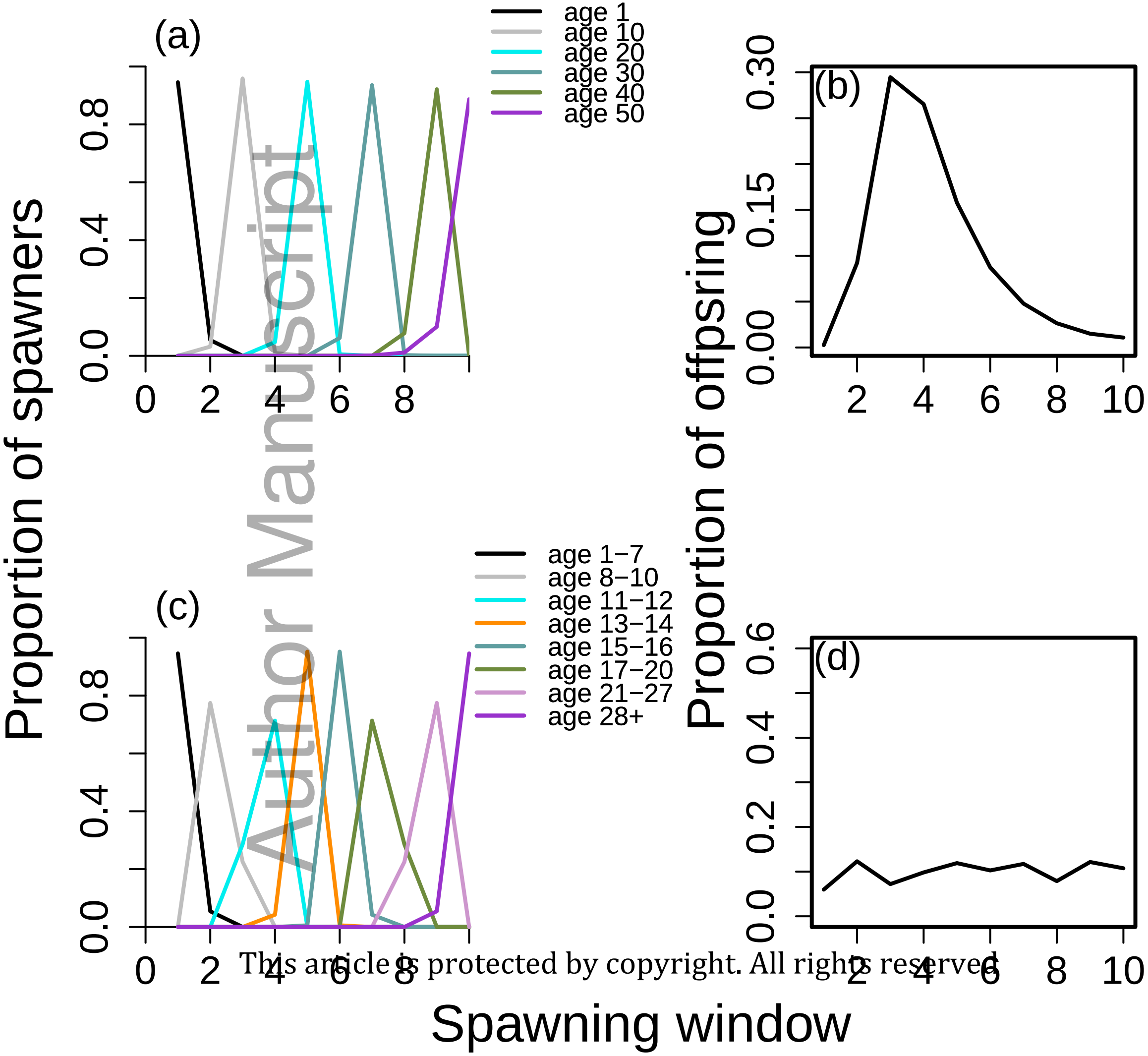
Figure 6. Recruitment variability (CV) over a range of fishing mortality rates and depletion levels (B/B_0 shaded in grayscale; a-c) for offspring size models and corresponding control models with reproductive rate standardized (steepness is equal to 0.6). F_{MSY} is shown for the offspring size model (*) and for the corresponding control model (o). Graphs d-f show the relationship between spawning stock biomass relative to unfished spawning stock biomass and recruitment with data points (grey dots), mean stock-recruit relationship (red solid line), and 90% intervals (red dashed line). The black line shows the deterministic Beverton-holt stock-recruit curve with the same reproductive rate (steepness) and R_0 as for the stochastic simulations with reproductive rate (steepness) standardized. Offspring size model with a Berkeley (a & d), linear (b & e), and exponential (c & f) relationship between maternal age and time to 50% mortality.

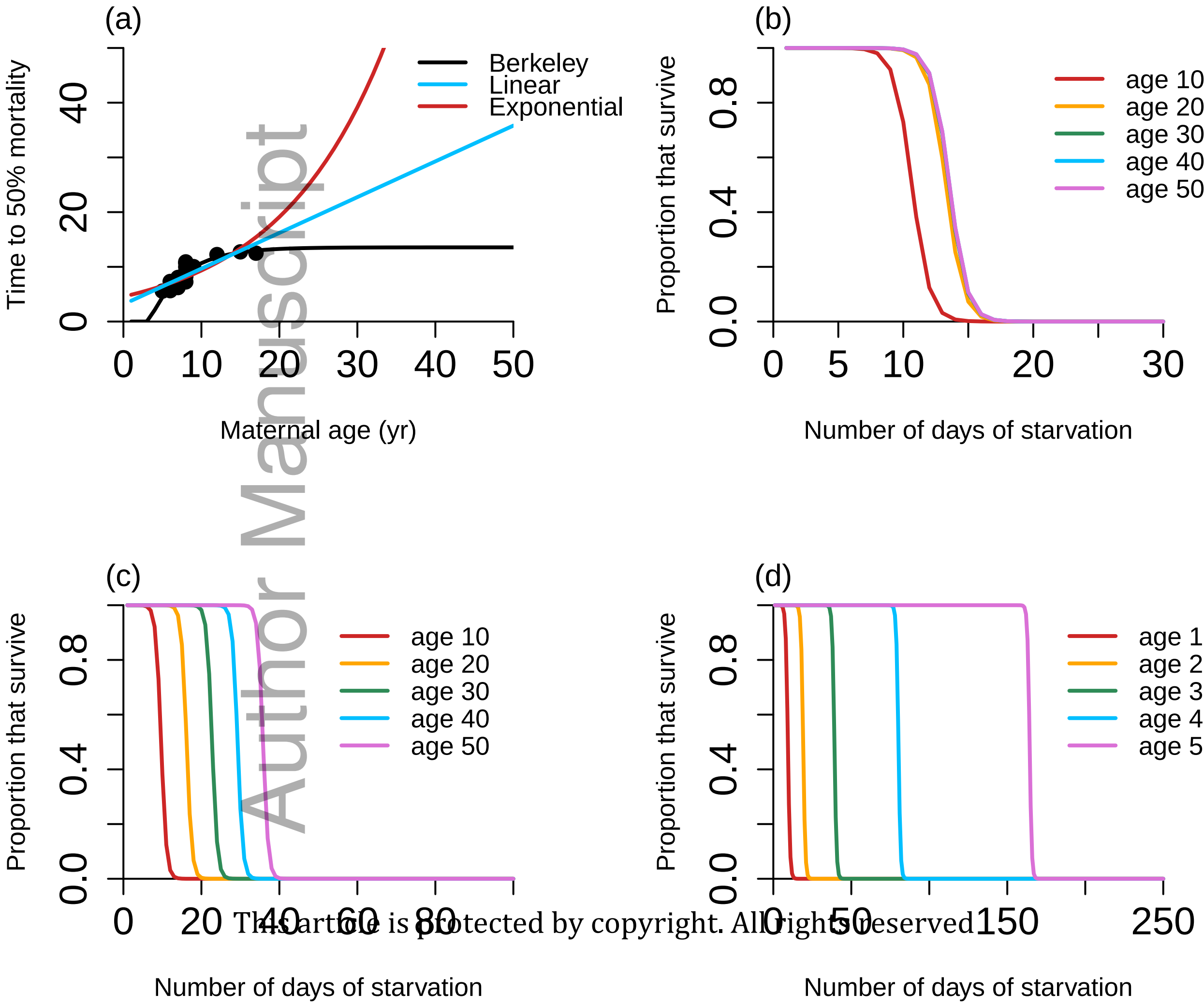
Figure 7. Distribution of catch over a range of fishing mortality rates (F) for the stage-specific spawning window model (a) and the offspring size model with steepness standardized and a linear relationship between the maternal age and time to 50% mortality (b). Distribution of catch for the spawning window and offspring size models are shown in pink and face to the right and the corresponding control models are in black and face to the left.

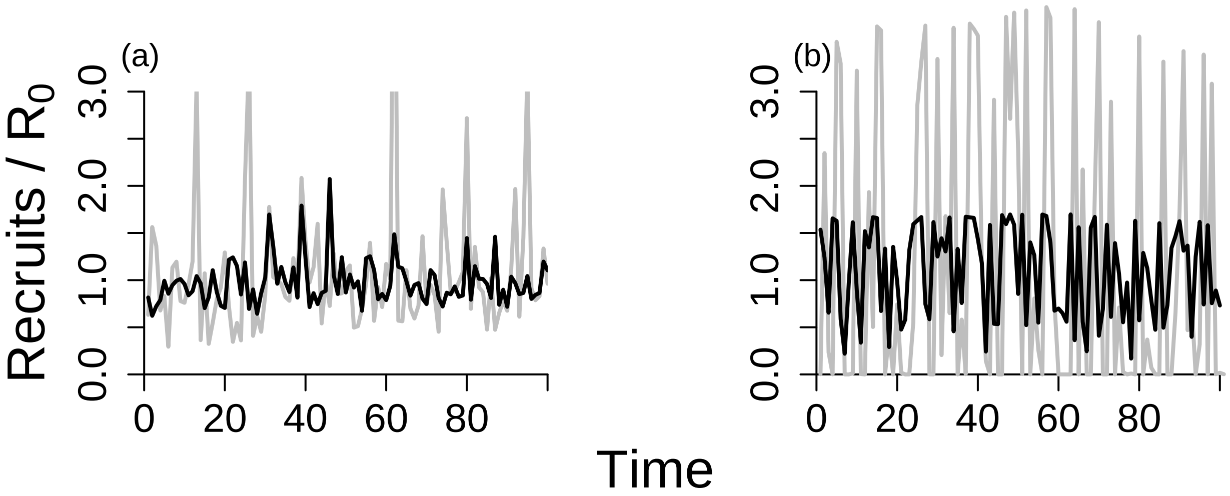
Figure 8. Recruitment variability (CV) over a range of fishing mortality rates (*F*) for a management scenario with no marine reserve (a &d), a marine reserve covering 20% of the area applied to (1) a population with sedentary larvae and adults (b & e), and (2) a population with a high larval movement rate and sedentary adults (c & f). Panels a-c show an age-specific spawning window model (grey dashed lines) with corresponding control models (black solid lines). Panels d-f show offspring size models with standardized steepness and a linear relationship between maternal age and time to 50%

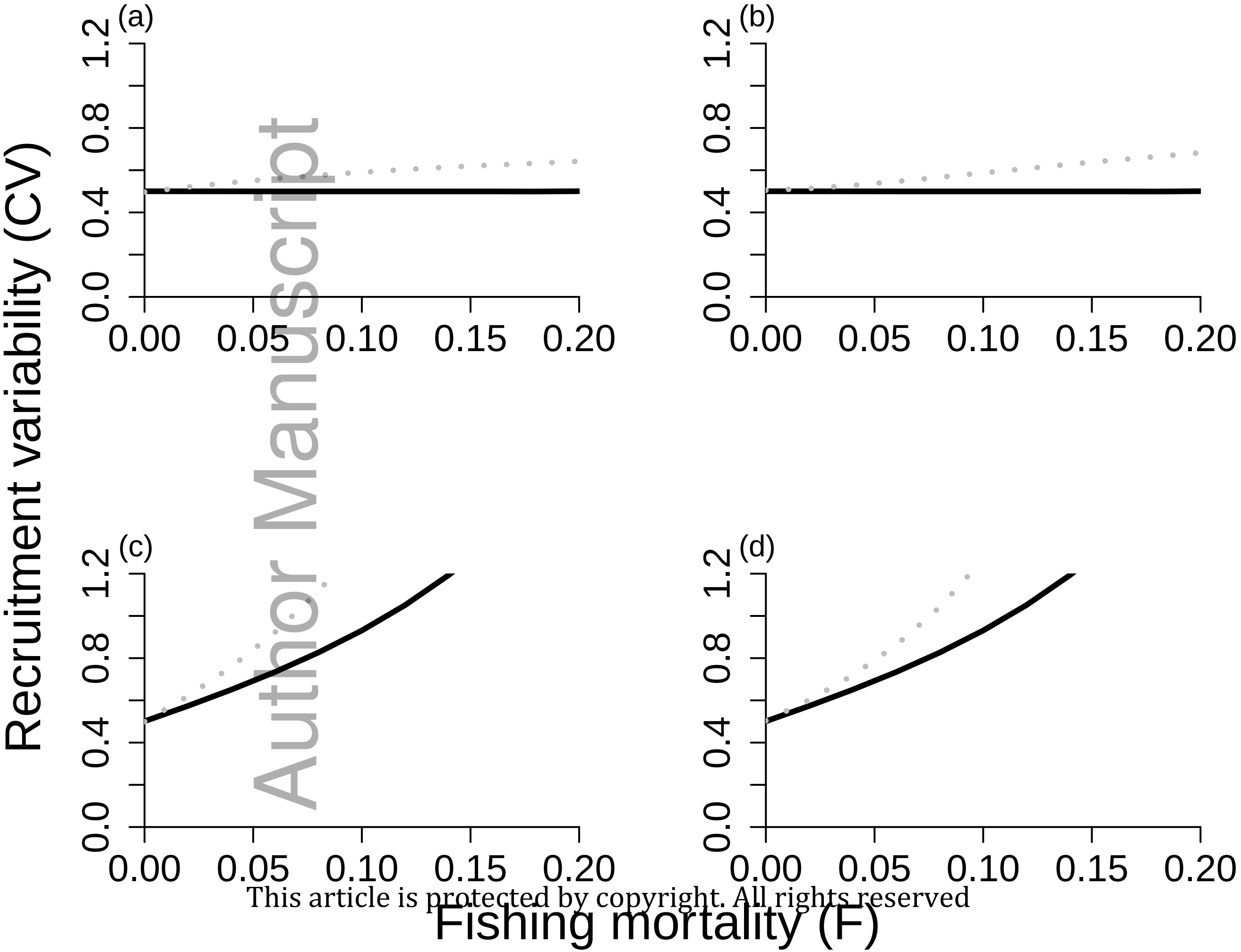
mortality of offspring. F_{MSY} is shown for the offspring size model (*) and for the corresponding control model (o).

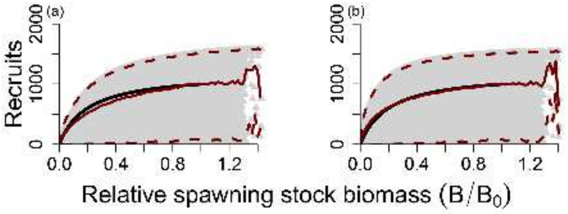
Figure 9. Relative cumulative catch (a & d), probability of spawning stock biomass falling below 20% of unfished spawning stock biomass (b & e), and recruitment variability (c & f) over a range of exploitation rates (catch/total biomass) for the spawning window model (a-c) and the offspring size model (d-f). Solid black lines represent a constant F policy with no marine reserve, dashed black lines indicate a marine reserve applied to a sedentary fish stock, dotted grey lines indicate a marine reserve applied to a fish stock with long larval dispersal rates. Lines are drawn over a range of fishing mortality rates (*F*s), starting at $F = 0$ to $F = 0.4$ (indicated with an asterisk).


(a)
age 1
age 10
age 20
age 30
age 40
age 50
(b)
0.00
0.15
0.30
2
4
6
8
10
(c)
age 1−7
age 8−10
age 11−12
age 13−14
age 15−16
age 17−20
age 21−27
age 28+
(d)
0.0
0.2
0.4
0.6
0.0
0.4
0.8
0
2
4
6
8
Proportion of spawners
Proportion of offpsring
Spawning window


(a)
Time to 50% mortality
0
20
40
0
10
20
30
40
50
Maternal age (yr)
Berkeley
Linear
Exponential
(b)
Proportion that survive
0.0
0.4
0.8
0
5
10
20
30
Number of days of starvation
age 10
age 20
age 30
age 40
age 50
(c)
Proportion that survive
0.0
0.4
0.8
0
20
40
60
80
Number of days of starvation
age 10
age 20
age 30
age 40
age 50
(d)
Proportion that survive
0.0
0.4
0.8
0
50
150
250
Number of days of starvation
age 10
age 20
age 30
age 40
age 50


(a)
(b)
Recruits / R_0
0.0
1.0
2.0
3.0
0
20
40
60
80
Time


(a)
(b)
(c)
(d)
1.2
0.8
0.4
0.0
0.00
0.05
0.10
0.15
0.20
Recruitment variability (CV)
Fishing mortality (F)



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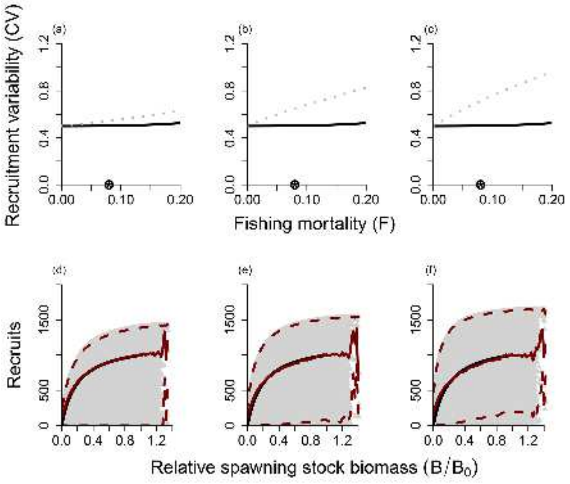

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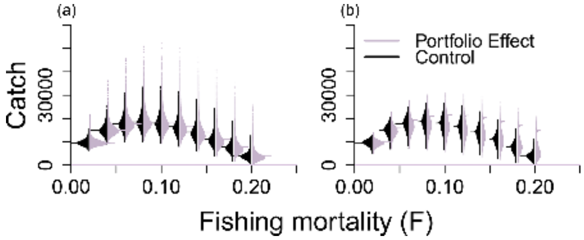

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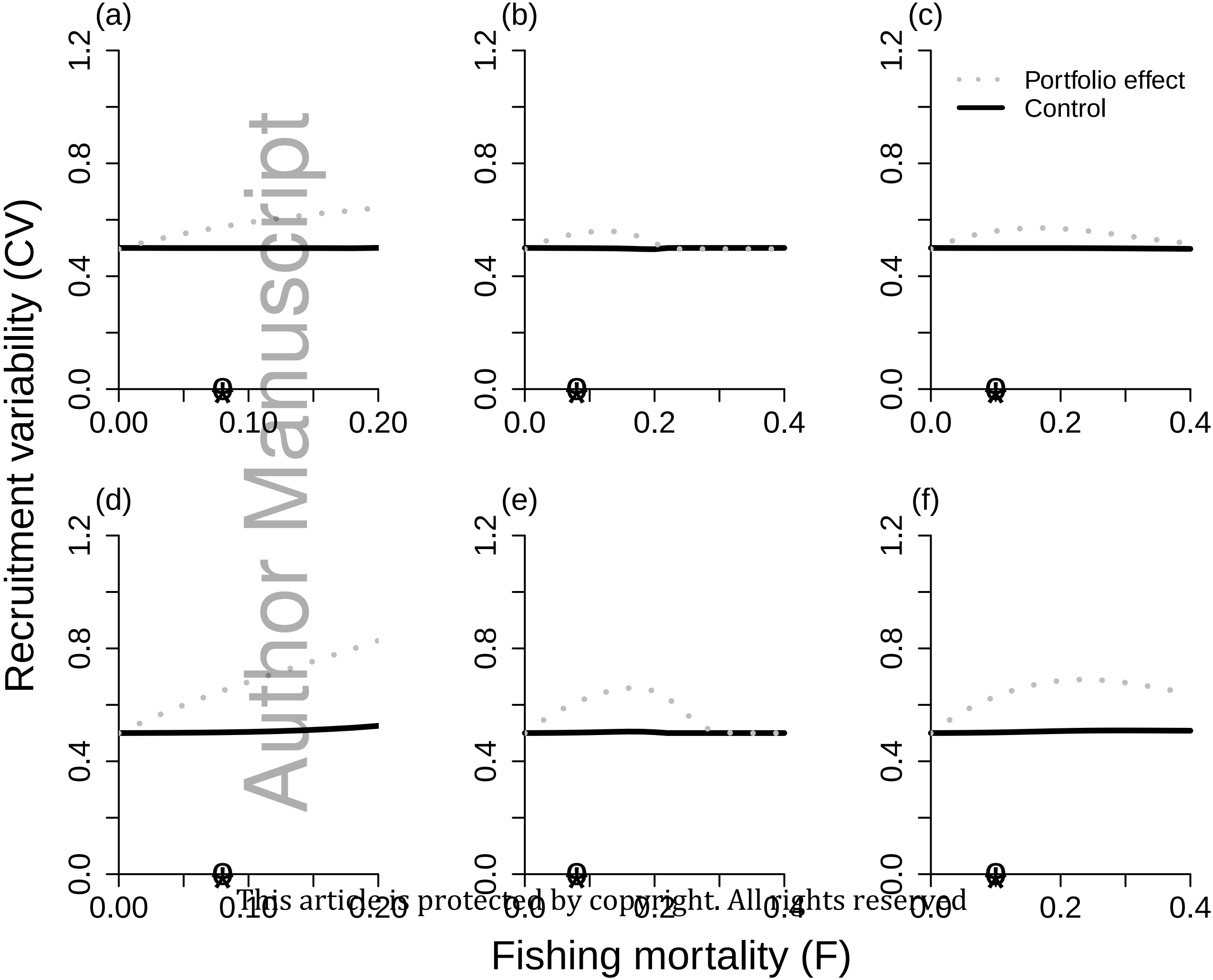

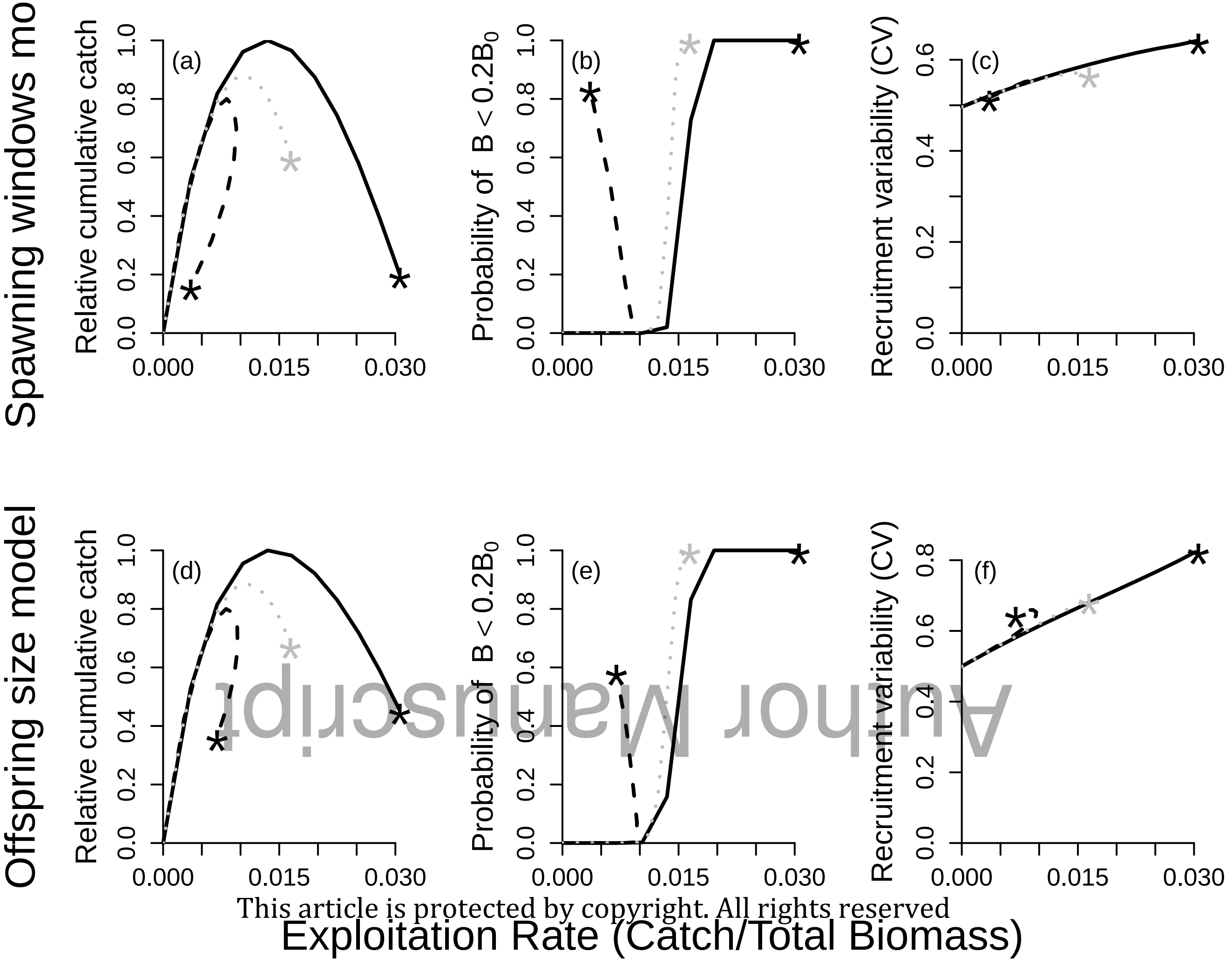
Spawning windows model
Offspring size model
Relative cumulative catch
Probability of $B < 0.2B_0$
Recruitment variability (CV)
(a)
(b)
(c)
(d)
(e)
(f)
0.0
0.2
0.4
0.6
0.8
1.0
0.000
0.015
0.030
Exploitation Rate (Catch/Total Biomass)