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Utility and implications of no-take marine reserves in fishery management strategies

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Abstract

Utility and implications of no-take marine reserves in fishery management strategies

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This work explores (1) the potential for using marine reserves to manage data-poor fish populations, (2) the potential for marine reserves to influence the performance of commonly used stock assessment approaches relative to alternative approaches that explicitly account for a marine reserve, and (3) hypotheses about the role of older females to population persistence and arguments that marine reserves are needed to maintain this role.

In Chapter 1, the potential use of the ratio of the density of fish outside a marine reserve to that inside the reserve in a fishery management control rule (DRCR) is evaluated by Management Strategy Evaluation. The cumulative catch under the optimal DRCR was 90% of the cumulative catch from an optimal constant effort rule (CER). A small range of parameter values for the DRCR produced 75% or more of the cumulative catch produced from optimal CERs for a variety of assumptions about biology and initial stock status. The optimal DRCR was most sensitive to movement patterns of larvae and adults and survey variability.

In Chapter 2, a simulation model was used to analyze the ability of several stock assessment approaches to estimate current biomass after the implementation of a marine reserve. Results show that assessing populations as a single stock without accounting for a no-take marine reserve and performing separate assessments for fished and protected areas can lead to severely biased estimates of biomass. An assessment approach which explicitly accounted for fish movement was robust to uncertainty in movement patterns.

In Chapter 3, two popular hypotheses are modeled; one assumes that older mothers produce larger offspring capable of surviving longer starvation periods than offspring from younger mothers. The other modeled hypothesis is that mothers of different ages spawned in different times or locations. Recruitment variability was 55-65% lower than for control models in the absence of fishing and increased with increases in fishing mortality rates for both models. A marine reserve policy did not benefit measures of sustainability for either model.

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General Introduction

A marine reserve is an area of the ocean where fishing and other development activities are restricted or prohibited. Thousands of marine reserves exist worldwide and are implemented to meet diverse objectives, such as increasing biomass and catch of targeted or bycatch species, maintaining biodiversity, and protecting or rehabilitating bottom habitat. Some marine reserves have been implemented in areas that are severely overfished and where other fisheries management regulations have not existed previously or have been ineffective (e.g. Horigue et al., 2012). However, many marine reserves are implemented in addition to other fisheries management regulations, such as catch or effort limits (MLPA, 2008). For example, federally managed U.S. fisheries are managed using catch limits that are required by law (MSRA, 2007), and many are affected by various types of marine reserves (e.g. CFR, 2010). Numerous scientists have argued for the implementation of marine reserves as fishery management tools (e.g. Pauly et al., 2005, Berkeley et al., 2004b, Hastings and Botsford, 1999, Pikitch et al., 2004, Birkeland and Dayton, 2005, Worm et al., 2006, Lester et al., 2009). However, scientific study of these arguments is incomplete and in many cases fails to show a benefit of using marine reserves for accomplishing typical fisheries management objectives.

A brief review of current knowledge about marine reserves as tools for fisheries management

The results of marine reserve modeling studies converge on several points. First, no-take marine reserves (NTMRs) are expected to lead to increases in total biomass and (unless larvae and adults are both entirely sedentary) biomass of catch if a population is

overfished and in decline (Lauck et al., 1998, DeMartini, 1993, Roberts and Polunin, 1993, Hilborn et al., 2006, McGilliard and Hilborn, 2008, Holland and Brazee, 1996, Hart, 2006, Beverton and Holt, 1957, Quinn et al., 1993). Many empirical studies corroborate this modeling result (e.g. Goni et al., 2010, Garcia-Charton et al., 2008, Lester et al., 2009).

Second, an NTMR cannot control fishing mortality rates in fished areas. Hilborn et al. (2006) and Beverton and Holt (1957) note that when an NTMR is implemented it can displace fishing effort from the location where the NTMR is implemented to fished areas, thus increasing fishing effort in fished areas. An NTMR cannot control overfishing in fished areas.

Third, the extent to which biomass can build within an NTMR and spill over to fished areas will depend on larval and adult movement patterns and the spatial scale and timing of density-dependent mortality relative to the timing of larval movement (e.g. McGilliard and Hilborn, 2008, Gerber et al., 2003, Gaylord et al., 2005, Ralston and O'Farrell, 2008). Many models of NTMRs are composed of two boxes with one box as the NTMR, where larvae from both boxes are assumed to experience global density-dependent mortality and adults are sedentary. Larvae are then re-distributed in proportion to the size of each area (e.g. Hastings and Botsford, 1999). In these models, there is no adult spillover, but larval export is maximized among models that do not assume any advection of larvae. Larval export is reduced if density-dependent mortality is local to area because the density of larvae within NTMRs is greater than the global density of larvae, hence fewer larvae in total survive. In addition, a smaller proportion of larvae from the NTMR may move to the fished area than is assumed by these models and a two-box model assumes

that the whole fished area is seeded with larvae, rather than only locations close to the NTMR. Many alternative assumptions have been made about larval movement and density-dependent mortality. McGilliard et al. (2008), Ralston et al. (2008), and Gaylord et al. (2005) explore the influence of the timing of local density-dependent mortality of larvae and establish that larval export and catch is greatest in these models under the assumption of post-dispersal density-dependent mortality, combined with long-distance larval dispersal.

Larval dispersal distances and the timing and spatial scale of density-dependent mortality are open areas of research for most fish and invertebrate species (e.g. Petersen et al., 2010, Kinlan and Gaines, 2003, Siegel et al., 2003, Di Franco et al., 2012, Buston et al., 2012, Cowen and Sponaugle, 2009, Wiedenmann and Essington, 2006, Munday, 2004). Many biophysical models suggest that there is potential for larvae to disperse long distances (e.g. Kinlan and Gaines, 2003, Siegel et al., 2003, Largier, 2003), but that swimming, vertical movements, and particle size can limit dispersal distances (North and Houde, 2001, North and Houde, 2004). Empirical studies using otolith microchemistry, dye-marking mothers, and genetic techniques show a variety of larval dispersal distances among species (Cowen and Sponaugle, 2009, Kinlan and Gaines, 2003). However, several empirical studies suggest that realized larval dispersal distances may be much shorter than potential for dispersal for some species (Cowen and Castro, 1994, Cowen et al., 2000). Adult fish movement patterns are much easier to observe than larval movement patterns and information exists on movement of some species (Jorgensen et al., 2006), but is still uncertain for many species. Hence, any evaluation of management strategies that include NTMRs should test whether the candidate strategies are robust to

uncertainty about larval and adult movement characteristics of the species being managed.

Fourth, while NTMRs may increase catch when a population is overfished, most models show that NTMRs lead to a lower optimal long-term catch than conventional regulations such as catch limits (Hilborn et al., 2006, McGilliard and Hilborn, 2008). Hart (2006) shows that an increase in the fraction of habitat within NTMRs will increase catch only if the slope of the stock–recruit curve at an equilibrium spawning stock biomass is greater than $1/\text{spawning biomass per recruit when } F = 0$ for a population with sedentary adults and well–mixed larvae. Hart (2006) applied this modeling framework to two species with very different life histories (Canary rockfish and George’s Bank sea scallops), finding that the above condition is only met at fishing mortality rates above F_{MSY} . The assumptions in Hart (2006) that adults are sedentary, larvae are well–mixed, and density–dependent mortality is global will together provide a larger supplement of larvae to the fished area than for most alternative assumptions; hence, reasonable alternative model assumptions about movement and density–dependent mortality are not likely to provide any further benefits to catch with an NTMR. This corroborates the wealth of modeling literature which indicates that an NTMR will increase catch for an overfished population with mobile larvae.

Gaylord et al. (2005) and Neubert (2003) argue that optimal catch can be greater with an NTMR policy than with conventional regulations, but both assume strong source–sink dynamics. Neubert (2003) assumes a source population that is fully protected by an NTMR with highly mobile larvae and a sink population capable of no reproduction that is open to fishing. Gaylord et al. (2005) find that catch is maximized by a network of

NTMRs for a population with two life stages, where fecundity increases in the second life stage, but body mass is the same for the two stages. Both stages are fully selected to the fishery. In addition, Gaylord et al. (2005) report using a Beverton-Holt stock recruit curve with inter-cohort density-dependent mortality (but do not include the equation for density-dependent mortality in their manuscript). Typically, fisheries models assume that density-dependent mortality occurs among larvae only. The assumption of inter-cohort, post-dispersal density-dependent mortality, in combination with no individual growth (a one-year old is the same weight as a 50 year-old) means that catch is optimized by fishing the fished areas to extinction each year and evenly distributing new larvae among the cleared areas so as to minimize density-dependence in each fished area which eliminates the influence of inter-cohort density-dependent mortality. The assumption that fecundity, but not body mass, increases with age means that there is no benefit to yield-per-recruit of allowing individuals in the fished areas to grow older. With the exception of extremely short-lived species, this is a very unrealistic assumption. Interestingly, the model configuration assuming long-lived fish is the very scenario for which optimal catch with a network of NTMRs is substantially higher than for management with no NTMRs in their study. White et al. (2008) argue that profits are maximized with a network of NTMRs, but make a number of the same assumptions as in Gaylord et al. (2005) and additionally assume that the value of each fish caught is independent of fish size, which is quite unrealistic (Hart and Sissenwine, 2009). Results of Ralston and O'Farrell (2008) also model the influence of inter-cohort density-dependent mortality, finding that catch can exceed MSY when fishing mortality rates are above F_{MSY} when there is spatial variation in fishing mortality (the extreme case of spatial

variation in fishing mortality is an NTMR) and inter-cohort, post-dispersal density dependent-mortality occurs. However, Ralston and O'Farrell (2008) do not find that spatial variation in fishing mortality enhances catch for fishing mortality levels at or below F_{MSY} .

Fifth, an NTMR will change the relationship between fishery catch-rates and abundance (McGilliard and Hilborn, 2008). This is important because fishery catch-rate data are often used as indices abundance in stock assessments (e.g. Stewart et al., 2009). Hence, changes in stock assessment methods may be necessary after NTMRs are implemented. Punt and Methot (2004) and Garrison (2011) explore the performance of stock assessment methods that are currently used for assessments of groundfish on the U.S. West Coast after the implementation of an NTMR for simple assumptions about fish movement (a simple exchange rate between a fished and a closed area). Their results confirm that biases in stock assessments may occur for assessments conducted after NTMR implementation in some scenarios (see Introduction to Chapter 2 for more details).

Sixth, several studies have shown that catch-rates are highest in the fished areas closest to a closed area (Murawski et al., 2000, 2005). Using data from vessel monitoring systems, Murawski et al. (2005) found that fishing boats concentrated close to the border of closed areas in the Gulf of Maine. Catch-rates close to an NTMR may not reflect abundances in fished locations further from an NTMR. Hence it is important to consider whether fishing fleet behavior may influence the meaning of fishery catch-rate data after NTMR implementation. In addition, it is often argued that NTMRs benefit fisheries because catch and catch-rates close to NTMRs are higher than those before NTMR

implementation, but this argument is fundamentally flawed because overall catch and catch-rates for the entire geographic range of the fishery may still be lower than those prior to NTMR implementation.

Motivation

Three broad topic areas concerning NTMRs warrant further scientific exploration. First, little research has been done on what we can learn from NTMRs to inform management, particularly in data-poor systems. Second, several scientists have argued that NTMRs are necessary for the sustainability of some fish species, but these arguments have not been validated by scientific exploration. Third, further exploration of the potential influence of NTMRs on the performance of stock assessments and stock-assessment-based management is needed to explore potential impacts of a variety of fish movement patterns on the performance of assessments, beyond the assumption of a simple exchange rate between fished and closed areas.

World War I and World War II are known in the history of fisheries science as the first and second “Great Fishing Experiments,” whereby war led to cessations of fishing on North Sea plaice (Smith, 1994). A great deal was learned about the population dynamics of plaice based on measurements of catch-rates, total catch, and fish length before and after each war (Smith, 1994). Typically, we learn about fish population dynamics from historical catch, catch-rate, and catch-at-age data. The historical catch data provide crucial information on the magnitude of fish stocks and are necessary to inform stock assessments (Shepherd, 1984). In many nearshore fisheries worldwide, historical catch data do not exist and management regulations are relatively arbitrary or non-existent due to a lack of information on stock status and population dynamics. While it is impossible

to collect historical catch data retroactively, we know from history that an alternative way to learn about fish population dynamics is to stop fishing. While it might not be possible to close an entire fishery for multiple years, as during WWI and WWII, it may be possible to implement NTMRs. Little research has been done on what can be learned about fish population dynamics from NTMRs and whether such information could be used to manage fish populations in the absence of the data necessary to conduct stock assessments.

Despite the wealth of research on NTMRs that has occurred over the past two decades, several arguments for the implementation of NTMRs have been made by scientists, the validity of which have not been explored by scientific study. These scientists argue for the use of NTMRs to increase and maintain the proportion of older females of long-lived species, such as rockfish (Berkeley et al., 2004a, Sogard et al., 2008, Birkeland and Dayton, 2005). Studies show that older spawners have much higher fecundity and may produce larger eggs or offspring with larger oil globules than young spawners (Berkeley et al., 2004a, Sogard et al., 2008, Trippel, 1998). Berkeley et al. (2004a) showed in the laboratory that larvae with large oil globules (born to older spawners) were able to withstand longer periods of starvation than larvae with small oil globules (born to younger mothers). In addition, it is thought that larger larvae and juveniles have higher survival rates (e.g. Hare and Cowen, 1997). Finally, it is thought that older spawners may spawn in different times or locations than younger spawners (Berkeley et al., 2004b), creating a bet-hedging effect over spawner age. Berkeley et al. (2004b) argue that maintaining older spawners in the population by way of NTMRs is necessary for sustainability of long-lived species such as rockfish. However, no modeling efforts have

explored the implications of management with NTMRs as compared to catch or effort regulations for these species.

Objectives

The objectives of this dissertation are as follows:

Develop and explore a management strategy that uses data gathered from an NTMR to inform effort regulations in surrounding fished areas. In particular, the potential use of the ratio of the density of fish outside an NTMR to that inside one each year in a control rule is evaluated to determine the direction and magnitude of change in fishing effort in the next year.

Use simulation modeling to analyze the ability of several stock assessment configurations to estimate current biomass after the implementation of a single, large NTMR for three fish populations with distinct ontogenetic movement patterns.

Model two mechanisms by which reducing the proportion of older fish in a population has been hypothesized to influence sustainability and explore whether these mechanisms influence mean population dynamics and the characteristics of recruitment variability. Explore whether populations with these mechanisms could be managed more sustainably with an NTMR policy in addition to a constant fishing mortality rate than with a constant fishing mortality rate alone.

Chapter 1. Can information from marine protected areas be used to inform control-rule-based management of small-scale, data-poor stocks?

Abstract

Many small-scale, nearshore fisheries lack the historical catch and survey information needed for conventional stock-assessment-based management. The potential use of the ratio of the density of fish outside a marine protected area to that inside one each year (the density ratio) in a control rule is evaluated in order to determine the direction and magnitude of change in fishing effort in the next year. Management Strategy Evaluation was used to evaluate the performance of this density ratio control rule (DRCR) for a range of movement rates of larvae and adults and other biological scenarios, and the parameters of the control rule that maximized cumulative catch (over 95 years) for each scenario were found. The cumulative catch under the optimal DRCR was 90% of the cumulative catch from an optimal constant effort rule (CER). A small range of parameter values for the DRCR produced 75% or more of the cumulative catch produced from optimal CERs for a variety of assumptions about biology and initial stock status. The optimal DRCR was most sensitive to movement patterns of larvae and adults and survey variability.

Introduction

Many nearshore fisheries are difficult to manage because the data required for conventional stock-assessment-based management, such as historical catch, and catch and discard rates, are missing or uncertain (Leonart and Maynou, 2003; Key *et al.*, 2008). Further difficulties associated with managing nearshore fisheries include problems tracking catches accurately, lack of species-specific catch data, infrequent (or nonexistent) fishery-independent survey data, and an uncertain relationship between fishery catch per unit effort (cpue) and abundance owing to changes in the geographic location of fishing effort, the implementation of MPAs, and other management regulations. Information for these fisheries is commonly aggregated over large spatial areas, even though the spatial scale of both biological and physical dynamics, and the corresponding spatial extent of fish stocks and fisheries, are often much smaller (Gunderson *et al.*, 2006, 2008). For example, the stock assessment for blue rockfish (*Sebastes mystinus*) aggregates data over most of the coastline of California (Key *et al.*, 2008), whereas Jorgensen *et al.* (2006) found that these fish have a home range of 100 m or less. Managing resources at a spatial scale larger than that of the system dynamics means that the fishing intensity on individual populations may be too high in some locations, e.g. locations close to a fishing port, and too low in others, leading to the possibility of localized depletions or forgone catch (Walters and Martell, 2004). The absence of informed management at an appropriate spatial scale leaves nearshore fisheries vulnerable to rapid overexploitation owing to the classic boom-and-bust cycle that follows when a new market is found for a resource (Berkes *et al.*, 2006).

In recent years, marine protected areas (MPAs) have been implemented in many marine ecosystems to conserve biodiversity, highly vulnerable species, and habitats (Anon., 1979, 1992; HDAR, 1992; GBRMPA, 2004; MLPA, 2008;). Modelling studies show that MPAs can be expected to increase biomass in the absence of other fishing regulations for populations that are overexploited and in decline (Holland and Brazee, 1996; Lauck *et al.*, 1998; Gerber *et al.*, 2003). Nevertheless, they do not protect areas that are open to fishing from overexploitation (Horwood *et al.*, 1998; Hilborn *et al.*, 2006; McGilliard and Hilborn, 2008). Moreover, MPAs are often located on the basis of objectives other than those of conventional fisheries management, such as increasing biodiversity, protecting bottom habitat, or achieving socio-economic or political goals, so may not protect a significant proportion of the range of a target species (Ward *et al.*, 1999; Sala *et al.*, 2002; Sorensen and Thomsen, 2009; Semmens *et al.*, 2010). Therefore, management measures are needed in addition to MPAs to minimize the risk of severely overexploiting nearshore resources.

In addition to MPAs, the nearshore rockfish fishery along the California coast, the Australian North West Slope and Western Deepwater Trawl Fisheries, and the Australian Coral Sea Fishery set catch limits as a fraction of the highest historical catch (NFMP, 2002; Dowling *et al.*, 2008). However, the highest historical catch contains little information about the dynamics of a stock. Moreover, historical catch is often based on and applied to a multispecies assemblage, rather than to a single species. New methods are needed to manage nearshore fish stocks that will ensure sustainable fishing practices at appropriate spatial scales, do not require reliable historical information on the fisheries

or unbiased information on current catch, and will provide quality data to inform and improve future management.

We evaluate here a survey-based control rule (the density ratio control rule, DRCR). The density ratio (DR) is the ratio of the fish density outside an MPA to that inside it, based on stratified random sampling. The DR is used as an indicator of stock status where the density inside an MPA is the best available representation of unfished conditions. Unlike a point estimate of unfished biomass from a typical stock assessment, the density inside an MPA is subject to the same fluctuations in environmental conditions as the fished portion of the stock. The DRCR that we evaluate uses the DR in the current year to determine a multiplier specifying a direction and magnitude of change in allowable effort that is implemented in the subsequent year. Fishing effort rather than catch is assumed to be controlled. Effort controls are more common than catch controls in many recreational and artisanal nearshore fisheries. For example, several fisheries are managed by various combinations of gear restrictions, time-area closures, and limited entry rules, including Argentinian scallops, Chilean loco and sea urchin, nearshore Mediterranean fisheries, and assemblages of coral reef species worldwide (McClanahan and Mangi, 2001; Orensanz *et al.*, 2005; Hilborn *et al.*, 2005; Little *et al.*, 2009; Campbell *et al.*, 2008; Morales-Nin *et al.*, 2010).

In this paper the performance of the DRCR as a management strategy is assessed for small-scale nearshore fisheries, and the DRCR is compared with a constant effort rule (CER), determining the parameters of the DRCR that maximize cumulative catch over 20, 30, 60, and 95 years. Optimal values for the parameters of the control rule are always unknown because of irreducible uncertainties. Therefore, we evaluate the long-term

effects of using a range of non-optimal DRCRs relative to those of non-optimal constant effort strategies. In data-poor situations, successful management strategies need to be robust to uncertainties about biology and stock status, so it is necessary to evaluate the sensitivity of outcomes to a range of assumptions on life history, movement patterns of larvae and adults, initial stock status, spatial heterogeneity in abundance, and alternative sample sizes.

Methods

We used Management Strategy Evaluation (MSE; Punt, 2006) to evaluate the performance of the DRCR. MSE tests strategies for assessing and managing fisheries by (i) simulating the true biology of the natural system (referred to as the operating model, OM), (ii) sampling from the true population, (iii) calculating measures of stock status (assessment), (iv) calculating recommended fishing restrictions using control rules, and (v) applying updated restrictions to the fishery, which allows the dynamics of the true population to be updated. Although MSE can allow for implementation error, i.e. where the restrictions on the fishery differ from those inferred from the control rule, the analyses conducted here ignore this source of uncertainty, for simplicity.

The DRCR tested is a control rule in which a change in effort for the subsequent year is linearly related to the value of the DR in the current year (Figure 1). The DRCR has two parameters: the x -intercept and the slope. The x -intercept is the DR at which no change in effort is recommended by the control rule (0.4 in Figure 1), and the slope of the control rule controls the magnitude of the change in allowable effort as a function of the DR.

The OM was age- and space-structured with a fishery taking place in the middle of the year (see the Appendix A for more detail). It consisted of 30 cells alongshore and 5 cells representing the inshore–offshore direction (Figure 2). Two spatial dimensions are modelled to capture the effects of sampling a population that is distributed heterogeneously over its geographic range. Larvae and adults move during each time-step.

Management strategy

Simulations were initiated with fishing effort at the constant level that brought the fishery from unfished to a specified initial depletion level over 60 years. A single no-take MPA was implemented in the middle 6 cells in the alongshore direction and spanned the inshore–offshore cells (Figure 2). Management strategies (a DRCR or a CER) were implemented five years after the MPA came into effect.

Sampling

Sampling followed a stratified random design with three strata: (i) cells open to fishing and within a distance of three cells from the MPA; (ii) cells open to fishing and farther than three cells from the MPA; and (iii) cells within the MPA (Figure 2). Fished areas closest to the MPA are expected to have higher densities of fish and therefore will be subject to more fishing effort. Dividing the fished area into two strata is expected to lower survey variance and ensures that both strata are sampled each time there is a survey. Within strata, cells were selected for sampling randomly without replacement each year. In the base-case scenario, 1/8th of the cells of each stratum were sampled. Samples within each surveyed cell were represented by the true abundance prior to removals in the middle of the year, modified by survey selectivity, which was assumed to

be the same as fishery selectivity, and subject to lognormal observation error with a standard error of the log σ_{survey} .

Assessment

Stock status was determined as the ratio of the sampled density in fished areas, $\tilde{D}_{\text{open},t}$, to that in the MPA, $\tilde{D}_{\text{closed},t}$, where the simulated sample densities were

$$(1) \quad \tilde{D}_{\text{open},t} = \left(\frac{\tilde{N}_{\text{near},t} + \tilde{N}_{\text{far},t}}{n_{\text{near},t} + n_{\text{far},t}} \right); \quad \tilde{D}_{\text{closed},t} = \frac{\tilde{N}_{\text{closed},t}}{n_{\text{closed},t}},$$

where $n_{\text{near},t}$, $n_{\text{far},t}$, and $n_{\text{closed},t}$ were the number of cells open to fishing (near and far from the MPA), and in the MPA, respectively; and $\tilde{N}_{\text{near},t}$, $\tilde{N}_{\text{far},t}$, and $\tilde{N}_{\text{closed},t}$ were the sampled number of fish in each stratum. The DR, $\tilde{\rho}_t$, was $\tilde{D}_{\text{open},t} / \tilde{D}_{\text{closed},t}$.

Control rule

The control rule was a linear function where the change in effort from year t to year $t+1$ (ΔE_{t+1}) was a function of the DR ($\tilde{\rho}_t$), an x -intercept, and a slope (Figure 1).

$$(2) \quad \Delta E_{t+1} = \text{slope}(\tilde{\rho}_t - x\text{intercept}); \quad \text{i.e. } E_{t+1} = E_t + \Delta E_{t+1}.$$

A grid of control-rule parameters consisting of 20 x -intercepts over the range [0,1] and 20 slopes over the range [0,4] was evaluated to identify the “optimal” set of parameters, i.e. those that produced the maximum cumulative catch summed over 95 years of simulation and 50 sets of random deviates. In addition, control-rule parameters were found that maximized cumulative catch summed over 20, 30, and 60 years, and 50 sets of random deviates.

Constant effort rules (CERs) as an alternative to the control rule

CERs were evaluated as a reference for comparison with DRCRs. Simulations were conducted to determine the cumulative catch when a single effort level was applied for the entire duration of a simulation. Simulations were conducted for each of 200 effort levels (E where $E_t=E$ for all t), for the same 50 sets of random deviates used for testing the DRCR. The optimal constant effort levels which produced the maximum cumulative catch over 20, 30, 60, or 95 years were identified.

Base-case operating model

The optimal values for the control-rule parameters were found for a base case OM which had an initial depletion (spawning-stock biomass, SSB, divided by unfished equilibrium SSB) equal to 25% of that at maximum sustainable yield (MSY). The initial effort level ($E_t=0$) was the constant effort level required to achieve a depletion level of 25% of that at MSY over 60 years, starting at MSY conditions. Larvae and adults were sedentary, and larvae experienced density-dependent mortality locally in each cell. The base-case OM accounted for process and observation uncertainty by including local and global recruitment variation with a total recruitment variance of 0.72, and $\sigma_{\text{survey}} = 0.2$. Additional base-case OM conditions are listed in Table A1 of Appendix A.

Sensitivity analyses

Sensitivity analyses explored the extent to which initial stock size, biological parameters, and sampling error influenced which DRCRs and CERs were optimal, and the potential consequences of using suboptimal control rules. Sensitivity analyses examined initial depletion levels of 10, 50, 100, and 200% of the depletion corresponding

to MSY, alternative steepness (h ; Francis, 1992) levels of 0.3, 0.5, and 0.9, natural mortality (M) values of 0.05, 0.2, and 0.4 year⁻¹, survey CV s of 0.1, 1, and 1.5, and spatial CV s of catchability of 0.2 and 0.42. Sensitivity analyses were selected to represent a range of uncertainties common to nearshore fisheries where few data exist and few analyses have been performed to determine initial stock status and biological parameters. In addition, survey CV s may vary as a consequence of the patchy distribution of fish, the small scale of nearshore fish populations, and the small sample sizes caused by funding constraints.

Several scenarios were conducted to examine the impact of assumptions on movement of larvae and adults (Tables 1 and 2; the phrases in these Tables are used as abbreviations for the scenarios). Table 1 describes scenarios in which larvae experienced density-dependent mortality after larval diffusion and Table 2 those in which density-dependent mortality applied to the entire larval pool, the survivors of which then recruited to a diffuse patch of spatial cells. The scenarios in Table 2 captured the hypothesis that density-dependent mortality is caused by global environmental conditions such as food availability during a planktonic stage (Hjort, 1914; Cushing, 1990), rather than habitat availability for juveniles at the time of settlement, as for the scenarios in Table 1 (Myers and Cadigan, 1993a, 1993b). The scenario “recruitment to inside the MPA and adult diffusion” (Table 2) was similar to the scenario “recruitment to outside the MPA and adult diffusion”, except that larvae recruited to a patch of cells inside the MPA.

Performance measures

The main performance measure was the cumulative catch (over 95 years and 50 sets of random deviates) relative to that under the optimal CER. Other performance measures

were the cumulative catch over 20, 30, and 60 years, the probability of falling below 25% of $BMSY$, average and 5% and 95% quantiles of the CV of catch and cpue interannually and among simulations in year 100 (termed “intersimulation CV ”), average depletion in year 100, and the average catch and cpue in year 100 relative to that at MSY . For each scenario, the optimal values of x -intercept and slope were found and used to assess whether the optimal set of values defining the control rule was similar across biological and sampling scenarios, and hence the potential for the same set of values to be used for more than one scenario.

In addition, the parameter values for a max–min DRCR (defined below) and CER were identified based on all scenarios (the base-case OM and all the sensitivity analyses). The max–min rule was the DRCR (x -intercept and slope) or CER (effort) that maximized the lowest cumulative catch across all scenarios. More specifically, the max–min rule was found by (i) identifying, for each parameter value (for CERs) or each combination of parameter values (for DRCRs), the scenario that led to the lowest cumulative catch, and then (ii) finding the parameter value or combination of parameter values for which the lowest cumulative catch was greatest. The max–min rule minimized potential losses assuming that nothing was known about the biology, survey CV , or initial status of the stock being managed.

Results

Base-case scenario

The base-case scenario resulted in an optimal DRCR in which (x -intercept, slope) = (0.42,1.05). An example realization of the base-case scenario using the optimal DRCR (Figure 3) shows that initially there was little difference between densities inside and outside the MPA because of the similar fishing history before MPA implementation. The true and sampled DR began to follow the true trend in depletion after 15–20 years with no fishing in the MPA. The sampled DR was sometimes very different from the true depletion level, but major shifts in true depletion levels were captured in sample DRs (Figure 3).

Profiles of cumulative catch calculated over 30 years for a range of parameter values are influenced by transient dynamics such as stochasticity and oscillations in dynamics after the control rule is implemented (Figure 4b). After 95 years, the length of the catch series is sufficient to identify the parameter values that are optimal without the substantial influence of transient dynamics (Figure 4a). The parameter space producing high cumulative catches changes depending on the period over which the control rule is evaluated, but converges after ~60 years (Figure 5). Results for shorter periods (i.e. 5–10 years) are not shown in Figure 5 because the optimal DRCR caused the population to collapse quickly. Over 30 years, the optimal DRCR produced ~60% of the cumulative catch produced by the optimal CER (Figure 4b). In contrast, over 95 years, the optimal DRCR produced 90% of the cumulative catches produced by the optimal CER (Figure 4a). We focus on the cumulative catch over 95 years for the balance of this paper to avoid confounding optimality with the effects of transient dynamics.

The cumulative catch over 95 years was insensitive to the value of the DRCR slope (Figures 4a, 5d). With the DRCR x -intercept fixed at its optimal value, the cumulative catch was maintained near the maximum for slopes ranging from 20 to 300% of the optimal slope (Figure 4a). In contrast, the cumulative catch was highly sensitive to the x -intercept (Figure 4a). Cumulative catches under constant-effort policies were maintained at high values for a fairly wide range of effort levels (Figure 4a).

Interannual variability in catch under DRCRs was smallest when a small slope was used and for x -intercepts close to the optimal x -intercept (Figure 6a). The probability of falling below 25% of $BMSY$ was greatest when the slope was large and the x -intercept was small relative to the optimal x -intercept (Figure 6b).

Sensitivity analyses

Fish movement

The optimal DRCR x -intercept and slope were most sensitive to movement patterns of larvae and adults (Table 3, Figure 7a). The scenarios with short-, medium-, and long-distance larval diffusion only had a small effect on the optimal DRCR (Table 3, Figure 7a), but the optimal x -intercept increased as diffusion rates of adults increased (Table 3, Figure 7a). The x -intercept was larger for higher diffusion rates of adults because adult diffusion dampened the magnitude of difference between fished areas and MPAs. In addition, catches in year 100 were greater for higher diffusion rates of adults (Table 3).

The optimal x -intercept was very large (0.79) for the scenario with recruitment to outside the MPA and adult diffusion. More fish (especially young fish that were newly available to the survey catch) were concentrated in fished areas for this scenario, causing

DRs to be higher. Hence a larger x -intercept was required to limit fishing effort (Table 3, Figure 7a).

Observation error

The optimal x -intercept increased as survey CV increased, forcing decreases in effort over a wider range of DRs (Table 3, Figure 7b). Optimal slope decreased as survey CV increased, indicating that the largest cumulative catches were produced when changes in effort were small as the quality of data declined (Table 3).

Initial stock status

The initial size of the stock relative to $BMSY$ before the implementation of the DRCR did not affect the optimal x -intercept (Appendix A, Table A2). Optimal slopes were largest when the stock was initially overfished or very lightly fished (150–200% of depletion at MSY ; Table A2). The optimal slope was 0 when the population was initially at MSY (Table A2; the long-term effort level was already optimal, so changes in effort only lowered long-term cumulative catch). When initial stock size was small, a greater decrease in effort caused the population to recover to biomass levels and productivity close to that at MSY more rapidly. Likewise, when stocks were initially lightly fished, a control rule that allowed large increases in effort behaved like a constant escapement policy, reducing the population size quickly to MSY conditions, and maximizing productivity by reducing the effects of density-dependent mortality.

Steepness and natural mortality

The optimal slope was 0 at very low steepness ($h = 0.3$; Appendix A, Table A2) because the stock was very sensitive to changes in effort and even a small increase in effort resulted in long recovery times; it was better to use an effort level that did not

result in population collapse over 60 years of fishing. The optimal slope increased with steepness and the optimal x -intercept decreased, so it was optimal to make large changes in effort and to allow increases in effort at lower DRs for a stock with a steepness of $h = 0.9$ (Figure 7c, Table A2). Such a stock is very productive, so higher fishing levels can be sustained.

The optimal x -intercept increased with increasing values for natural mortality (Figure 7d, Table A2). The population was spread over a wide range of age classes when natural mortality was low (e.g. $M = 0.05 \text{ year}^{-1}$) so the proportion of mature fish for a particular population level was larger than for a population with high rates of natural mortality (e.g. $M = 0.3$ or 0.4 year^{-1}). Therefore, a population with low natural mortality can be fished relatively harder and produces more eggs than if it were fished at the same level with higher natural mortality. Optimal slope was larger for populations with low rates of natural mortality than for populations with high rates; making large reductions in effort on fish populations with higher natural mortality results in lost catches that cannot be taken later, because fish that are not caught are more likely to die of natural mortality. Typically, age-at-maturity is higher for fish with low rates of natural mortality; changing the age-at-maturity concurrently with changes in natural mortality rates would likely dampen the effects of changing the rates of natural mortality.

Max–min rules

The max–min DRCR had a larger x -intercept and a smaller slope than the optimal DRCR for the base-case scenario (Table 4). The max–min DRCR lowered the probability of falling below 25% of $BMSY$ for most scenarios, with the exception of three scenarios ($h = 0.3$, medium-distance larval and adult diffusion, and recruitment to outside the MPA

and adult diffusion) where optimal x -intercepts were larger than the x -intercept for the max–min DRCR (Tables 4, A3). In most scenarios, catches were smaller and cpue higher for the max–min DRCRs than for the optimal DRCRs (Tables 4, A3). The max–min effort rule was based on a slightly lower level of effort than the optimal CER for the base-case scenario and led to lower probabilities of falling below 25% of *BMSY* and larger catches than the DRCR, except where h was 0.3.

Discussion

A DRCR may be a viable strategy for managing fish stocks for which the data needed to use conventional stock assessment tools are unavailable, and when catches are uncertain. A DRCR with an x -intercept of 0.4–0.5 and many values for the slope produced a form of so-called pretty good yield (PGY; Hilborn, 2010), defined here as 75% or more of the cumulative catch over 95 years produced by the optimal CER for a variety of assumptions about fish biology and initial stock status. Therefore, a DRCR has the potential to produce high cumulative catches (PGY) when biological information on fish stocks is uncertain, except for the most extreme life histories. Setting the x -intercept just above its optimal value reduced the probability of falling below 25% of *BMSY* while maintaining high cumulative catches. The slope of the DRCR did not have a great effect on cumulative catch, but smaller slopes minimized the probability of falling below 25% of *BMSY*, lowered interannual variation in catch and cpue, and widened the range of x -intercepts over which the cumulative catch remained high. CERs may outperform DRCRs, assuming that the correct level of effort can be identified.

The MPA and reference points

The population both inside and outside the reference MPA may be affected in the same way, causing no change in the DR during a period of high natural mortality or low productivity as a result of environmental conditions. In this way, the DRCR is subject to additional risk because fishing effort will not be lowered immediately in response to declines in productivity. However, a year of successful recruitment throughout the range of a stock would also not change the DR and fishing effort would not be increased in response to the increased recruitment (although catch would increase because of greater abundance). Steepness and natural mortality did not change the parameter values of the optimal DRCR, nor those producing large cumulative catches (Figures 7c and 7d); this means that the same parameter values should be appropriate if there were changes in productivity or natural mortality. However, future studies should explore the implications of using the DRCR in the presence of shifts in productivity and natural mortality.

The DRCR will not be effective when an MPA is new because the DR does not mimic the true depletion level then. For example, a DRCR that is implemented before enough build-up of biomass within the MPA will result in a management recommendation that effort be increased for fisheries that are severely overexploited. Wilson *et al.* (2010) suggest a way to adjust for this when using information from an MPA as a reference point; further simulation testing would be necessary to determine whether this correction factor is appropriate in the absence of knowledge regarding initial depletion.

Nevertheless, established MPAs exist worldwide and they could, in principle, be used for management with DRCRs (HDAR, 1992; McClanahan and Mangi, 2001; GBRMPA, 2004).

Multispecies perspective

Most nearshore fisheries target an assemblage of species, so a need exists for multispecies management tools. This study considered single-species scenarios, but offers insights about the performance of the DRCR in a multispecies context. A multispecies DRCR could calculate the DR for each species and use an arithmetic or geometric mean of the ratio of the DR to the x -intercept for each species as input to the control rule, rather than the DR itself. This would allow the use of different x -intercepts for different species. DRCRs could be combined with additional regulations for species that do not follow the general trend in DR across species, because abundance does not increase notably for all species within a MPA (Bohnsack *et al.*, 2003). In some instances, effort could be lowered for species with the lowest DR : x -intercept ratios through non-retention of those species on particular days, seasons, or in particular fishing areas.

Implementing a DRCR

The DRCR is effort-based; effort-based management can be used when catches are difficult to track. However, increases in the efficiency of fishing gear and new technology cause increases in effort for which there is no accounting under a CER. A control rule that adjusts allowable effort based on continually updated information on stock status will diminish the effects of effort creep by continually lowering effort, unless the DR is high enough. A DRCR could be created to manage catch rather than effort, even when the magnitude of unreported catch is uncertain, particularly where legal constraints require defined catch limits (MSFCMA, 2007). Further analysis would be needed to assess the performance of a catch-based DRCR.

Another challenge for fisheries management is that many nearshore fish stocks with low rates of movement and local, port-based fisheries are currently managed at a coastwide spatial scale; localized depletion and forgone catch are risks when management is at a larger spatial scale than that of the fish stocks and fisheries. The DRCR is a potential tool for managing fish stocks at the spatial scale at which the population and fishery dynamics occur. The DRCR can be used without a high level of quantitative expertise, so is a candidate for use at a local level as part of community-based monitoring and fishery management.

Finally, implementation of a DRCR would benefit from some knowledge of larval dispersal and adult movement to determine an appropriate x -intercept. Exploration of movement patterns of larvae and adults is an active area of research, and much information exists for many nearshore species (e.g. Jorgensen *et al.*, 2006; Hyde and Vetter, 2009). Changing the rate of diffusion is expected to have similar effects on optimal parametrization of the DRCR as changing the size of the MPA or allowing fishing mortality within the MPA. Therefore, successful implementation of the DRCR would benefit from careful consideration of the size of the MPA relative to movement rates and the rate of fishing mortality expected within the MPA.

Potential for future work

Several changes could be made to the DRCR.

- (i) First, many large and sudden changes in effort regulations could be destabilizing for fishing communities, so future studies should find ways to minimize the variance in sample DRs, which would in turn lower variability in effort recommendations generated by the control rule (Figure 3). For example, time-

averaged DRs, e.g. averaging the DR over the previous three years, could be used as an input to the DRCR. Further, the use of a more sophisticated survey design could lower the variance among years in sample DRs. Some management systems do not allow conventional surveys within MPAs, and future studies should explore the implications of basing the DR on non-extractive surveys.

- (ii) This study used cumulative catch to evaluate the performance of control rules. Control rules could be analysed using other performance measures, depending on fishery objectives (Quinn and Deriso, 1999; Deroba and Bence, 2008), such as those related to fluctuations in catch, cumulative net profits (Clark, 1973), or differences between current depletion and a target depletion level (Deroba and Bence, 2008).
- (iii) As historical data accumulate, it may be more effective to carry out conventional quantitative stock assessments than to continue to use the DRCR. Future work should explore whether this is true, and if so, find the average number of years required to produce a stock assessment containing better quality information than the DR.
- (iv) Other ratios than that based on density could be used, for example, to capture more information on age or length structure, fecundity, or maturity. For instance, a ratio could be formulated based on a rough estimate of spawning biomass per recruit (SBPR) or lifetime egg production (LEP; O'Farrell and Botsford, 2005).
- (v) The control rule could be implemented based on fishery cpue data, rather than survey data. Cpue data are often biased and are not linearly related to density, but often more cpue data exist than could be gathered using a small survey. Future

analyses that consider the use of cpue data could examine whether or not the use of biased cpue data is better than using an unbiased, but smaller, survey.

- (vi) Only linear control rules were considered in this study; non-linear control rules may have desirable properties. For instance, a control rule that has constraints on the maximum and minimum extent of change in effort in a given year may produce more stable catches and could lessen the probability of falling below a biomass threshold by not allowing very large increases in effort.
- (vii) Other data-poor methods of providing fisheries management advice exist and are in various stages of development (O'Farrell and Botsford, 2005; Kai and Shirakihara, 2008; Cope and Punt, 2009; MacCall, 2009; Wilson *et al.*, 2010). A comparative analysis of data-poor methods, including the approach developed here, would illustrate which methods are likely to perform best given the shortcomings of data and the dynamics of fish species and fisheries in particular data-poor situations.

Tables

Table 1. Descriptions and parameter values for sensitivity tests of larval and adult movement for scenarios with local (within-cell), post-dispersal density-dependent mortality; $(\sigma_{Lalong}, \sigma_{Loff})$ represents the extent of larval diffusion in the north–south and east–west directions, respectively, and $(\sigma_{Aalong}, \sigma_{Aoff})$ represents the same for adult diffusion.

Description	Larval diffusion $(\sigma_{LAlong}, \sigma_{LOff})$	Adult diffusion $(\sigma_{Aalong}, \sigma_{Aoff})$
Short-distance larval diffusion	(1,0.5)	(0,0)
Medium-distance larval diffusion	(5,0.5)	(0,0)
Long-distance larval diffusion	(10,0.5)	(0,0)
Short-distance larval and adult diffusion	(1,0.5)	(1,0.5)
Long-distance larval and short-distance adult diffusion	(10,0.5)	(1,0.5)
Medium-distance larval and adult diffusion	(5,0.5)	(5,0.5)

Table 2. As for Table 1, but for scenarios with global (pooled) density-dependent mortality; $\sigma_{Lnorth}, \sigma_{Lsouth}, \sigma_{Least}, \sigma_{Lwest}$ are standard deviations of larval movement in each cardinal direction, and σ_{Aalong} and σ_{Aoff} represent the extent of adult diffusion in the north–south and east–west directions, respectively.

Description	Central cell of larval settlement	Alongshore spatial spread of larvae around central cell $(\sigma_{Lnorth}, \sigma_{Lsouth})$	Offshore spatial spread of larvae around central cell $(\sigma_{Least}, \sigma_{Lwest})$	Adult diffusion $(\sigma_{Aalong}, \sigma_{Aoff})$
Recruitment to outside the MPA and adult diffusion	(6,2.5)	(7,7)	(7,7)	(3,0.5)
Recruitment to inside the MPA and adult diffusion	(15.5,2.5)	(7,7)	(7,7)	(3,0.5)

Table 3. Performance measures for scenarios using optimal DRCRs and CERs.

Description	Optimal x -intercept	Optimal slope	Optimal effort relative to optimal effort for the base case	Probability of $B < 0.25B_{MSY}$ after time-step 5	Average depletion in year 100	Average cpue in year 100 relative to cpue at MSY	Average catch in year 100 relative to MSY	Average interannual CV of catch (5%, 95% quantiles)	
Base case									
CER			1.00	0.00	0.45	0.90	0.76	0.22	(0.15, 0.29)
DRCR	0.42	1.05		0.28	0.44	0.86	0.72	0.62	(0.45, 0.82)
Short-distance larval diffusion only									
CER			1.09	0.02	0.43	0.84	0.78	0.22	(0.15, 0.29)
DRCR	0.42	0.84		0.26	0.43	0.84	0.78	0.54	(0.40, 0.70)
Medium-distance larval diffusion only									
CER			1.18	0.02	0.41	0.82	0.83	0.22	(0.15, 0.29)
DRCR	0.42	0.84		0.30	0.39	0.76	0.80	0.42	(0.32, 0.55)
Long-distance larval diffusion only									
CER			1.27	0.02	0.39	0.79	0.85	0.22	(0.16, 0.29)
DRCR	0.47	0.84		0.26	0.40	0.82	0.82	0.41	(0.31, 0.53)
Short-distance larval and adult diffusion									
CER			1.27	0.02	0.35	0.84	0.90	0.22	(0.15, 0.29)
DRCR	0.53	1.26		0.52	0.31	0.74	0.89	0.53	(0.39, 0.67)
Long-distance larval and short-distance adult diffusion									
CER			1.36	0.06	0.33	0.81	0.92	0.22	(0.15, 0.29)
DRCR	0.58	2.11		0.54	0.31	0.77	0.96	0.76	(0.56, 0.98)
Medium-distance larval and adult diffusion									
CER			1.27	0.06	0.31	0.88	0.95	0.22	(0.14, 0.29)
DRCR	0.79	0.21		0.80	0.29	0.82	0.88	0.25	(0.15, 0.39)
Recruitment to outside the MPA and adult diffusion									
CER			1.00	0.02	0.32	0.89	0.93	0.22	(0.14, 0.29)
DRCR	0.95	1.05		0.74	0.34	0.94	0.96	0.57	(0.45, 0.71)
Recruitment to inside the MPA and adult diffusion									
CER			1.36	0.06	0.30	0.81	0.97	0.22	(0.14, 0.29)
DRCR	0.47	3.16		0.68	0.26	0.70	0.99	0.82	(0.63, 1.04)
Survey $CV = 0.1$									
CER			1.00	0.00	0.45	0.90	0.76	0.22	(0.15, 0.29)
DRCR	0.42	1.89		0.26	0.46	0.91	0.71	0.63	(0.48, 0.85)
Survey $CV = 1$									
CER			1.00	0.00	0.45	0.90	0.76	0.22	(0.15, 0.29)
DRCR	0.79	0.21		0.28	0.43	0.82	0.64	0.94	(0.43, 1.97)
Survey $CV = 1.5$									
CER			1.00	0.00	0.45	0.90	0.76	0.22	(0.15, 0.29)
DRCR	0.89	0.42		0.62	0.40	0.70	0.29	2.80	(1.38, 5.14)

Table 4. Performance measures for scenarios using the max–min CER and DRCR (relative to those using the optimal rules for all performance measures except “probability of $B < 0.25B_{MSY}$ after time-step 5”). The max–min DRCR was (x-intercept, slope) = (0.74, 0.21); the max–min CER was 0.91 of the optimal constant effort for the base-case scenario.

Description	Max–min x-intercept relative to optimal x-intercept	Max–min slope relative to optimal slope	Max–min effort relative to optimal effort	Probability of $B < 0.25B_{MSY}$ after time-step 5	Average depletion in year 100 relative to that for the optimal rule	Average cpue in year 100 relative to cpue for the optimal rule	Average catch in year 100 relative to that for the optimal rule	Average interannual CV of catch relative to that for the optimal rule
Base case								
CER			0.91	0.00	1.06	1.10	1.00	1.02
DRCR	1.75	0.20		0.16	1.70	2.27	0.78	0.59
Short-distance larval diffusion only								
CER			0.83	0.00	1.11	1.20	1.00	1.04
DRCR	1.75	0.25		0.16	1.71	2.27	0.73	0.63
Medium-distance larval diffusion only								
CER			0.77	0.00	1.16	1.28	0.98	1.04
DRCR	1.75	0.25		0.16	1.76	2.34	0.76	0.64
Long-distance larval diffusion only								
CER			0.71	0.00	1.22	1.36	0.97	1.04
DRCR	1.56	0.25		0.16	1.67	2.08	0.77	0.62
Short-distance larval and adult diffusion								
CER			0.71	0.00	1.30	1.36	0.97	1.07
DRCR	1.40	0.17		0.36	1.78	1.96	0.91	0.56
Long-distance larval and short-distance adult diffusion								
CER			0.67	0.00	1.38	1.44	0.96	1.07
DRCR	1.27	0.10		0.38	1.54	1.63	0.90	0.35
Medium-distance larval and adult diffusion								
CER			0.71	0.00	1.36	1.35	0.97	1.07
DRCR	0.93	1.00		0.90	0.46	0.47	0.81	0.95
Recruitment to outside the MPA and adult diffusion								
CER			0.91	0.02	1.10	1.10	1.00	1.02
DRCR	0.78	0.20		1.00	0.01	0.01	0.04	1.59
Recruitment to inside the MPA and adult diffusion								
CER			0.67	0.00	1.45	1.45	0.96	1.08
DRCR	1.56	0.07		0.50	3.18	3.19	0.32	0.28
Survey $CV = 0.1$								
CER			0.91	0.00	1.06	1.10	1.00	1.02
DRCR	1.75	0.11		0.16	1.69	2.20	0.74	0.54
Survey $CV = 1$								
CER			0.91	0.00	1.06	1.10	1.00	1.02
DRCR	0.93	1.00		0.34	0.95	0.90	0.99	0.98
Survey $CV = 1.5$								
CER			0.91	0.00	1.06	1.10	1.00	1.02
DRCR	0.82	0.50		0.60	0.76	0.50	1.53	0.70

Figures

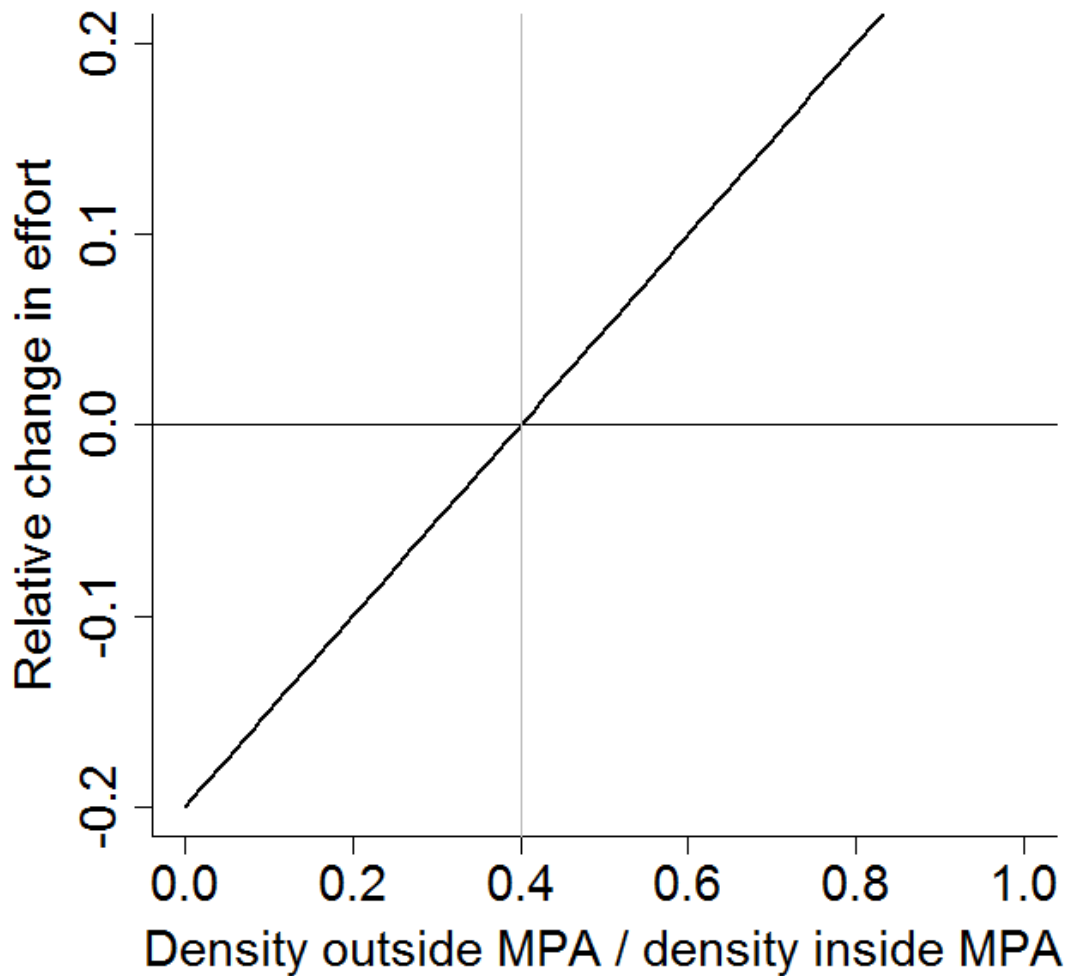


Figure 1. Example of a DRCR. The ratio of the density outside to inside the marine protected area (x-axis) determines the direction and relative amount of recommended change in fishing effort in the following year (y-axis). The vertical grey line shows the x-intercept of the DRCR.

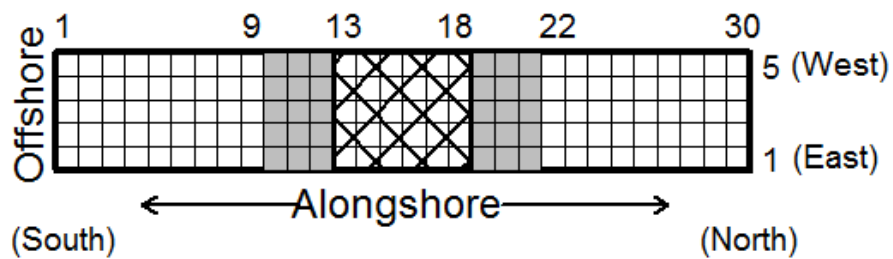


Figure 2. The spatial configuration of the OM. A no-take MPA is implemented in year 1 in cells 13–18 alongshore and 1–5 in the offshore direction (black hatched). Stratified random sampling occurs in three strata: the MPA (black hatched), the open areas near the MPA (grey), and the remaining open areas (white). The labels east, west, north, and south denote the orientation of directional larval movement.

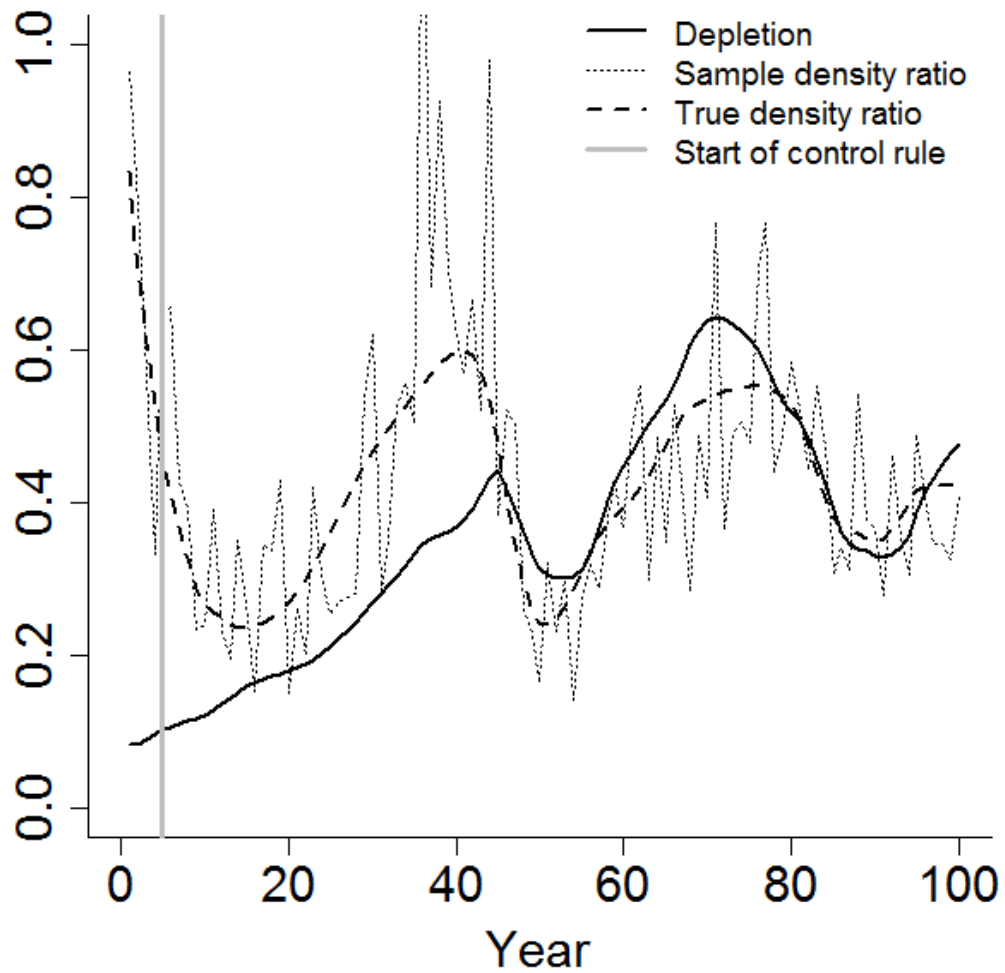


Figure 3. An example realization of the DRCR for the base-case scenario. An MPA is implemented in year 0, and the DRCR with $(x\text{-intercept, slope}) = (0.42, 1.05)$ in year 5 (vertical grey line). Depletion (solid black line), the true DR with no observation error (heavy dashed line), and the sample DR (light dotted line) are shown.

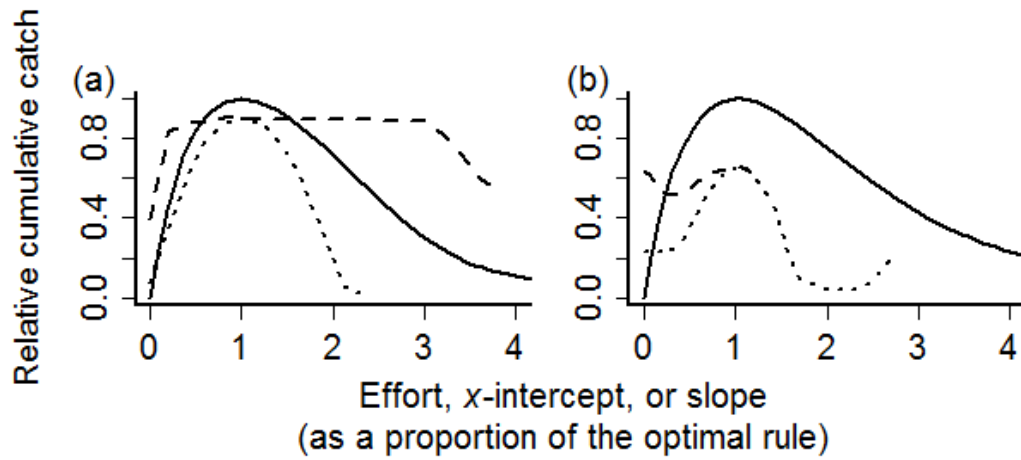


Figure 4. Profiles of cumulative catch calculated over (a) 95 years and (b) 30 years (scaled to the cumulative catch of the optimal CER) over CERs (solid lines), and x -intercepts (dotted lines) and slopes (dashed lines) under DRCRs for the base-case scenario. For the profile over x -intercepts, the slope is fixed at its value for the optimal DRCR (optimal slope was (a) 1.05, and (b) 3.37)), for the profile over slopes, the x -intercept is fixed at its value for the optimal DRCR (optimal x -intercept was (a) 0.42, and (b) 0.37)).

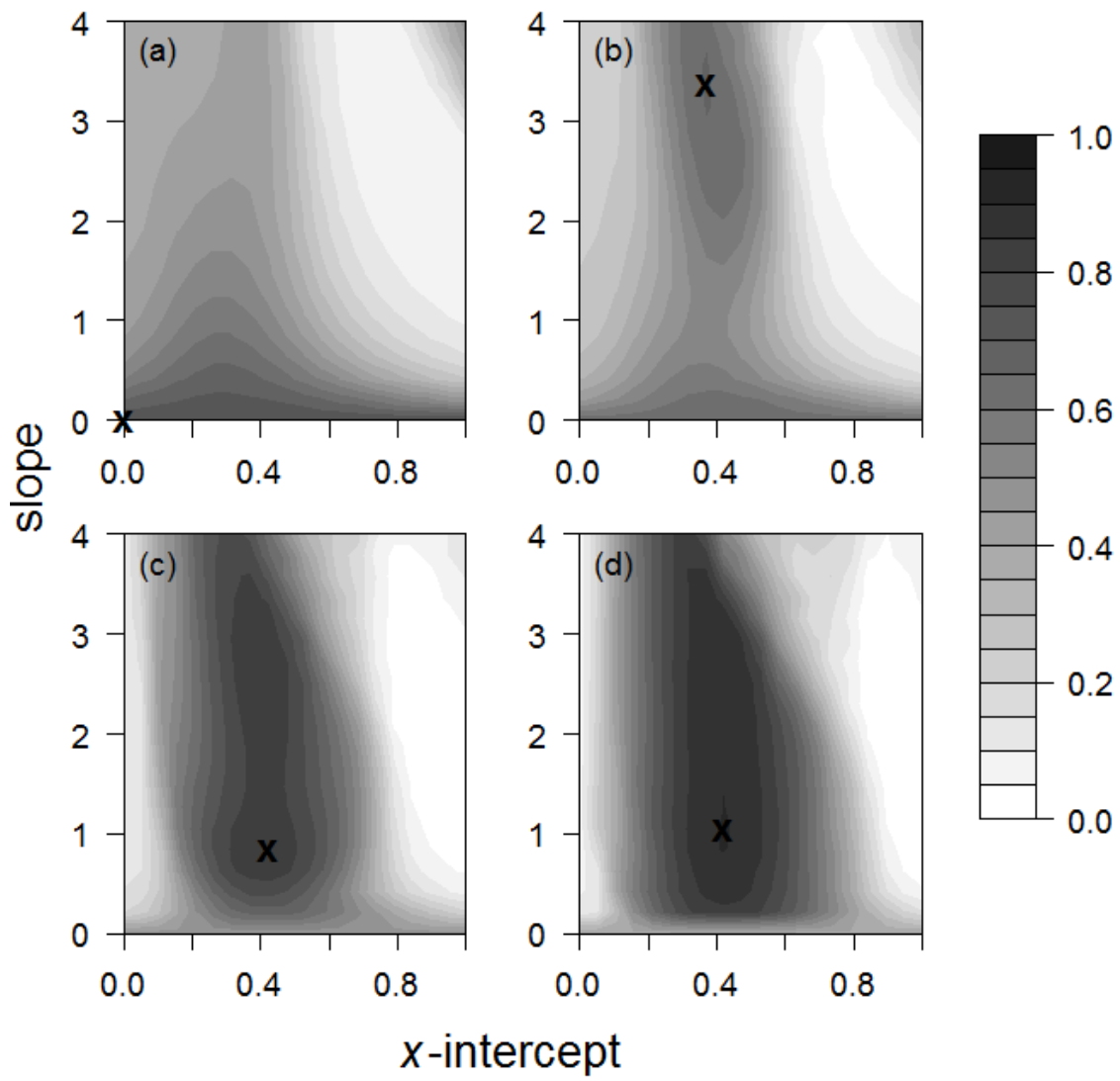


Figure 5. Profiles of cumulative catch calculated over (a) 20, (b) 30, (c) 60, and (d) 95 years over a range of x-intercepts and slopes relative to the cumulative catch for the optimal CER. The maximum cumulative catch is marked with a black cross.

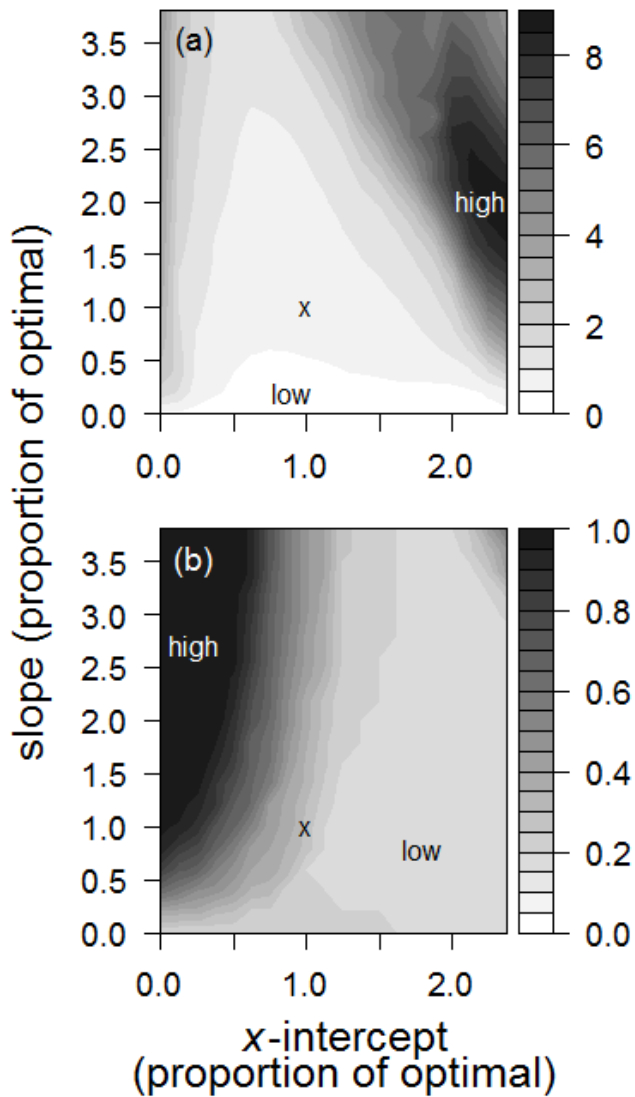


Figure 6. Two-dimensional profile of (a) the interannual variation (CV) of the catch (averaged over simulations), and (b) the probability of falling below 25% of B_{MSY} during any time-step after year 5 (the time of control-rule implementation) over values for x -intercepts (as a proportion of the optimal x -intercept) and slopes (as a proportion of the optimal slope) of DRCRs for the base-case scenario. The optimal DRCR is marked with a black cross.

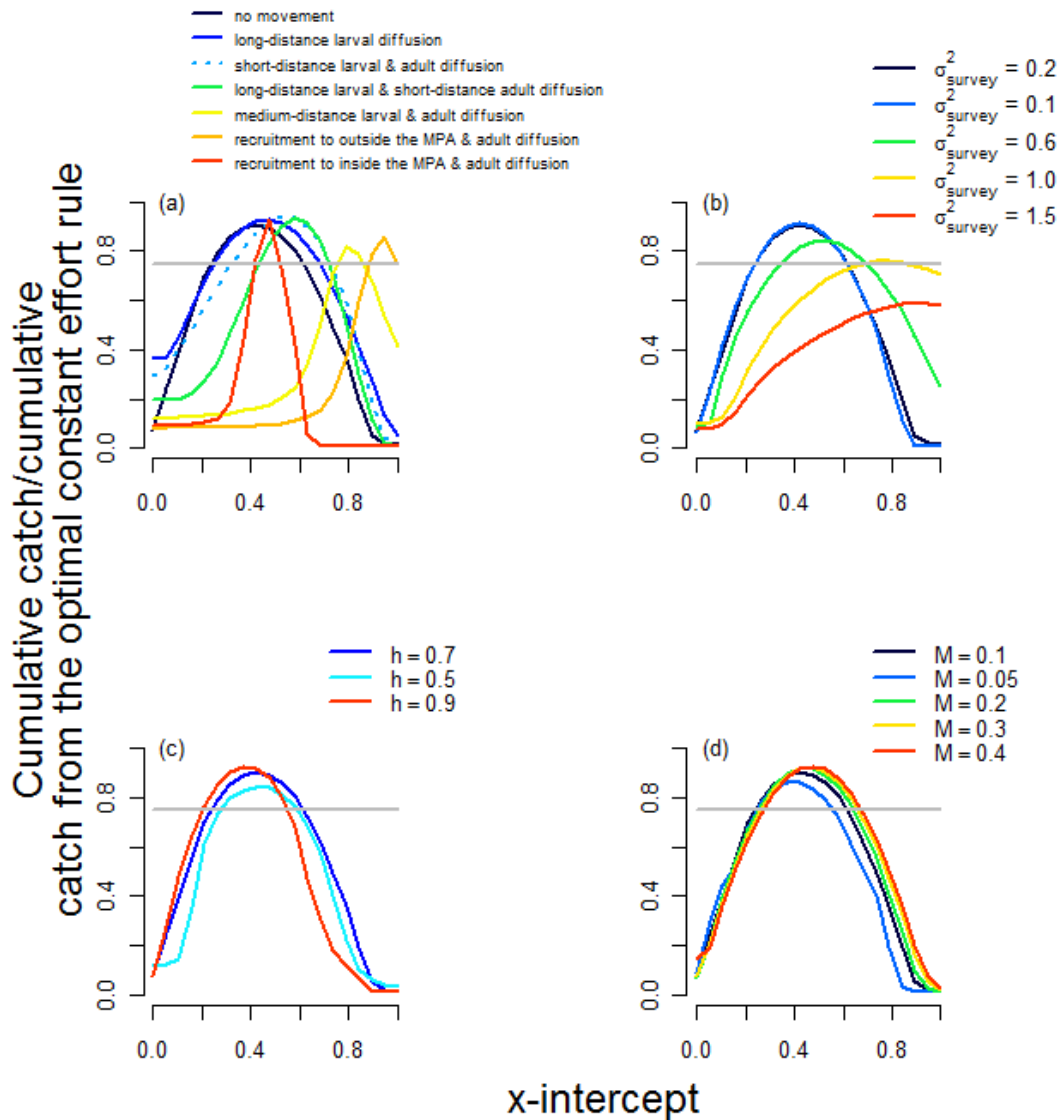


Figure 7. Cumulative catch (scaled to the cumulative catch of the scenario-specific optimal CER) for values of the x -intercept of the DRCR for (a) movement patterns of larvae and adults, (b) survey CV s (σ_{survey}^2), (c) steepness (h), with $h = 0.3$ omitted because the optimal slope was 0, so all x -intercepts produced the same cumulative catch, and (d) natural mortality (M). For each line (scenario), the slope of the DRCR was fixed at the value for the scenario-specific optimal DRCR. The horizontal grey line shows 75% of the cumulative catch under the optimal CER for each scenario.

Chapter 2. Accounting for marine reserves using spatial stock assessments

Abstract

Some fish stock assessments are conducted in regions that contain no-take marine reserves. Marine reserves can cause substantial spatial heterogeneity in fish biomass by allowing a build-up of biomass inside their borders while fishing pressure is maintained or increased outside. Spatial heterogeneity in the distribution of fish biomass is a known issue for stock assessments, potentially leading to bias in estimates of current biomass, but stock assessments do not typically account for the spatial heterogeneity caused by marine reserves. We use simulation modeling to analyze the ability of several stock assessment configurations to estimate current biomass after the implementation of a single, large no-take marine reserve. We use age-structured two-dimensional spatial operating models with three patterns of ontogenetic movement to represent the “true” underlying population dynamics. Results show that assessing populations as a single stock without accounting for the no-take marine reserve results in severe underestimation of biomass for two of the three patterns of movement. Performing separate assessments for fished and protected areas leads to improved estimation performance in the absence of movement between assessment areas, but can severely overestimate biomass otherwise. Performing a spatial assessment with estimation of movement parameters between areas was the best way to assess a species with non-directed, low movement rates and for situations where movement patterns were unknown. This assessment model was unable to estimate movement for two of the three movement patterns, but correctly estimated

current biomass in the absence of a marine reserve. Applying this assessment method when there is a marine reserve shows that differences in biomass and proportions of older fish in the marine reserve and that in adjacent fished areas informs many of the movement parameters.

Introduction

No-take marine reserves (NTMRs) have been implemented in many marine ecosystems to conserve biodiversity, reduce bycatch, and protect valuable habitat (Anon., 1979, Anon., 1992, HDAR, 1992, GBRMPA, 2004, MLPA, 2008). Many of these NTMRs are implemented in addition to other fishery management regulations, such as catch limits. For example, groundfish species off the U.S. West Coast are affected by various types of closed areas and are managed using catch limits that are required by federal and state law (MLPA, 2008, CFR, 2010, MSRA, 2007). Catch limits for federally managed fish stocks off the U.S. West Coast are based on control rules, functions that link the estimated biomass from a stock assessment to an “Overfishing Level” (OFL) and an “Acceptable Biological Catch” (ABC). The catch limit that is implemented (the Annual Catch Limit; ACL) must not exceed the ABC (MSRA, 2007), creating a direct linkage between estimated biomass from stock assessments and catch regulations.

NTMRs may affect the performance of stock assessment methods and, consequently, the specification of catch regulations (Punt and Methot, 2004, Holland, 2002, Field et al., 2006). Many empirical studies show evidence of fish biomass building within NTMRs over time, creating spatial heterogeneity between the biomass of fish inside and outside of NTMR boundaries (e.g. McCook et al., 2010, Aburto-Oropeza et al., 2011, Lester et al., 2009). The magnitude of difference in density will depend on fishing pressure outside

NTMRs, stock status prior to NTMR implementation, productivity, movement characteristics, habitat, and other environmental factors (Hilborn et al., 2006, Claudet et al., 2010). Spatial heterogeneity in the distribution of fish biomass and changes in the distribution of biomass and fishing effort are known problems for stock assessment methods, leading to biased assessment results and subsequent mis-specification of catch limits if not adequately taken into account (Walters, 2003, Maunder et al., 2006). After an NTMR is implemented, fishery catch-rates will not reflect abundance within NTMRs; if biomass increases within NTMRs, fishery catch-rates may remain low even as total biomass increases (hyperdepletion; Walters and Martell, 2004). In addition, fishing effort has been shown to concentrate along the border of marine reserves (“fishing the line”), where catch-rates may be higher than in fished areas further from NTMRs (Murawski et al., 2000). Hence, fishery catch-rates may not reflect abundance for all fishable areas; if abundance is lower in fishable areas further from the NTMR where effort is lower, “fishing the line” could cause hyperstability in fishery catch-rate data.

It is typical to ignore the presence of NTMRs in stock assessments and to conduct a single assessment for the entire range of the fish stock, using fishery catch-rate data that is aggregated over the entire range (e.g. Hamel et al., 2009, Cope and Key, 2009). Monte Carlo simulation (e.g. Patterson and Kirkwood, 1995, Punt et al., 2002) has been used to explore the implications of assessing fish stocks affected by NTMRs with statistical catch-at-age models that are commonly used to assess U.S. West Coast fish stocks. Punt and Methot (2004) showed using simulations that conducting a single assessment (using a statistical catch-at-age model) with fishery and survey catch-rate data aggregated over the stock distribution could result in underestimates of spawning stock biomass and depletion

when there is an NTMR. The magnitude of bias increased with the number of years since NTMR implementation and increased faster for a species with higher productivity (lingcod) than for a species with lower productivity (widow rockfish). Punt and Methot (2004) showed that problems with underestimation could be resolved by conducting separate assessments for the fished area and the NTMR, assuming that survey data were available for the NTMR. However, this method overestimated biomass when movement rates between the fished area and NTMR were high for a model with diffusive movement rates that increased with age. Garrison et al. (2011) showed that when conducting separate assessments (using Stock Synthesis (SS), a statistical catch-at-age model; Methot 2009) for a fished area and an NTMR, the NTMR could inform natural mortality estimates for a sedentary species. However, improvements in natural mortality estimates were lost when there was movement between the fished area and the NTMR. Garrison et al. (2011) then showed that estimates in natural mortality once again improved by estimating movement rates between the fished area and the NTMR. However, Garrison et al. (2011) assumed that the movement model on which the assessment was based was correct and that movement was diffusive (non-directional) and increased with age.

Realistically, the spatial dynamics of fish populations will be more complex and will occur at a finer scale than those that could be included in an assessment model without an unreasonably large increase in model complexity. For instance, some rockfish species are thought to exhibit ontogenetic movement across depths or habitats. Although the exploration of the movement characteristics of fish species is an active area of research (e.g. Jorgensen et al., 2006, Hyde and Vetter, 2009), little is known about larval and adult movement characteristics for many species. Therefore, assessment methods are needed

that can estimate biomass without prior knowledge or data about fish movement.

Furthermore, potential biases in assessments from hyperstability in fishery catch–rate data (due to fishing fleets “fishing the line” of NTMRs) have not been explored.

This study evaluates (1) the ability of a spatially–structured Stock Synthesis model with estimation of movement among areas (the MULTI configuration) to estimate spawning stock biomass (SSB) given an operating model with movement dynamics that occur at a finer spatial resolution than the spatial structure of the assessment model (as is realistically the case); (2) the ability of the MULTI configuration to estimate SSB for the same operating models as for (1), but when there is an NTMR in the middle of the spatial grid of the operating model (OM) for the last 30 years of an 80-year simulation period; and (3) the ability of the MULTI configuration to estimate movement parameters with and without an NTMR to determine whether additional information on movement parameters is necessary to estimate SSB and whether an NTMR could provide information on movement.

Performance of the MULTI configuration was compared to that of two other commonly-used assessment configurations: (a) one aggregated assessment (the SINGLE configuration), which is the method most commonly used for assessments currently, regardless of movement dynamics and the influence of NTMRs; and (b) three separate assessments (the 3ASMT configuration), one assessment for each of two fished areas (Areas 1 and 3 in Figure 1) and a third assessment for the NTMR (Area 2 in Figure 1).

Methods

We evaluated the performance of the assessment methods using Monte Carlo simulation, which involves five steps. (i) creation of an age- and spatially-structured fish

population dynamics model (the operating model (OM); Appendix B) to represent the “true” biological state of the system, (ii) specification of the 80-year time-trajectory of fishing mortality based on pre-determined management regulations, (iii) generation of data from the OM, (iv) application of the assessment model configurations to the simulated data, and (iv), evaluation of the performance of the configurations by comparing the predictions from the assessment model to the true spawning stock biomass (SSB) in the OM. We describe each of these steps in more detail below.

The Operating Model

The OM was an age- and spatially-structured population dynamics model (see Appendix B for details). Population dynamics occurred within each of 90 spatial cells, with 18 cells alongshore and 5 inshore-offshore (Figure 1a) to explore the impacts of assessing fish species with population and movement dynamics that occur at a much finer spatial resolution than can be taken into account in the data collection and assessment process. Fish in each spatial cell were connected via the distribution of recruitment over space and diffusion and advection of adults. Several studies have shown that fishing fleets tend to fish near the border of NTMRs because biomass (and hence catch-rates) are higher due to spillover of fish from the NTMR to the fished areas (Murawski et al., 2000). Therefore, the distribution of fishing effort over space occurred as a function of the relative biomass in each spatial cell, with more fishing effort applied in the areas with the highest levels of biomass (Equation B.14).

OM Scenarios

The OM was used to conduct projections over 80 years (Figure 1b), starting at unfished equilibrium. We modeled a long time-series of data (50 years) with considerable contrast in catch history. This eliminated the possibility of simultaneously testing the role of limited data and the role of an NTMR in contributing to bias and variance in assessments. We found the catchability, q , that resulted in an SSB of 40% of unfished SSB after 50 years of fishing given an assumed effort series where effort increased for 10 years, remained constant for 6 years, and then declined. An NTMR was then implemented in the middle 1/3 of the alongshore cells, covering all of the cells in the inshore-offshore direction (Figure 1a, grey shading; Figure 1b). Fishing was simulated at an effort level so that the SSB was 40% of the unfished level (averaged over simulations) in year 80 (Figure 1b).

We simulated three movement scenarios that represent a range of the types of movement thought to occur across rockfish populations (Figure 2 and Table S.1); the phrases in quotes will be used to refer to these movement scenarios throughout the text: (1) the “alongshore diffusion” pattern, where recruits were distributed among the alongshore cells that were furthest inshore, after which animals move ontogenetically from “inshore” to the “shelf” with simultaneous diffusion alongshore; (2) the “sedentary” pattern where fish recruited to all spatial cells with no movement thereafter; (3) the “alongshore advection” pattern where fish recruited to the southeast corner of the grid and advected ontogenetically towards the northwest corner of the grid with low diffusion rates (Figure 2).

We conducted a base-case scenario, parameterizing the model to resemble a rockfish-like species (see Table S.2 for parameter values).

Generation of Data

Catch (in weight), fishery and survey catch-per-unit effort (cpue) data, and age-composition data from both surveys and catches were generated and used in assessments. Age-composition data were assumed to be multinomially distributed about the true age composition. Catch in each year was assumed to be known without error. Catch data were generated yearly, while it was assumed that surveys occurred every two years. Assessments were conducted either using data from three assessment areas (Areas 1-3 in Figure 1a which correspond to alongshore areas 1-6, 7-12, and 13-18, respectively, and included all cells in the inshore-offshore direction) or using data aggregated over all cells.

Generation of data by assessment area

Fishery catch-per-unit-effort (cpue) indices were simulated by assuming that observed effort is log-normally distributed about the true fishing effort, where $\varepsilon_{A,t}^{obs} \sim N(0, \sigma_{obs,A}^2)$.

The cpue for assessment area A at time t is therefore

$$(1) \quad \text{cpue}_{A,t} = \frac{\left(\sum_{i,j \in A} \dot{C}_{i,j,t} \right)}{\sum_{i,j \in A} E_{i,j,t} \exp\left(\varepsilon_{A,t}^{obs} - \frac{\sigma_{obs,A}^2}{2} \right)},$$

where $\dot{C}_{i,t}$ is the catch (in biomass) in cell (i,j) at time t and $E_{i,j,t}$ is the true effort in area (i,j) at time t .

Survey cpue was generated as a function of the biomass available to the survey and lognormal observation error by assessment area, A , where $\varepsilon_{A,t}^{Sobs} \sim N(0, \sigma_{Sobs,A}^2)$.

$$(2) \quad \text{cpue}_{A,t}^{\text{survey}} = \sum_{i,j \in A} \sum_a \left[\left(N_{a,i,j,t} e^{-M/2} - C_{a,i,j,t} / 2 \right) S_a w_{a,\text{mid}} \right] \exp(\varepsilon_{A,t}^{\text{Sobs}} - \sigma_{\text{Sobs},A}^2 / 2)$$

Generation of aggregated data

Lognormal observation error was applied at the area (A) level and the observed effort was summed over cells and areas such that the aggregated fishery cpue index for a given time–step was the total catch (in biomass) divided by the total observed effort for that time–step. Aggregated survey cpue data was the sum of survey cpue values over assessment areas. Survey and fishery cpue CVs were defined at the spatial scale of assessment area ($\text{CV}_{\text{Sobs},A} = \sigma_{\text{Sobs},A}$, $\text{CV}_{\text{obs},A} = \sigma_{\text{obs},A}$ for survey and fishery cpue CV, respectively) and so the aggregated survey (CV_{Sobs}) and fishery (CV_{obs}) cpue CVs were:

$$(3) \quad \text{CV}_{\text{Sobs}} = \sqrt{\sum_A \left(\frac{\sigma_{\text{Sobs},A}}{N_{\text{area}}} \right)^2}, \quad \text{CV}_{\text{obs}} = \sqrt{\sum_A \left(\frac{\sigma_{\text{obs},A}}{N_{\text{area}}} \right)^2},$$

where N_{area} is the number of assessment areas.

Age composition data was generated with a sample size of 67 for each of three assessment areas when data are generated spatially (for each of three assessment areas) and a sample size of 201 when aggregated data are generated. Survey and fishery cpue CVs at the spatial scale of the assessment area were assumed to be $\sigma_{\text{Sobs},A} = \sigma_{\text{obs},A} = 0.2$.

Assessments

Assessments were conducted using Stock Synthesis v3.22b (Methot, 2009), which is a statistical catch-at-age model allowing for one or multiple assessment areas. The population dynamics in SS and in the OM are identical except for the way that space is modelled (i.e. running the OM with one spatial cell will produce identical results to

running SS with the same parameter values). See Appendix C for further details on the SS assessment model.

Three assessment configurations were evaluated in this study. The phrases used to refer to each are: (1) the SINGLE configuration, where data were aggregated across all spatial cells, including cells within the NTMR; (2) “three assessments”, one for each fished area and one for the NTMR (see Figure 1a), where the three assessments were completely distinct from one another; and (3) the MULTI configuration with estimation of movement parameters. The MULTI configuration utilized data aggregated across spatial cells within each assessment area (the two fished areas and the NTMR) and movement was estimated between these three areas. Referring to Figure 1, the assessment areas were Areas 1, 2, and 3 which corresponded to alongshore areas 1-6, 7-12, and 13-18, respectively, each spanning the cells in the inshore-offshore direction; movement parameters were estimated between each of the three areas.

In the base-case scenario, we estimated recruitment residuals starting in year 34 (2 years after the start of fishery), R_0 , and logistic fishery– and survey–selectivity–at–age. We conducted assessments in years 51, 66, and 81 (corresponding to 1, 16, and 31 years after the implementation of an NTMR in scenarios with an NTMR) to evaluate changes in bias and precision over time as a result of changes in the distribution of biomass after NTMR implementation. The CVs of generated data were set to their true values. Effective sample size was assumed to be 33 for each of the three spatial assessment areas (used for the 3ASMT and MULTI approaches) and 99 for the SINGLE assessment.

Sensitivity Analyses

Fish movement from the NTMR (where there may be a higher proportion of older fish than in fished areas) to the fished areas has the potential to change the proportions-at-age in fished areas. Therefore, the role of catch-at-age data was explored by setting the effective sample size in the assessment models to 1; this greatly diminishes the influence of catch-at-age data on the likelihood in the assessment. In addition, an analysis was conducted to explore the joint effect of catch-at-age data and spatial fishing fleet dynamics by both setting the effective sample size of catch-at-age data to 1 and changing fishing fleet dynamics so that fishing effort occurred uniformly over space.

Assessments conducted for the base case scenario estimated R_0 , selectivity parameters, and recruitment deviations, but correctly specified and did not estimate natural mortality. Natural mortality estimates can be confounded with estimates of other parameters (movement parameters in particular). Therefore, a set of sensitivity analyses was conducted where natural mortality was estimated, rather than specified. In addition, the base case scenario assumed that no local recruitment variability occurred, but evidence exists that local variability may be substantial for some fish populations (Field and Ralston, 2005). Hence, sensitivity analyses were performed with local recruitment variability (σ_{R_L}) accounting for half of the total recruitment variability in the OM. Global recruitment variability (σ_{R_G}) was set to 0.42 and the amount of local recruitment variability that would lead to total recruitment variability of 0.6 was found; the values for σ_{R_L} were 1.31, 1.87, 1.23 for the alongshore diffusion, sedentary, and alongshore advection scenarios, respectively. These values are very high because the total variability

caused by local variability approaches 0 as the number of spatial cells becomes very large.

Performance Measures

The relative error ($100 \times (\text{estimated} - \text{true}) / \text{true}$) in each year included in the assessment, as well as the median relative error and the median absolute relative error (MARE: $100 \times |\text{estimated} - \text{true}| / \text{true}$) in SSB for years in which an assessment was conducted: 51, 66, and 81 (1, 15, and 30 years after the implementation of an NTMR) were calculated. The MARE measures the combined magnitude of bias and variance in assessment results, but bias and variance cannot be disentangled and the direction of bias cannot be ascertained from the MARE. The relative error and median relative error measure the magnitude and direction of bias in assessment results. In addition, 90% intervals of the relative error in SSB were calculated and graphed to show variance in assessment results.

The assessment method that would lead to the smallest potential errors in the estimation of SSB given no knowledge of, or an incorrect assumption about, the movement patterns of the species being assessed (thus minimizing the maximum potential errors in SSB) was found. This is called the minmax solution and was found by identifying the movement type with the largest MARE in SSB for each assessment method and then identifying the assessment method for which the species with the largest MARE in SSB was the smallest.

Results

Base case scenario

Estimation of spawning stock biomass

The SINGLE and MULTI assessments estimated SSB with negligible bias in the absence of an NTMR for all movement patterns with few differences in the magnitude of variance between assessment configurations (Figure 3, Table 1). The 3ASMT configuration resulted in underestimation of SSB for the alongshore advection movement patterns (Figure 3, Table 1).

The MULTI assessment led to the lowest MARE among the three assessment configurations in estimates of SSB for all three movement patterns in the presence of an NTMR for assessments conducted in year 81 (Figure 4, Table 2). The MULTI assessment was also the configuration with the lowest magnitude of MRE for the alongshore diffusion movement pattern (Table 2). The MULTI assessment did not have the lowest magnitude MRE for the sedentary and alongshore advection movement patterns in the presence of an NTMR, but led to estimates of SSB with relatively small MREs (Table 2, Figure 4). The SINGLE assessment substantially underestimated biomass and produced very negative MREs for the alongshore diffusion and sedentary movement patterns (-22.133 and -52.781, respectively) after the implementation of the NTMR (Table 2, Figure 4). The 3ASMT configuration substantially overestimated biomass for the alongshore diffusion and alongshore advection movement patterns, producing large MAREs and MREs for assessments conducted in years 81 and 66, but, as expected, led to the smallest-magnitude MRE among the assessment configurations for a stock with the

sedentary movement pattern in the presence of an NTMR for assessments conducted in years 81, 66, and 51 (Figure 4, Table 2).

The fishery catch–rate data caused the SINGLE assessment to underestimate SSB for all three movement patterns in the presence of an NTMR (Figure 4, Table 2) because the biomass that builds up within the NTMR is not captured by the fishery, which operates exclusively outside the NTMR (Figure 5). Figure 5 shows the relative catch–rates in aggregate and by area for the fishery and the survey for the alongshore diffusion movement pattern when there is no process or observation error. The aggregated survey catch–rate is substantially higher than the aggregated fishery catch–rate (black dots and line, respectively). The fishery catch–rate data have a substantially greater influence on assessment results than the survey data in part because there is twice as much fishery data. This underestimation when using the SINGLE assessment is negligible for the alongshore advection movement pattern because individuals pass through the NTMR at intermediate ages, but few stay within the NTMR permanently. Thus, biomass does not build up within the reserve to the same extent as for the other movement patterns and the fishery catch–rate data more closely reflect the total biomass.

Estimation of SSB using the 3ASMT configuration

The 3ASMT configuration most closely matches the true dynamics of the sedentary movement pattern in that there is no connectivity of adults among assessment areas in the operating or assessment model and the resulting bias in the estimation of SSB is negligible (Figure 4, Table 2). In the case of the alongshore diffusion movement pattern, older fish accumulate within the NTMR over time and some of these older fish diffuse into fished areas, increasing the proportion of older fish in the age composition data for

the assessments of the two fished areas and thus causing positive bias in biomass estimates for these areas (Table 2). When the influence of age composition data is diminished by setting the effective sample size to 1, the MRE decreases by 16%, confirming that proportions-at-age contribute to the overestimation of biomass when the 3ASMT configuration is applied to a stock with alongshore diffusion (Table 4). However, substantial positive bias remains after removing the influence of age composition data (Table 4).

Another potential cause of overestimation of SSB in this scenario is the influence of fishing fleet dynamics. Exploitable biomass is greatest in spatial cells closest to the NTMR, which can inflate fishery catch-rate indices and influence proportions-at-age in age composition data. However, a sensitivity analysis where spatial fishing fleet dynamics are removed (uniform fishing effort over space) did not decrease the magnitude of the MRE or MARE and an analysis where both catch-at-data and spatial fishing fleet dynamics are removed (uniform fishing effort over space) show that overestimation is not caused by spatial fishing fleet dynamics, or “fishing the line” (Table 4); the MARE and MRE for the sensitivity analysis with uniform fishing fleet dynamics are very similar to those for the base case scenario (Table 2). In addition, the MRE for the sensitivity analysis with an effective sample size of 1 with spatial fishing fleet dynamics (36.52) is almost identical to that for the sensitivity analysis with an effective sample size of 1 and uniform fishing effort over space (36.27, Table 4).

Figure 6a & e show that R_0 is overestimated in the fished areas, but that the 3ASMT configuration is able to estimate the trend in SSB over time. In addition, on average, the assessment estimates slightly negative recruitment deviations prior to implementation of

the NTMR and slightly positive deviations for many years after the NTMR is implemented (Figure 6c). (Results for assessments in the fished areas are identical, so results for only one fished area are shown in Figure 6.) After the NTMR is implemented, diffusion from the NTMR to the fished area becomes greater than diffusion from the fished area to the NTMR as biomass builds within the NTMR. Thus, there is a net contribution of biomass to the fished areas that was not produced in those areas. Natural mortality and steepness are not estimated, so the assessment accounts for this extra biomass by estimating larger values for R_0 (Figure 6e). The assessment in Area 2 where the NTMR is implemented in year 51 is able to estimate SSB prior to NTMR implementation, but overestimates SSB afterwards (Figure 6b). In the years just after NTMR implementation, the SSB does not build up as quickly as expected given that no catches are occurring and SSB never increases to B_0 due to alongshore diffusion (net emigration). This is likely why estimates of R_0 are smaller than true R_0 (Figure 6f) and recruitment deviations are negative for many years after NTMR implementation (Figure 6d). However, the assessment is still not able to fully account for the slow rate of build-up of biomass within the NTMR caused by net emigration after the NTMR is implemented. Much more data is available in this area prior to NTMR implementation than afterward (fishery and survey catch-rate data and catches, rather than just survey information) and therefore the assessment is able to estimate SSB quite well prior to NTMR implementation, making up for the underestimation of R_0 by estimating very large recruitment deviations in the initial years of the model to fit the data when the population is at or close to unfished (Figure 6d). Recruitment within Area 2 is local. A small proportion of a cohort will emigrate in each year such that net emigration of older cohorts

is a greater proportion of the cohort than for younger cohorts. In the last couple of years of simulation, only a small proportion of the youngest cohorts have already emigrated from the NTMR, perhaps making these cohorts appear large, relative to cohorts of older fish and this may be why recruitment deviations are positive in the last couple of years of estimation.

The alongshore advection movement pattern is an extreme violation of the assumption of the 3ASMT configuration that the fish stock is three separate, unconnected populations. Here, a proportion of the mid-aged fish that would typically be caught are protected within the NTMR and emerge from the reserve to one of the fished areas to be caught at an older age. This increases the proportion of older fish in the age-composition data for the rightmost fished area (Area 3), increasing biomass estimates (Figure 4).

Patterns in variance of SSB estimates

Variability in estimated SSB increases after the first couple of years included in the assessments in Figures 3 and 4. While no recruitment deviations are estimated in the assessments until year 34, process error on recruitment is modelled in the OM beginning in year 2. Hence, the additional variability in relative error in early years in assessments reflects a burn in period whereby the true spawning stock biomass becomes more variable over time as age classes with process error on recruitment become older and constitute a greater proportion of the SSB (and meanwhile SSB in the assessment model remains constant due to the absence of a fishery and recruitment deviations until year 32 and 34, respectively).

The min-max method: what assessment method would perform best in the absence of knowledge about movement patterns?

The minmax solution with and without an NTMR and for each assessment year was the MULTI configuration (highlighted in grey in Tables 1 and 2; Figures 3 and 4). The minmax solution minimizes the maximum potential MARE that would occur if an assessment were conducted for a species with an unknown movement pattern or a species for which the assessment author had misinformation about the movement pattern of the species being assessed.

Estimation of movement parameters for the MULTI configuration

The MULTI configuration was able to estimate SSB accurately for the alongshore diffusion and sedentary movement patterns when there was no NTMR (Figure 3), even though estimates of movement parameters were both very imprecise and inaccurate (Figures 3 & 7). The assessment model fit the data for numerous assumptions about movement parameters. This is sensible because there is no relevant contrast in the data from which the estimation model could estimate movement rates in the absence of the NTMR. Estimates of recruitment allocation parameters were both precise and accurate for the alongshore diffusion and sedentary movement patterns (Figure 7). Movement estimates for the alongshore advection species with no NTMR were very close to the true values; the spatial life history of the alongshore advection species informed the movement parameters (Figure 7). The assessment model slightly underestimated the proportion of recruits settling in Area 1 and slightly overestimated the proportion of recruits settling in Area 2 (Figure 7).

Having an NTMR led to substantial information about movement for the alongshore diffusion and sedentary movement patterns (Figure 8). For the alongshore diffusion and sedentary movement patterns, the assessment model correctly estimated the large proportion of fish that stay in the NTMR (Area 2; “TwoToTwo” in Figure 8) and the proportion of fishing moving in and out of the NTMR (Area 2). The model predicted a large exchange of fish between the fished areas for the sedentary movement pattern and estimates of movement among fished areas was uncertain for the sedentary and alongshore diffusion movement patterns (Areas 1 and 3; Figure 8). The dynamics are the same in each of the fished areas for these two movement patterns and thus the assessment has no information or defining feature on which to base estimates of exchange among the fished areas; a lower likelihood was often achieved by having a large exchange between the fished areas (“OneToThree” and “ThreeToOne”). The NTMR had little effect on the ability of the assessment to estimate parameters for the alongshore advection movement pattern (Figures 7 & 8). Likewise estimates of recruitment allocation were not influenced by the NTMR for any of the movement patterns (Figures 7 & 8).

Additional sensitivity analyses

Including local recruitment variability in the OM led to negative bias in estimates of SSB for the SINGLE and 3ASMT configurations for assessments with a sedentary movement pattern with no NTMR (Table 3, rows 16-17, column 4), scenarios for which there was no negative bias in the base case scenario (Figure 3). This phenomenon is explored further in Appendix D. The estimation of natural mortality (M) in assessments did not result in any substantial differences in the MARE from the base-case scenario

results for any of the scenarios or assessment configurations in the presence of an NTMR (Table 4).

Discussion

Estimates of SSB from the MULTI configuration were very precise and accurate, even though the assessment was often unable to estimate the movement parameters correctly among fished areas. The variation in estimates of the movement parameters for scenarios without an NTMR indicates that the MULTI configuration was able to fit the data using numerous assumptions for the movement parameters. The survey catchability was the same among the three assessment areas (Areas 1 -3 in Figure 1) in the OM and was restricted to be the same across these areas in the MULTI configuration; this restriction tells the assessment that the magnitude of the survey catch–rate data can be compared across areas and, with the help of age composition data, likely allows the assessment to correctly identify the allocation of recruitment among areas. Future studies could explore the influence of the assumption of spatially–invariant survey catchability by generating data from the OM with different catchability coefficients and allowing the MULTI configuration to estimate different survey catchability coefficients for each area.

The MULTI configuration led to the lowest MARE in SSB estimates among all assessment configurations for all of the movement patterns when there was an NTMR and thus was the minmax solution for assessing a species with an unknown movement pattern. That is, the MULTI configuration is the least likely of the three assessment configurations explored to produce an estimate of SSB with an extremely large MARE if the assessment author is mistaken or simply does not know anything about the movement patterns of the species that he or she is assessing. With the exception of a few well-

studied species and highly migratory species, often little is known about fish movement patterns and in these cases, it may be important to know which assessment method has the least potential for being very wrong. The SINGLE configuration produced reasonable estimates of SSB for the alongshore advection movement pattern and the 3ASMT configuration led to reasonable SSB estimates for the sedentary movement pattern and have the potential to perform well in these cases, given correct knowledge about movement parameters.

The NTMR provided considerable information on the movement parameters between a fished area and the area with the NTMR whereas little was known about movement parameters without an NTMR (i.e. for the alongshore diffusion and sedentary movement patterns). The estimates of movement in and out of the NTMR and the estimate of the proportion of individuals that stay in the NTMR were precise and accurate even for the two movement patterns where little was known about movement without an NTMR. This suggests that we might be able to learn something about fish movement from NTMRs, given that surveys occur within NTMRs and are able to use the same sampling methods and assume the same catchability both inside and outside NTMRs. However, an additional source of data, such as tagging data, would be needed to learn more about fish movement patterns between two fished areas. In addition, future study would be needed to determine whether movement parameters between fished areas and NTMRs could still be estimated accurately if additional parameters were estimated, such as steepness and growth parameters, mis-specification of natural mortality, as well as allowing movement in the assessment model to change with age. Furthermore, additional flexibility in the estimation of selectivity parameters, such as the ability for the model to estimate dome-

shaped selectivity or different selectivity patterns among areas and/or time blocks could confound the estimates of movement parameters.

Alternatively, flexibility and creativity in the design of the estimation of selectivity parameters within a single area or multi-area assessment could be utilized to account for the implementation of an NTMR and movement dynamics without estimating movement parameters. For instance, one way to account for an NTMR may be to allow a change in selectivity pattern after the implementation of an NTMR within a single, aggregated assessment. For a sedentary or alongshore movement scenario, the assessment may estimate dome-shaped selectivity after NTMR implementation, reflecting that a large proportion of older fish are protected within the NTMR. Future studies could compare approaches accounting for spatial dynamics by way of selectivity to approaches that explicitly estimate movement parameters.

Punt and Methot (2004) concluded that the 3ASMT configuration was superior to the SINGLE configuration; this work expands on Punt and Methot (2004) by showing that the SINGLE configuration may produce better estimates of SSB than the 3ASMT configuration for a species with directed ontogenetic movement across assessment areas. Additionally, this work expands upon by Punt and Methot (2004) by showing that the MULTI configuration with estimation of movement parameters may be a superior way to estimate SSB when non-directed movement occurs among assessment areas. Punt and Methot (2004) evaluated the performance of similar SINGLE and 3ASMT configurations with no estimation of movement parameters after the implementation of an NTMR. As in this study, Punt and Methot (2004) found that their SINGLE configuration resulted in underestimation of SSB for high values of steepness (0.7 in this study and 0.9 in Punt and

Methot (2004)). However, they found that for widow rockfish, a species with a low value for steepness (0.4), their SINGLE configuration produced reasonable estimates of SSB 20 years after NTMR implementation. With such a low value for steepness, the build-up of biomass within the NTMR occurred very slowly and differences between fishery and survey catch-rates from within the NTMR were minimized, reducing underestimation of SSB. Punt and Methot (2004) found that their 3ASMT configuration performed well for a species with little movement, but that SSB was overestimated at higher movement rates, corroborating the results of this study. Punt and Methot (2004) assumed that fishing effort was homogeneous among areas open to fishing. In this study, fishing fleets fished in cells of highest fish biomass and thus were able to “fish the line.”

Hypothetically, this could lead to increased fishery catch-rates, causing hyperstability in assessments of the fished areas and further contributing to overestimation of SSB for the 3ASMT configuration, but our results showed that spatial fishing fleet dynamics had little effect on the estimation of SSB for the 3ASMT configuration.

The OM includes one large NTMR in the middle of the unit stock, whereas a typical coastline might be a patchwork of small marine reserves (NTMRs and marine reserves that allow limited fishing) and fished areas with some connectivity between fished areas and marine reserves. For example, most assessments along the U.S. West Coast are coast-wide and marine reserves, such as those implemented as part of California’s MLPA process, are small, numerous, and dot the coastline (MLPA, 2008). The study design in this manuscript is an approximation of the patchwork of marine reserves and fished areas where movement represents the aggregate effect of movement in and out of these small areas. However, there are a few potential differences. Smaller marine

reserves are equivalent to higher movement rates and hence the magnitude of build-up within marine reserves may be smaller than for this study. This would decrease biases in the estimation of SSB because fishery and survey catch-rates would be more similar. With many small marine reserves, a higher proportion of the fished area will border a marine reserve such that “fishing the line” may be more representative of biomass in fished areas, reducing the potential magnitude of hyperstability; higher movement rates and less build-up within each marine reserve will reduce differences between fish densities bordering and further away from marine reserves, which would also reduce hyperstability in fishery catch-rate data. Effects of hyperstability may be caused more by differences in habitat or fish behavior in fished areas than by marine reserves. Future studies could explore whether and when a patchwork of small marine reserves would impact bias and variance in assessments.

Tables

Table 1. Median absolute relative errors (MAREs) and median relative errors in SSB (%) for scenarios without an NTMR and assessments conducted in years 81, 66, and 51. The movement scenario with the largest MARE within each assessment configuration is in bold and the min-max assessment configuration among movement methods is highlighted in grey.

	MARE in Year 81	Median Relative Error in Year 81	MARE in Year 66	Median Relative Error in Year 66	MARE in Year 51	Median Relative Error in Year 51
One Aggregated Assessment						
Alongshore Diffusion	0.106	-1.203	0.092	0.674	0.115	-0.723
Sedentary	0.101	-0.974	0.097	0.511	0.112	-0.051
Alongshore Advection	0.136	-7.440	0.107	-5.813	0.140	-9.306
Three Assessments						
Alongshore Diffusion	0.122	-3.101	0.104	-0.254	0.112	-0.770
Sedentary	0.122	-0.386	0.109	0.597	0.117	-0.533
Alongshore Advection	0.092	-5.158	0.126	-6.041	0.062	-4.309
One Multi-Area Assessment						
Alongshore Diffusion	0.097	-0.734	0.090	0.769	0.109	-0.916
Sedentary	0.095	0.069	0.095	1.051	0.109	-0.681
Alongshore Advection	0.096	3.179	0.096	4.347	0.110	0.462

Table 2. Median absolute relative errors (MAREs) and median relative errors in SSB (%) for scenarios with an NTMR implemented in year 51 and assessments conducted in years 81, 66, and 51. The movement scenario with the largest MARE within each assessment method is in bold and the min-max assessment method among movement scenarios is highlighted in grey.

	Median MARE in Year 81	Median Relative Error in Year 81	Median MARE in Year 66	Median Relative Error in Year 66	Median MARE in Year 51	Median Relative Error in Year 51
One Aggregated Assessment						
Alongshore Diffusion	0.231	-22.133	0.277	-27.571	0.116	-1.833
Sedentary	0.528	-52.781	0.518	-51.780	0.117	-0.666
Alongshore Advection	0.149	-11.414	0.141	-11.875	0.140	-8.764
Three Assessments						
Alongshore Diffusion	0.440	43.988	0.301	29.522	0.116	-0.747
Sedentary	0.140	3.228	0.143	3.427	0.119	-0.231
Alongshore Advection	0.567	56.664	0.336	32.425	0.065	-4.313
One Multi-Area Assessment						
Alongshore Diffusion	0.117	4.577	0.106	3.839	0.108	0.246
Sedentary	0.114	-9.421	0.092	-7.748	0.108	0.404
Alongshore Advection	0.128	11.574	0.159	14.515	0.110	1.095

Table 3. Median absolute relative error (MARE) and median relative error (MRE) in SSB (%) for each sensitivity analysis for simulations without an NTMR and with an assessment conducted in year 81 for each assessment configuration and movement scenario.

Sensitivity Analysis	Alongshore Diffusion		Sedentary		Alongshore Advection	
	MARE	MRE	MARE	MRE	MARE	MRE
Base case						
One Aggregated Assessment	0.11	-1.20	0.10	-0.97	0.14	-7.44
Three Assessments	0.12	-3.10	0.12	-0.39	0.09	-5.16
One Multi-Area Assessment	0.10	-0.73	0.10	0.07	0.10	3.18
Effective sample size of 1						
One Aggregated Assessment	0.14	-1.95	0.14	-3.13	0.16	-8.50
Three Assessments	0.17	-6.76	0.17	-5.65	0.11	-7.60
One Multi-Area Assessment	0.14	-1.29	0.14	-1.57	0.14	0.12
Uniform fishing effort						
One Aggregated Assessment	0.10	1.33	0.10	-0.05	0.12	-7.96
Three Assessments	0.11	1.95	0.12	-0.55	0.14	-14.00
One Multi-Area Assessment	0.09	1.71	0.09	0.97	0.10	3.61
Uniform fishing effort and Effective sample size of 1						
One Aggregated Assessment	0.15	2.50	0.14	0.55	0.16	-0.79
Three Assessments	0.18	-1.55	0.18	-3.52	0.18	-16.33
One Multi-Area Assessment	0.14	2.93	0.14	1.37	0.14	3.63
Estimation of natural mortality (M)						
One Aggregated Assessment	0.12	-0.42	0.12	-1.25	0.12	-2.07
Three Assessments	0.10	-0.39	0.10	-0.27	0.36	-35.60
One Multi-Area Assessment	0.12	-0.64	0.12	-1.13	0.11	1.05
Local recruitment variation in OM						
One Aggregated Assessment	0.11	-0.03	0.16	-8.36	0.12	-6.01
Three Assessments	0.14	2.33	0.16	-2.49	0.12	-5.34
One Multi-Area Assessment	0.10	1.43	0.10	1.43	0.10	1.43

Table 4. As for Table 3, but with an NTMR implemented in year 51 for an assessment conducted in year 81.

Sensitivity Analysis	Alongshore Diffusion		Sedentary		Alongshore Advection	
	MARE	MRE	MARE	MRE	MARE	MRE
Base case						
One Aggregated Assessment	0.23	-22.13	0.53	-52.78	0.15	-11.41
Three Assessments	0.44	43.99	0.14	3.23	0.57	56.66
One Multi-Area Assessment	0.12	4.58	0.11	-9.42	0.13	11.57
Effective sample size of 1						
One Aggregated Assessment	0.35	-34.87	0.61	-60.46	0.19	-13.78
Three Assessments	0.37	36.52	0.14	4.38	0.38	37.88
One Multi-Area Assessment	0.16	3.59	0.13	-12.82	0.17	8.75
Uniform fishing effort						
One Aggregated Assessment	0.25	-24.96	0.52	-52.49	0.14	-12.55
Three Assessments	0.44	43.99	0.14	3.89	0.43	42.97
One Multi-Area Assessment	0.13	7.66	0.11	-9.09	0.14	11.79
Uniform fishing effort and Effective sample size of 1						
One Aggregated Assessment	0.36	-35.72	0.60	-60.30	0.17	-10.73
Three Assessments	0.36	36.27	0.14	5.62	0.30	30.09
One Multi-Area Assessment	0.17	8.69	0.11	-11.26	0.18	13.59
Estimation of natural mortality (M)						
One Aggregated Assessment	0.28	-27.59	0.56	-55.64	0.13	-6.83
Three Assessments	0.53	53.38	0.13	5.16	0.53	53.27
One Multi-Area Assessment	0.13	4.87	0.12	-10.98	0.16	11.94
Local recruitment variation in OM						
One Aggregated Assessment	0.22	-21.25	0.56	-55.83	0.13	-8.13
Three Assessments	0.49	48.58	0.19	3.61	0.57	56.50
One Multi-Area Assessment	0.14	6.91	0.20	-12.73	0.15	13.79

Figures

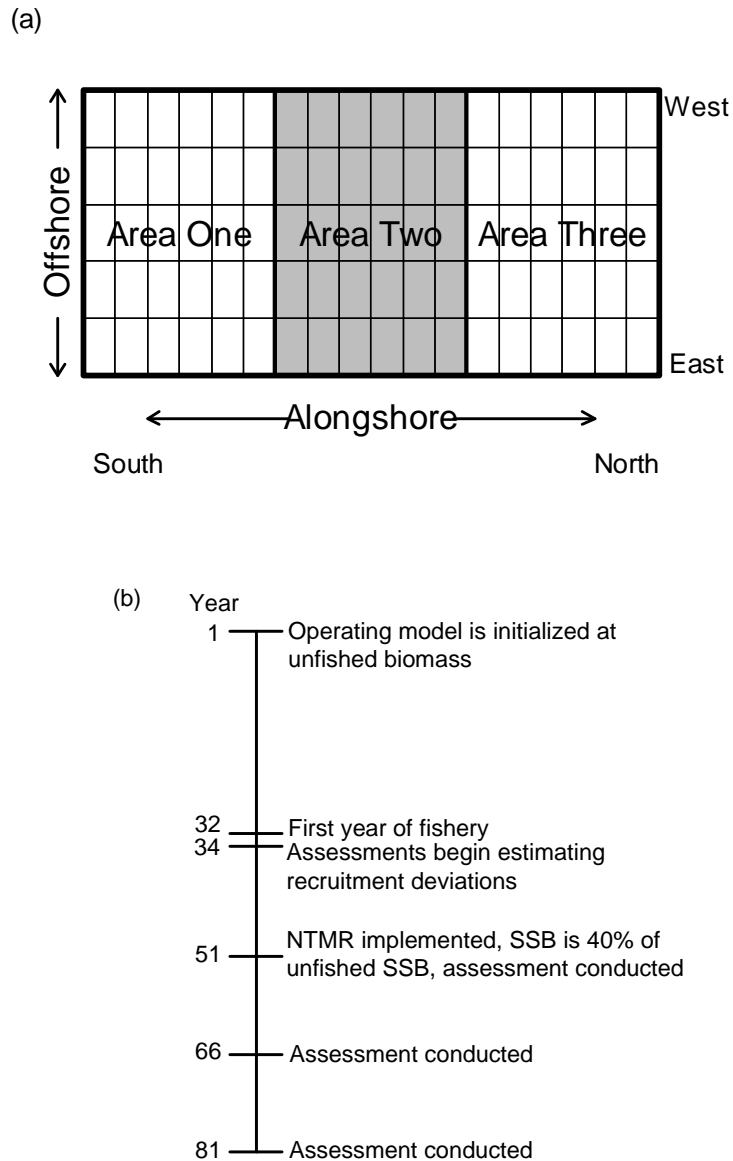


Figure 1. (a) A schematic of the spatial setup of the operating model. The operating model was a grid of 18 cells alongshore and 5 cells inshore-offshore. After 50 years an NTMR was implemented in the middle 1/3 of the alongshore areas (gray shaded region; cells 7-12 alongshore and 1-5 inshore-offshore). The 3ASMT and MULTI configurations used data aggregated within cells 1-6 (Area 1), 7-12 (Area 2), and 13-18 (Area 3) alongshore and the assessment areas spanned the inshore-offshore areas. The SINGLE configuration used data aggregated over all cells. (b) a schematic of the timeline of the simulations.

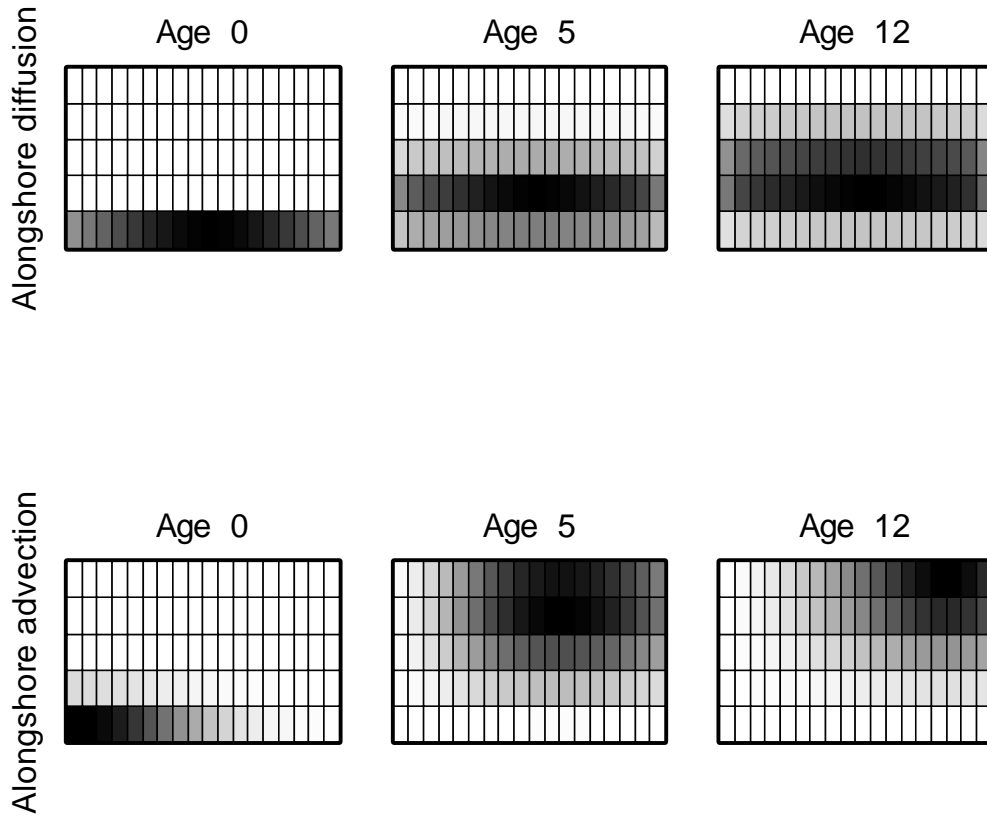


Figure 2. Relative spatial distribution of ages 0, 6, and 12 animals for the “alongshore diffusion” and “alongshore advection” movement scenarios modeled in the operating model.

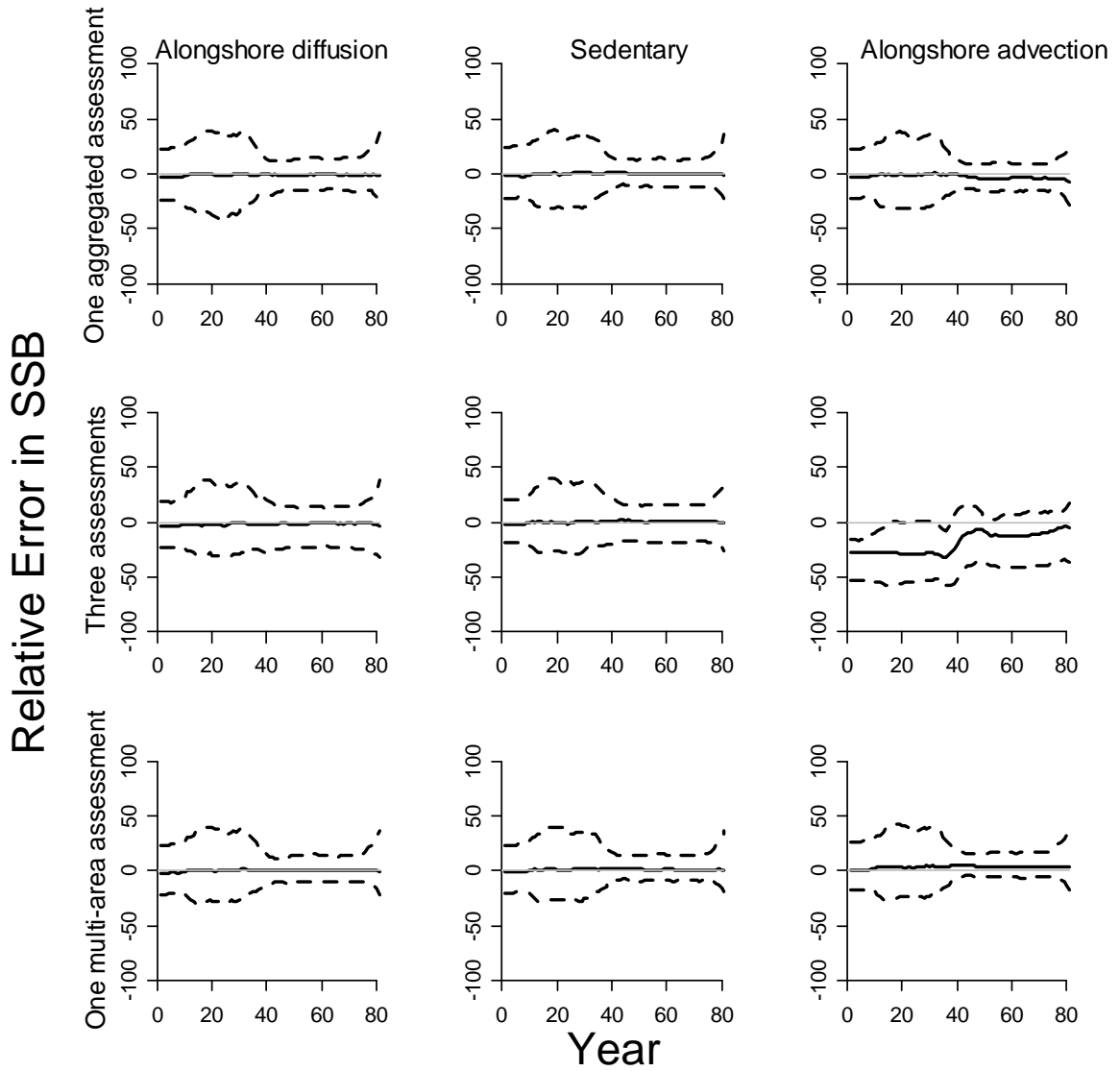


Figure 3. Relative error in spawning stock biomass (SSB) over time for base-case scenarios for each movement pattern and assessment configuration when there is no NTMR in the OM. Solid black lines indicate the median relative error and dashed lines show the 90% quantiles of relative error. Horizontal grey lines indicate no relative error.

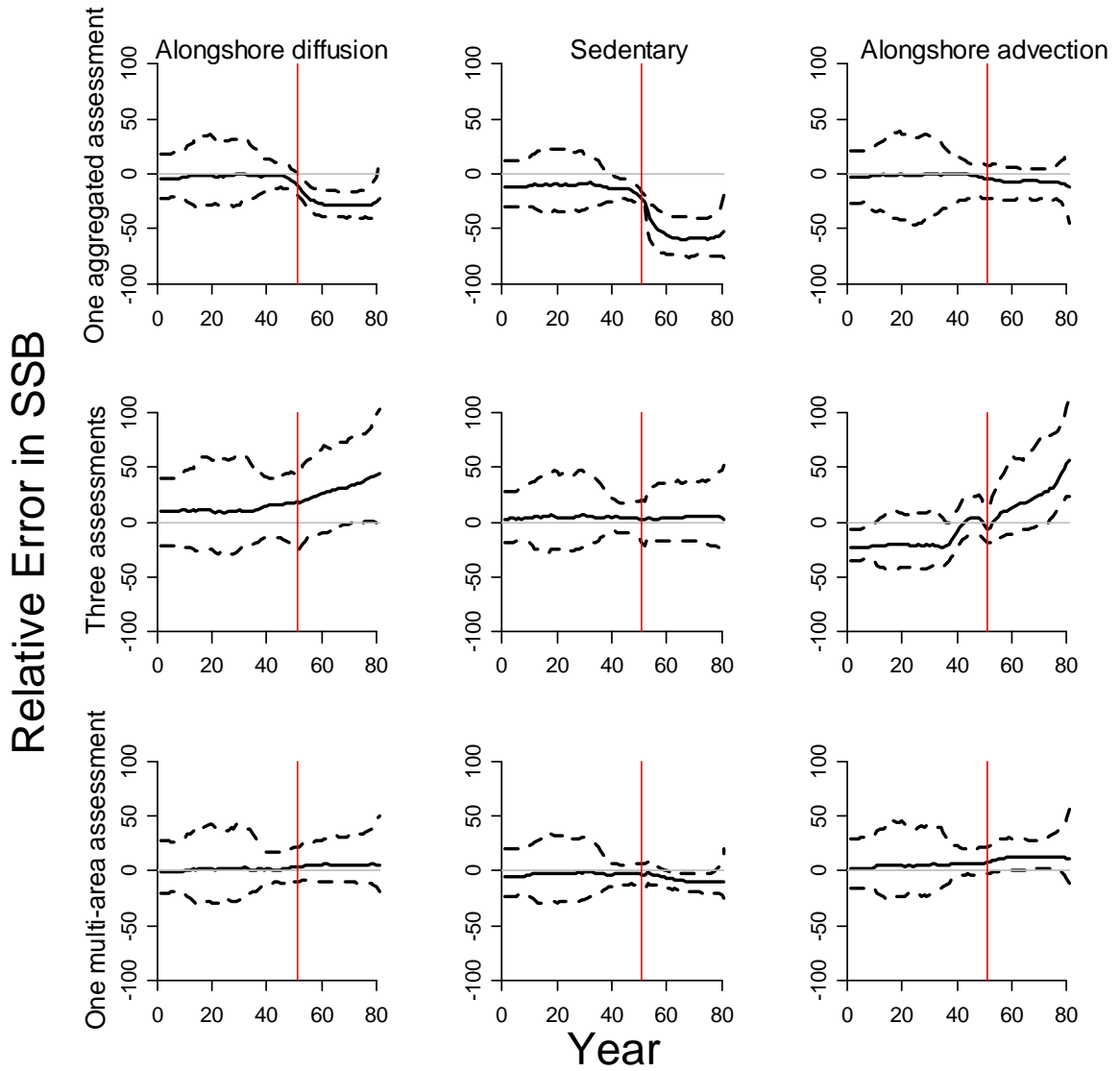


Figure 4. Relative error in SSB (%) over time for base-case scenarios for each movement pattern and assessment method when an NTMR is implemented in year 51 (vertical red line) in the OM. Solid black lines indicate the median relative error and dashed lines show the 90% quantiles of relative error. Horizontal grey lines indicate no relative error.

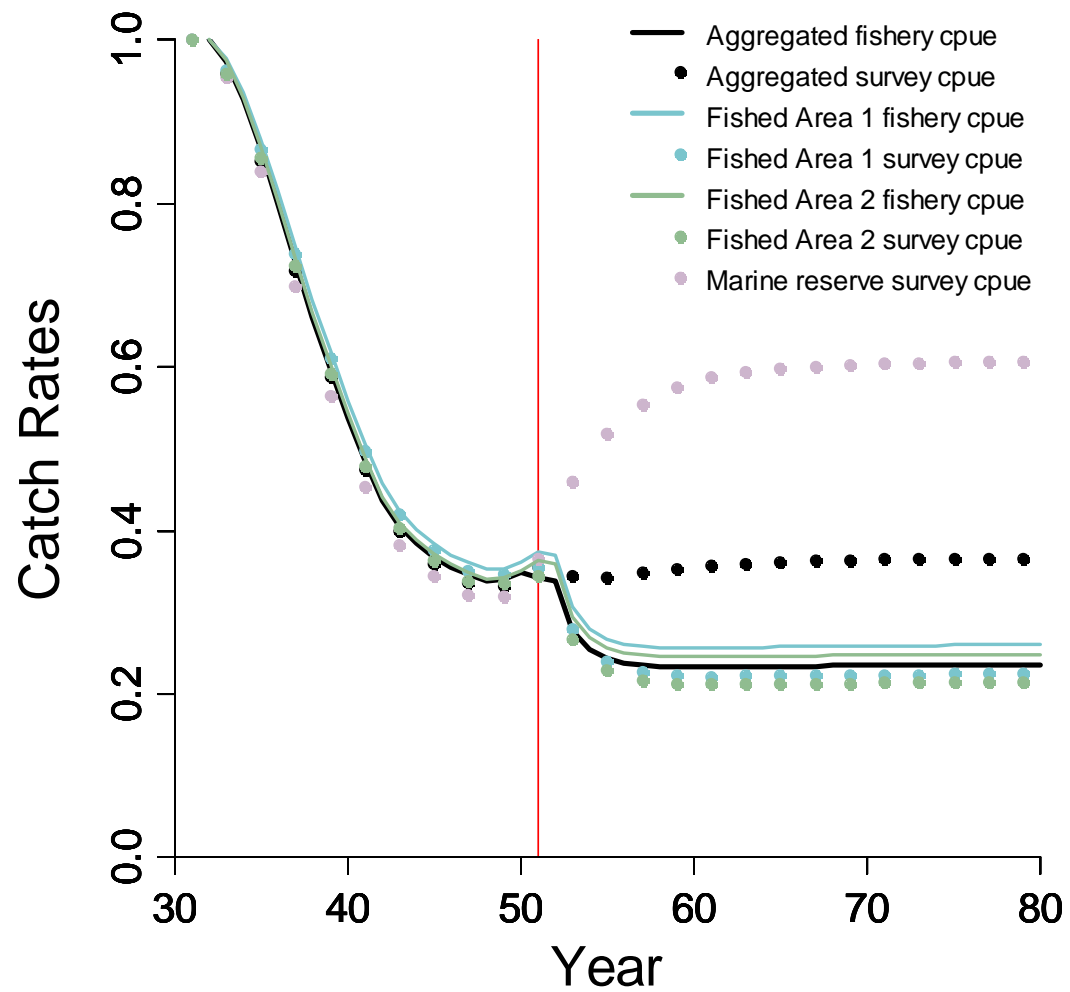


Figure 5. Fishery and survey catch-rate indices generated from the OM without process and observation error for the alongshore diffusion movement pattern when an NTMR is implemented in year 51. Lines indicate fishery catch-rate data and dots indicate survey catch-rate data.

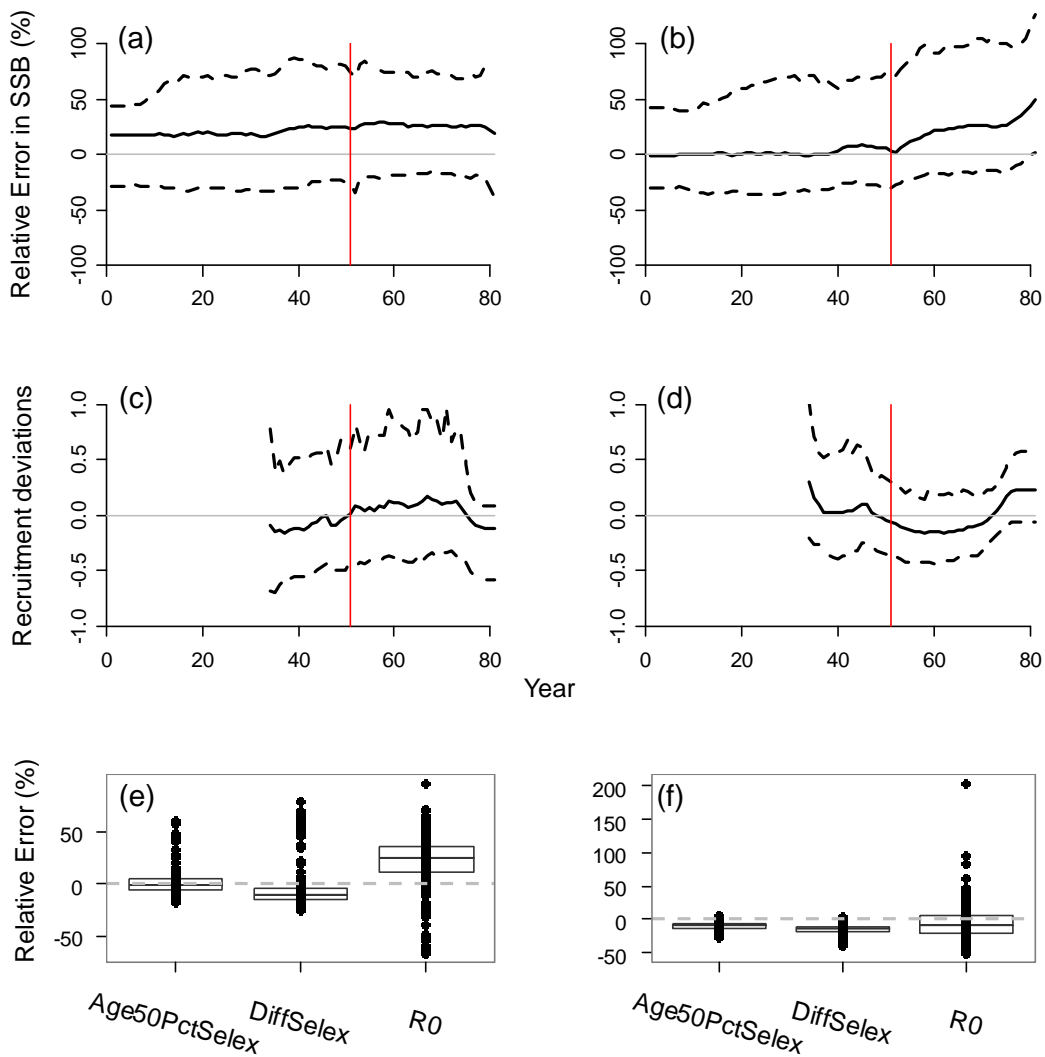


Figure 6. Relative error in SSB (%) and relative error (%) in parameter estimates (a_{50} , $a_{95-a_{50}}$, and R_0) for an assessment conducted in Area 1 (a fished area; a & c) and a separate assessment conducted in Area 2 (where a NTMR was implemented in year 51) where assessments were done in year 81 using a stock assessment configuration with an effective sample size of 1 (no catch-at-age data) and an OM with uniform fishing effort over space. Left panels show Area 1 and right panels show Area 2.

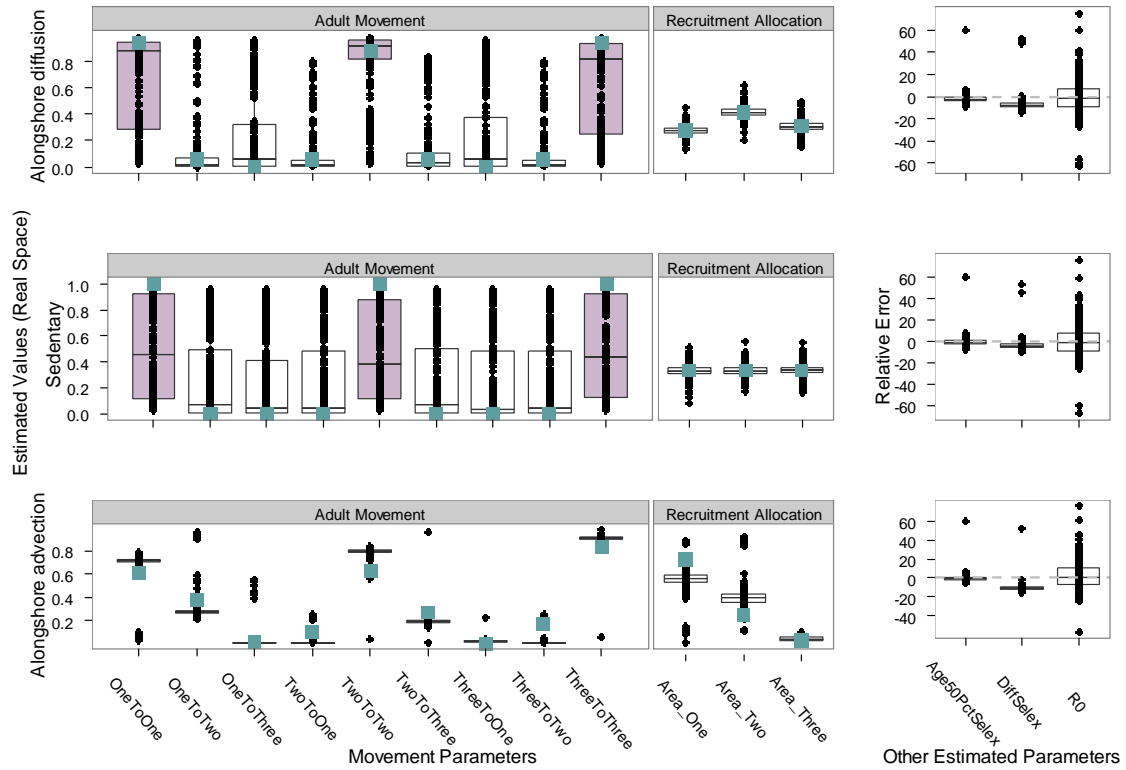


Figure 7. Box plots of estimates of movement, recruitment allocation, and relative error in selectivity parameters and R_0 for the MULTI configuration conducted in year 81 and for each movement pattern with no NTMR in the OM. Blue squares indicate true values from the OM. Black dots are individual estimates from each of the 300 simulations. Dotted grey line indicates no relative error.

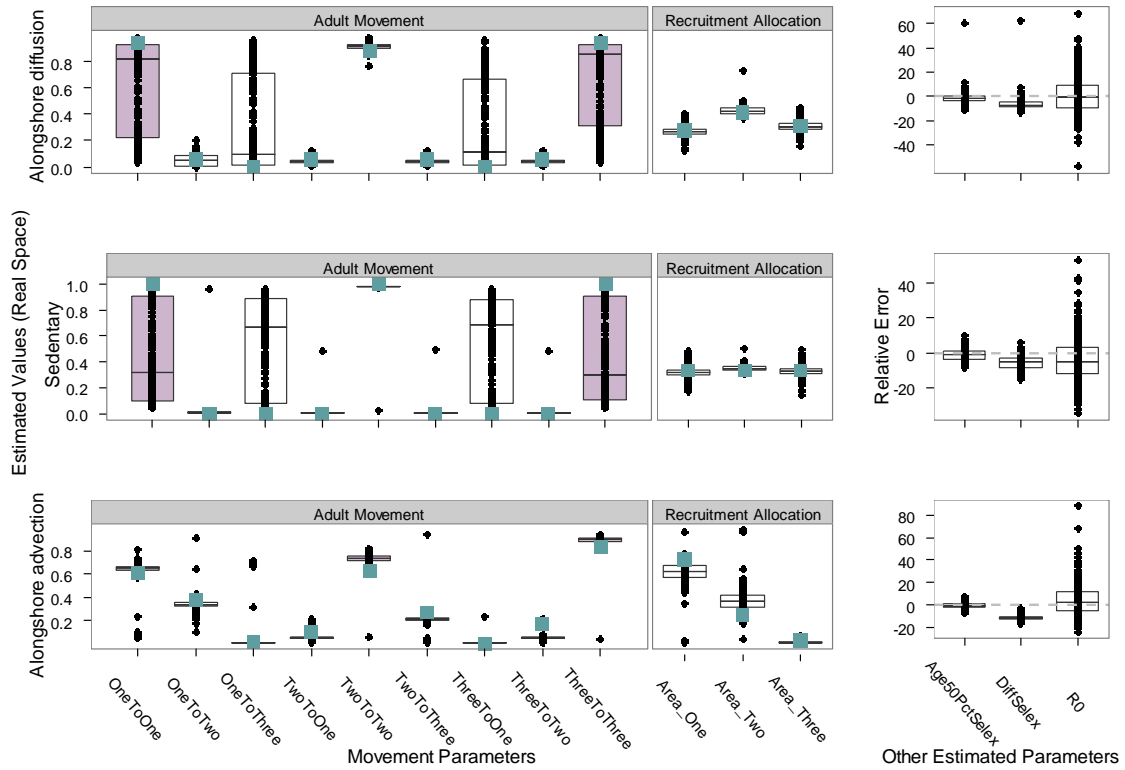


Figure 8. Box plots showing estimates of movement, recruitment allocation, and relative error in selectivity parameters and R_0 for the MULTI configuration conducted in year 81 and for each movement pattern with an NTMR implemented in year 51 in the OM. Blue squares indicate true values from the OM. Black dots are individual estimates from each of the 300 simulations. Dotted grey line indicates no relative error.

Chapter 3. Modeling the potential impacts of two age-related portfolio effects on recruitment variability

Abstract

Many rockfish species are long-lived and are thought to be particularly susceptible to being overfished. In recent years, 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 the characteristics of recruitment variability. In addition, we explored whether populations with these mechanisms could be managed more sustainably with a marine reserve policy in addition to a constant fishing mortality rate than with a constant fishing mortality rate 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 an offspring size effect which assumed that older mothers produced larger offspring than younger mothers where the survival rate of offspring was high regardless of maternal age when environmental conditions were favorable, but offspring of older mothers had higher survival rates than those of younger mothers when environmental conditions were poor. Secondly, we modeled a spawning site effect whereby mothers of different ages spawned in different times or locations. Thus, offspring of younger mothers experienced different environmental conditions than

those of older mothers within a single spawning season (year). Recruitment variability was 55-65% lower than for models without portfolio effects related to maternal age in the absence of fishing and increased with increases in fishing mortality rates (F s) for both the spawning site and offspring size effects. The reproductive rate specified in the model in a typical age-structured model is the same as that output from the model. However, an offspring size effect caused lower output reproductive rates such that the parameter specifying reproductive rate was no longer the realized rate. Therefore, a standardization was conducted such that offspring size effect and control models had the same realized reproductive rates. A flaw in previous analyses of offspring size effects is that reproductive rate is not standardized and thus comparisons of models with and without an offspring size effect (sometimes called a “maternal age effect”) are comparisons between two species with different 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 (catch divided by total biomass) 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 highly mobile larvae.

Introduction

Many rockfish species are long-lived and are thought to be susceptible to overfishing (Patrick et al., 2010, Love et al., 2002). 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 ensure sustainability given the complexities of old-growth age structure is through marine reserves. Berkeley et al. (2004b) suggested that maintenance of older rockfish in a population is essential for sustainability for two reasons. First, older fish may spawn in a different time or place than younger fish as a bet-hedging strategy. 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 (Figge, 2004, Hilborn et al., 2003, Schindler et al., 2010, Hooper et al., 2005). 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 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 site effect to influence population dynamics has not been fully explored, while the potential influence of a maternal age effect on population dynamics has been the subject of many studies and much debate (e.g. O'Farrell and Botsford, 2006, Spencer et al., 2007, Venturelli et al., 2009). 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 eggs 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 fecundity had only small effects on LEP. One reason that increases in the fecundity of older individuals has limited influence on population dynamics is that density-dependent mortality occurs after accounting for fecundity and this means that while older individuals may produce more eggs, this doesn't necessarily translate into the survival of more eggs than in models with no fecundity-related maternal age effect. Lucero (2008) explored how a maternal age effect influencing the characteristics of 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. (2007) modeled a maternal age effect acting on a stock-recruit curve for Pacific Ocean perch, showing that a maternal age effect causes 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 population response in a variable environment.

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 reduce 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.

In this study we model the two mechanisms described above, which are: (1) changes in the timing or location of spawning (spawning site) as a function of maternal age (a spawning site 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 E. The dynamics of larval dispersal are the same for both the offspring size and spawning site models and are described in Appendix E. We parameterized both models to represent black rockfish using parameters from Sampson (2007) with a steepness parameter of $h=0.6$, natural mortality of $M=0.12\text{yr}^{-1}$, age at which 50% and 95% of fish were selected in the fishery of $a_{50}=3\text{yr}$ and $a_{95}=6\text{yr}$, respectively. Growth parameters were $L_{\infty}=442\text{mm}$, $\kappa=0.33\text{yr}^{-1}$, and $t_0=0.75\text{yr}$, length-weight relationship parameters were $\alpha=0.00000168$, $\beta=3$, ages at 50% and 95% maturity were $a_{50}^{\text{mat}}=7.5\text{yr}$ and $a_{95}^{\text{mat}}=14\text{yr}$, respectively, and the plus group started at $a_{\text{max}}=50\text{yr}$.

Methods for the spawning site model

The spawning site model was an age-structured population dynamics model with ten spawning sites, which can be interpreted as spawning grounds or spawning times. Fish of different ages spawned at different spawning sites, where each site experienced independent environmental conditions within a year. Spawning sites were ephemeral structuring of the population that existed only at the time of spawning and not year-round. Year-round, the population occurred in one or two spatial areas with population dynamics occurring within each area. Populations within each area were sedentary and unconnected among areas, or were linked by larval movement between areas. The convention “spawning sites” 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 site model is described below with equations in Table 1; additional equations are specified in Appendix E.

Spawning and Recruitment for the “spawning sites” model

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

Distribution of spawning biomass across spawning sites

Two biological scenarios were modeled to represent potential ways that spawners could be distributed across spawning sites. First, spawners progress across spawning sites, shifting spawning sites by the same increment each year (age-specific distribution of spawners over spawning sites; Figure 1a). Figure 1b shows that most of the offspring were from younger mothers and therefore came from only a few of the spawning sites (sites 2-4 especially) when the age-specific distribution of spawners was applied.

Alternatively, spawners may shift to a new spawning site when reaching a new developmental stage (stage-specific distribution of spawners over spawning sites; Figure 1c). The stage-specific alternative was developed to create a scenario that would maximize a spawning site portfolio effect by resulting in a distribution of offspring over spawning sites that was as uniform as possible (Figure 1d). Both alternatives are described in more detail below.

Age-specific distribution of spawners over spawning sites

We modeled the process by which spawners distribute among spawning sites using a discrete Beta function (Equation 1). This parameterization allows flexibility in the

overlap of different ages in each spawning site, which impacts survival of recruits owing to stochastic events or density-dependent mortality.

$$(1) \quad P_{a,i} = \frac{i^{\alpha_a-1}(n-i+1)^{\beta_a-1}}{\sum_i i^{\alpha_a-1}(n-i+1)^{\beta_a-1}},$$

where $P_{a,i}$ is the proportion of age a spawners that spawn at spawning site i and n represents the total number of spawning sites. 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 site 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 sites was distinct for each age; a large value for the variance would dampen the influence of spawner age on resulting variation in recruitment. The parameters α_a and β_a are calculated from the mean and variance of the Beta function.

Stage-specific distribution of spawners across spawning sites

Here we represent a similar ontogeny of spawning sites, but instead presume that spawning site 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 .

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

These groupings and the number of groups were not based on black rockfish life history, but were chosen because they resulted in a uniform-looking distribution of offspring across spawning sites (Figure 1d). The standardized Beta function for each group, G , was:

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

The standardized Beta function for each age was

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

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 site model, environmental variation influences density-independent survival at each spawning site. 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 site (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 site i and area j produced when the number of eggs in spawning site i and area j is 20% of the number of eggs in spawning site i and area j when the population is in an unfished state, $B_{i,j,0}^E$; this definition of reproductive rate is often referred to as “steepness.” Environmental variation (process error) influences recruitment in each annual time-step and for each spawning site, i , with correlation, ρ , among spawning sites where $\varepsilon_{i,t} \sim N(0, \sigma_R^2)$ 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 sites were perfectly correlated ($\rho = 1$) were compared to scenarios where environmental conditions at each spawning site were uncorrelated ($\rho = 0$). A set of simulations for each biological and management scenario with and without a spawning site effect were conducted.

Scenarios with age- and stage-specific distribution of spawning biomass over spawning sites 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 sites, but local to spatial area (Table 1). A test simulation was conducted assuming that density dependence was local to spawning site 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 site were not explored further.

Model setup and standardization

Two main approaches were used to evaluate the spawning site 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 ($\sigma_R=0.5$) 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 site effect. We used this approach to evaluate whether the spawning site 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 site 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 this 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) to capture the uncertainty in this relationship at older ages (Figure 2a). Berkeley's model is:

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

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

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

The linear model is:

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

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 logistic model for each maternal age relating the number of days of starvation to offspring survival, $\gamma_{a,t}$ (Figure 2b-d).

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

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 site 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 , $\gamma_{a,t}$.

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

Spawning and recruitment for the offspring size model

As for the spawning site 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 site.

Density-dependent mortality followed by environmental variation

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 $R_{j,0}$.

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

Environmental variation followed by density-dependent mortality

The number of eggs in area j at time t is a function of the spawning stock biomass, $B_{j,t}^E$, the proportion of eggs that survival 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:

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

Biological scenarios

All simulations were conducted for the offspring size model and a control model which assumed that all offspring had the size and characteristics of offspring from an age 15 mother 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 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 (although confounded with observation uncertainty) is often assumed to be in the vicinity of $CV = 0.5$ or 0.6 (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 site 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 site 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 site 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 correct survival multiplier (ϕ), as mentioned previously, for which 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, and a no-take marine reserve covering 20% of the area with a constant F

strategy in the fished area. Choice of spawning site 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 conducted for two movement scenarios: (1) a sedentary population with no larval and adult movement, and (2) a population with sedentary adults and extensive larval dispersal (Equations E.15-E.18).

Performance Measures (both models)

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

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, (2) the probability of spawning stock

biomass falling below 20% of unfished spawning stock biomass, and (3) the long-term (cumulative) catch averaged over simulations. We also measured the largest long-term catch, averaged over simulations, for each policy. Long-term catch is measured to evaluate long-term sustainability, the probability of falling below a biomass threshold is used to measure population persistence, and recruitment variability is measured to assess whether lower variability results from a marine reserve policy by way of protecting older mothers.

Results

The structure of the results section is as follows. First, we show that a portfolio effect exists for both the spawning site and offspring size models in the absence of fishing whereby recruitment variability is lower with an offspring size or spawning site effect. Next, we discuss the effects of fishing on recruitment and catch variability for the spawning site 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 sites 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 site model ($\rho = 0$, purple line) results in inter-annual recruitment variability in the absence of fishing mortality that is 55% lower than a model with only one spawning site ($\rho = 1$)

when both models have 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 have the same mean number of days of starvation (μ_d).

Effects of fishing on the spawning site portfolio effect

Figure 4 shows the influence of fishing mortality on recruitment variability when the recruitment variability is standardized to be $CV = 0.5$ for spawning site models and corresponding control models for populations in an unfished state. Recruitment variability increases as a function of increasing fishing mortality for both the age- and stage-specific spawning site models, while it remains constant for all fishing mortality and spawning stock biomass levels in the control models when environmental variation occurs after density-dependent mortality (Figures 4a & b). The recruitment variability also increases as a function of increasing fishing mortality and decreasing spawning stock size when environmental variation occurs before density-dependent mortality (Figures 4c & d), but the increase in recruitment variability due to the declining influence of density-dependent mortality on offspring at lower spawning stock sizes (which applies to the spawning site and control models alike) is much greater in magnitude than the influence of age- or stage-specific spawning sites (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 0.5 rather than 0.6) 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 (Figure 6a-c). The increases in recruitment variability with increases in fishing mortality are least pronounced for the Berkeley relationship (Figure 6a) and largest for the exponential relationship (Figure 6c). Figure 6d-6f confirm that the mean stock recruit curves for each of the offspring size model scenarios are nearly identical to the deterministic Beverton-Holt stock recruit curve after the reproductive rates are standardized.

Simulations where environmental variation occurred before 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 site and offspring size models than for the corresponding control models (Figure 7). However, the increase in variability is mostly due to outlying 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 site and offspring size models in Figure 7 (relative to the control models). In contrast, the lower tails of the distributions are similar with and without an offspring size or spawning site effect (Figure 7). The largest catches for the spawning site model (Figure 7a) are approximately double those for the offspring size model (Figure 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 F s for a population with sedentary larvae and adults influenced by a spawning site 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 F_{MSY} 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 site 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 site and offspring size models.

Results for the spawning site 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 largest long-term catch; the marine reserve policy applied to a population with highly mobile larvae could produce up to 90% of the largest long-term catch, while a marine reserve policy applied to a population with sedentary larvae could produce 80% of the largest long-term catch (Figure 9a & d). In the case of the population with sedentary larvae managed with a marine reserve, long-term 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 (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 site and offspring size mechanisms acted as portfolio effects for all biological scenarios (the age-specific, stage-specific spawning site 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). 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} for all biological scenarios (e.g. Figures 4 & 6).

While the spawning site portfolio effect was large relative to larval survival, the portfolio 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-dependence. 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 site or offspring size portfolio 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 (when settlement occurs) and how much environmental variation occurs before versus after density-dependent mortality is an open area of research (e.g. Myers

and Cadigan, 1993a, Myers and Cadigan, 1993b, 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 eggs that survive starvation in a given year, rather than spawning stock biomass. The number of eggs that survive environmental variation in a year with favorable environmental conditions can be much greater than the deterministic number of eggs produced at unfished biomass. However, at this magnitude of eggs, there is an asymptote in the Beverton-Holt stock-recruit curve such that a very large number of eggs still translates 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 produce negative deviations such that recruitment variability is equal to $CV = 0.5$ is very high. This suggests that 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

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 for all of the sustainability metrics that we 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 exploitation rates (however, a marine reserve limits the maximum exploitation rate that can occur). Lastly, recruitment variability was a monotonically increasing function of exploitation rate, regardless of the presence of a marine reserve, except in the most extreme case where 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 (Hilborn et al., 2006, McGilliard and Hilborn, 2008, Gerber et al., 2005). A wealth of previous marine reserve modeling efforts have explored 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 long-term catch (e.g. Botsford et al., 2001, Moffitt et al., 2009, Hart and Sissenwine, 2009, Hart, 2006). This manuscript addresses only whether there is a particular benefit of marine reserves for sustainability due to age-related portfolio effects.

Spawning site model conclusions

Results for the age-specific spawning site 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 areas, offspring are aggregated in areas 2-5, a minority of the spawning sites. Although the older fish spawn in different times or spaces 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 site model maximizes the portfolio effect by spreading offspring evenly among spawning sites 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, Lucero, 2008, Venturelli et al., 2009). However, this study shows that 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 – we never observe a fish stock prior to the occurrence of a mean offspring size effect and hence the mean effect of the offspring size model is irrelevant for stock assessment and management, though perhaps still of theoretical interest to biologists.

It is of interest, however, that 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 site 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 (ages 18+) that is outside of the range of the data and we wanted to know 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, the possibility that older spawners may utilize a larger range of spawning sites than younger individuals could be explored as an extension to the spawning site 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 times or places, but this may be genetic and unrelated to age (Hauser and Carvalho, 2008, Palof et al., 2011). Several studies have found evidence of multiple genetic sub-populations of rockfish over their geographic range (Buonaccorsi et al., 2002, Withler et al., 2001). Future modeling studies could evaluate the relative influence of these portfolio effects on overall recruitment variability and associated implications for management.

Tables

Table 1. Recruitment equations for the spawning site model

Type of recruitment	Equations
Local density-dependent mortality followed by environmental variation	T.1 $B_{i,j,t}^E = 0.5 \sum_a N_{a,j,t} P_{a,i} O_a w_a$
	T.2 $R'_{i,j,t+1} = R_{i,j,0} \frac{4h(B_{i,j,t}^E / B_{i,j,0}^E)}{(1-h) + (5h-1)(B_{i,j,t}^E / B_{i,j,0}^E)} \exp(\eta_{i,t} - \sigma_R^2/2)$
Global density-dependent mortality followed by environmental variation	T.3 $R''_{j,t+1} = R_{j,0} \frac{4h(B_{j,t}^E / B_{j,0}^E)}{(1-h) + (5h-1)(B_{j,t}^E / B_{j,0}^E)}$
	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 $R'_{i,j,t+1} = R''_{j,t+1} \Omega_{i,j,t} \exp(\eta_{i,t} - \sigma_R^2/2)$
Environmental variation followed by global density-dependent mortality	T.6 $E_{i,j,t} = 0.5 \sum_a N_{a,j,t} P_{a,i} O_a w_a \exp(\eta_{i,t} - \sigma_R^2/2)$
	T.7 $E_{j,t} = \sum_i E_{i,j,t}$
	T.8 $R'_{j,t} = R_{j,0} \frac{4h(E_{j,t} / B_{j,0}^E)}{(1-h) + (5h-1)(E_{j,t} / B_{j,0}^E)}$
Environmental variation then local density-dependent mortality	T.9 $R'_{i,j,t} = \frac{4h(E_{i,j,t} / B_{i,j,0}^E)}{(1-h) + (5h-1)(E_{i,j,t} / B_{i,j,0}^E)}$

Figures

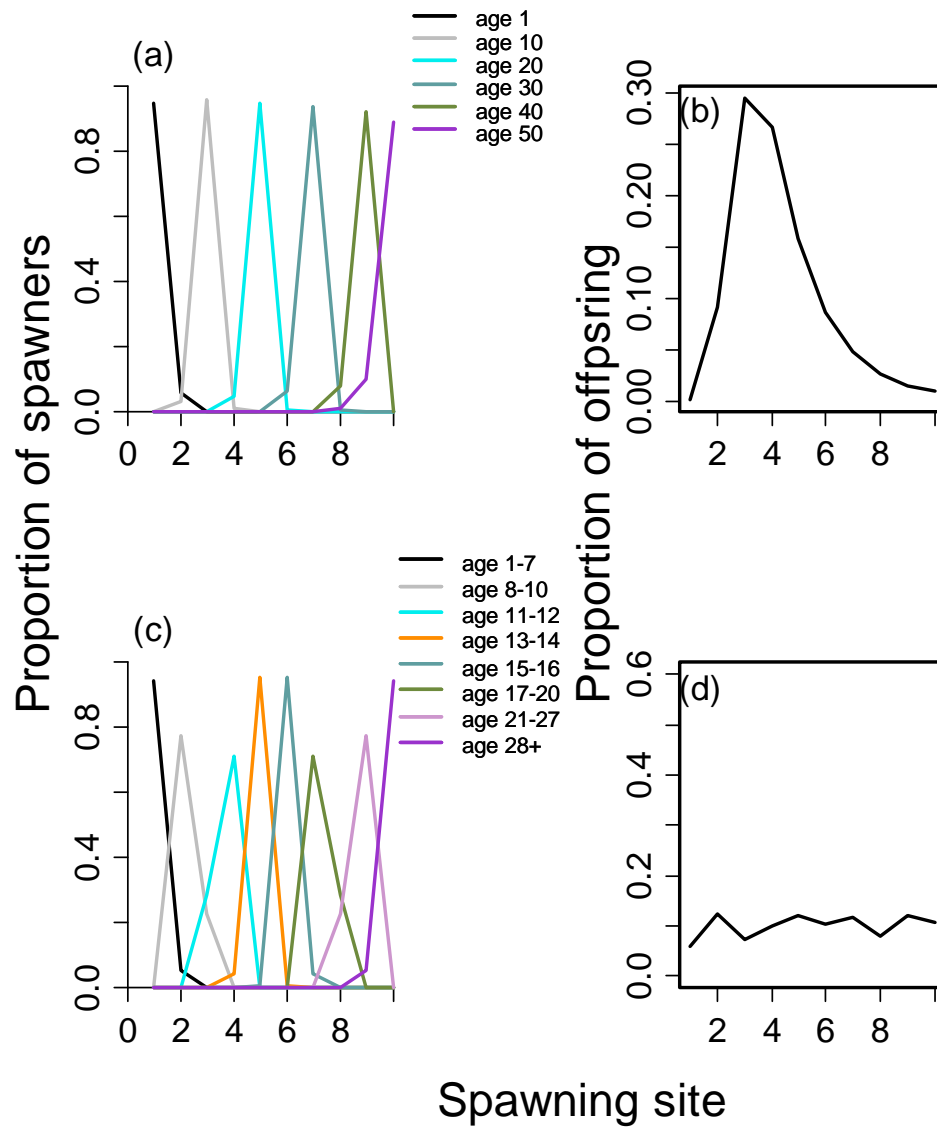


Figure 1. Distribution of spawners over spawning sites by age (a & c) and the resulting distribution of offspring over spawning sites (b & d) for the spawning site models. Graphs a & c show age-specific distribution of spawners over spawning sites and graphs b & d show stage-specific distribution of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

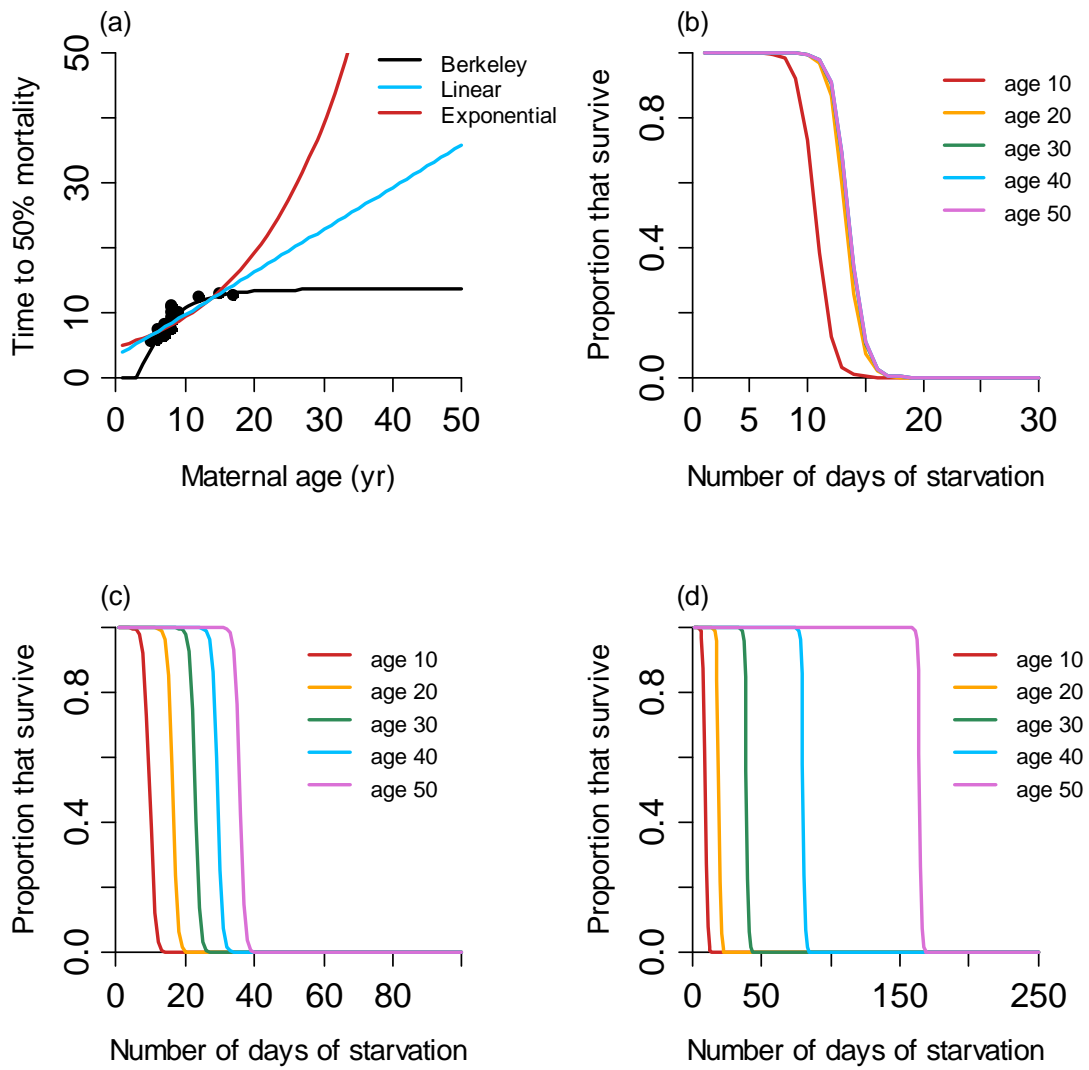


Figure 2. Panel (a) shows time to 50% mortality ($D_{50,a}$) for maternal age a in the offspring-size model. Dots are data from Berkeley et al. (2004a) and lines are three models fit to the data used as hypotheses about the relationship between maternal age and $D_{50,a}$: a model fit by Berkeley et 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).

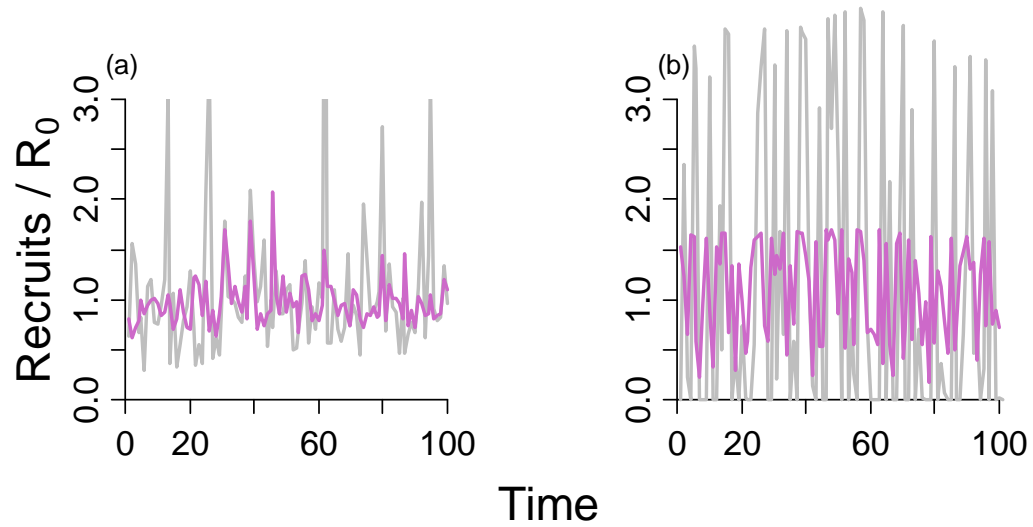


Figure 3. Recruitment relative to R_0 for a sample simulation for (a) the age-specific spawning site model with simulated environmental variability of $\sigma_R = 0.5$ and (b) the offspring size model with an exponential relationship between maternal age and time to 50% mortality of offspring; mean number 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 site effects (the portfolio effects) are shown in purple.

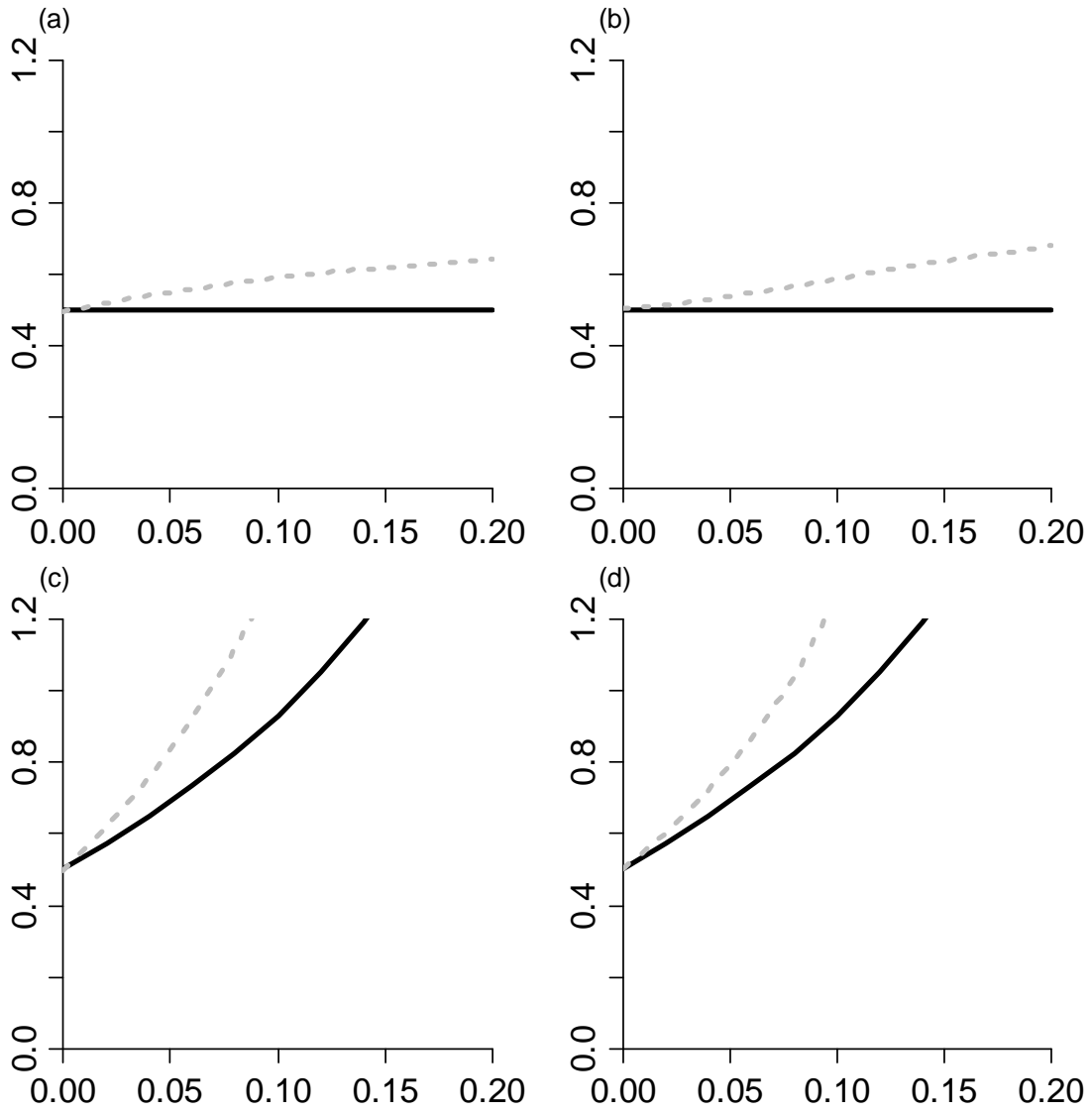


Figure 4. Recruitment variability (CV) for the spawning site model when density-dependent mortality occurs before environmental variation (a & b) and after environmental variation (c & d); (a & c) show results for an age-specific distribution of offspring across spawning sites, (b & d) show a stage-specific distribution of offspring across spawning sites. Control scenarios ($\rho = 1$) are solid black lines and spawning site models are grey dotted lines ($\rho = 0$).

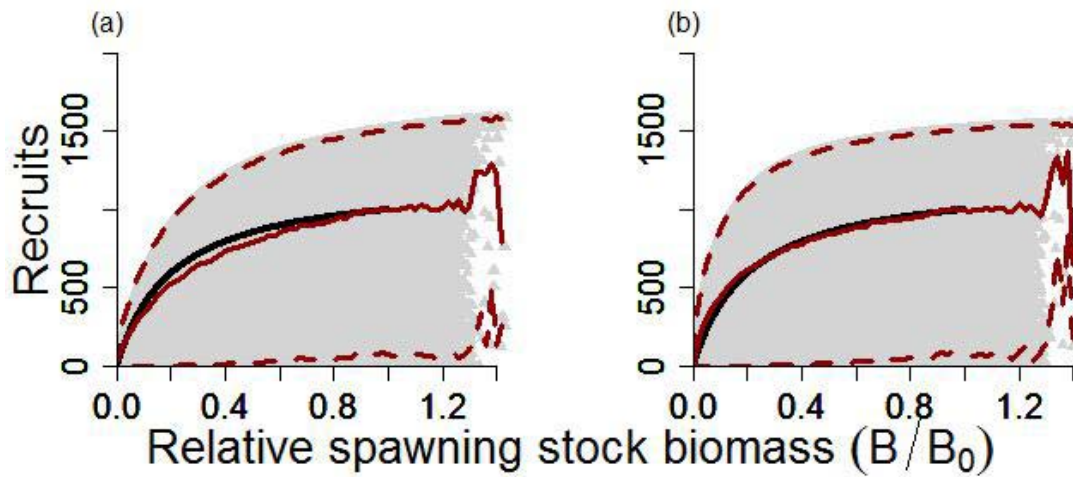


Figure 5. The relationship between spawning stock biomass relative to unfished spawning stock biomass and recruits for the offspring size model with a linear relationship between maternal age and time to 50% mortality for (a) an input reproductive rate of $h = 0.6$ and (b) an input reproductive rate (h) standardized such that the output reproductive rate (steepness) is equal to $z = 0.6$. The relationships between spawning stock biomass and recruits for each model realization 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.

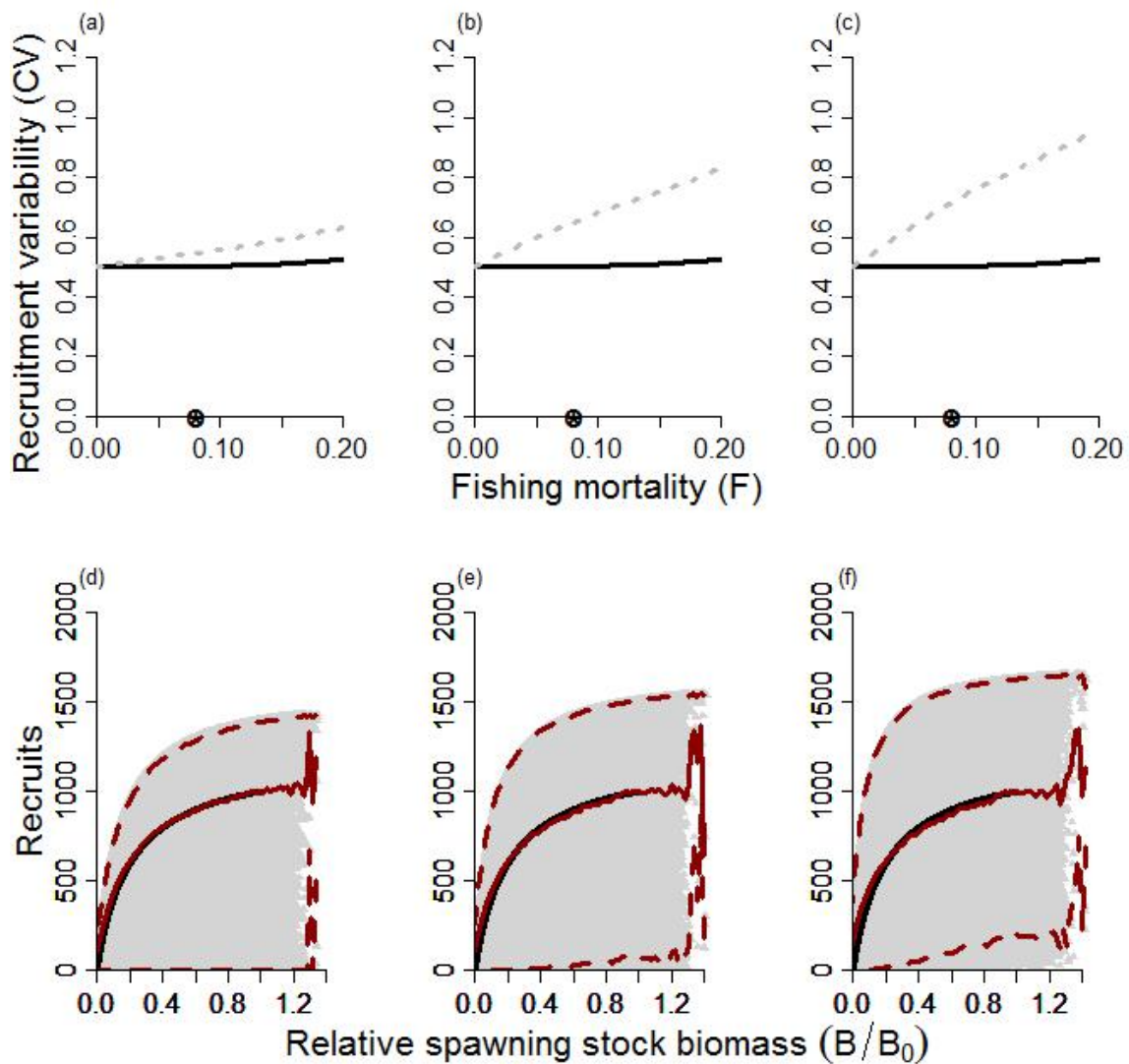


Figure 6. Recruitment variability (CV) over a range of fishing mortality rates (a-c) for offspring size models and corresponding control models with reproductive rate standardized (steepness is equal to 0.6). F_{MSY} is shown for the offspring size model (*) and for the corresponding control model (o). Graphs d-f show the relationship between spawning stock biomass relative to unfished spawning stock biomass and recruitment for each model realization (grey dots), the 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.

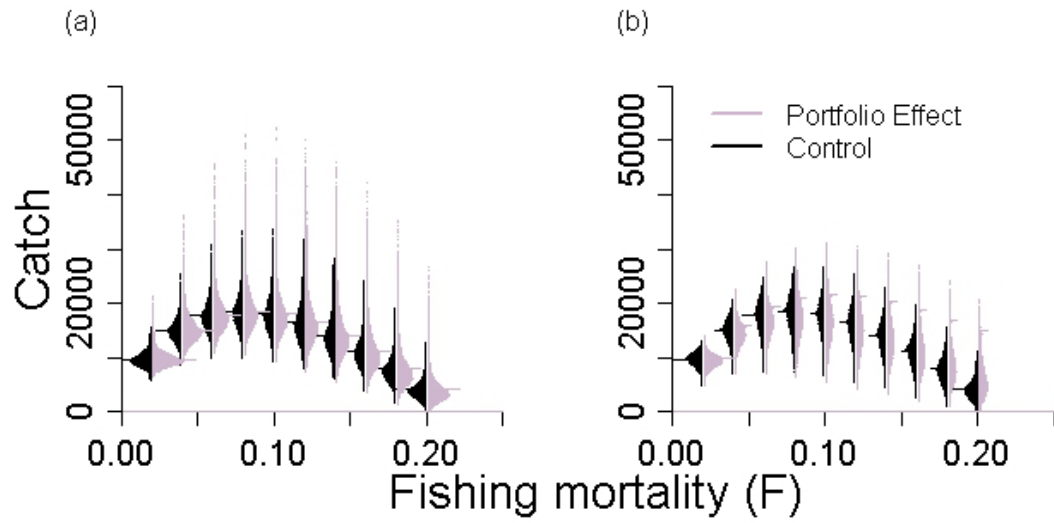


Figure 7. Distribution of catch over a range of fishing mortality rates (F) for the stage-specific spawning site model (a) and the offspring size model with steepness standardized and a linear relationship between the maternal age and time to 50% mortality (b). Distribution of catch for the spawning site 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.

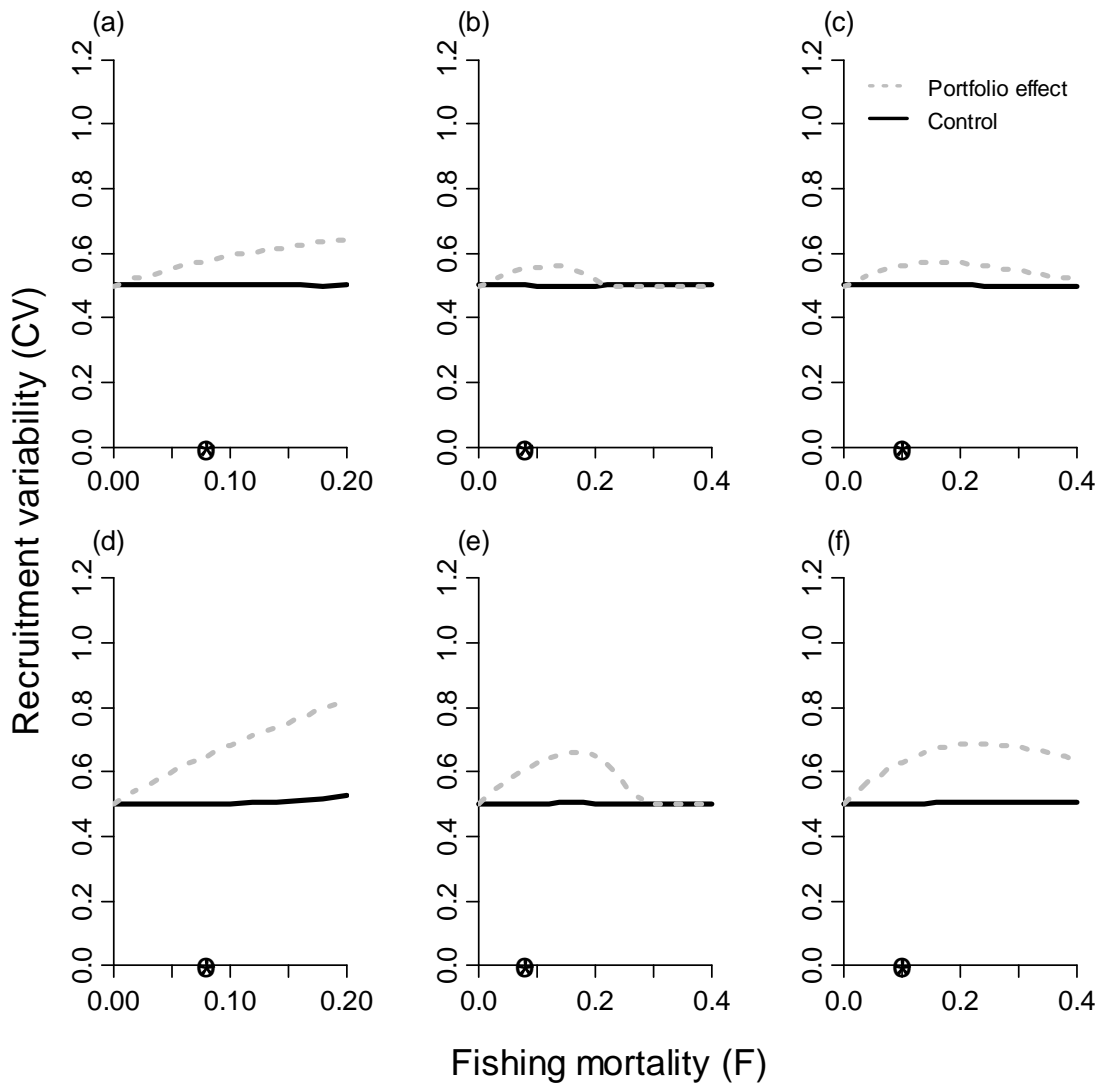


Figure 8. Recruitment variability (CV) over a range of fishing mortality rates (F) for a management scenario with no marine reserve (a & d), a marine reserve covering 20% of the area applied to (1) a population with sedentary larvae and adults (b & e), and (2) a population with a high larval movement rates and sedentary adults (c & f). Panels a-c show an age-specific spawning site 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).

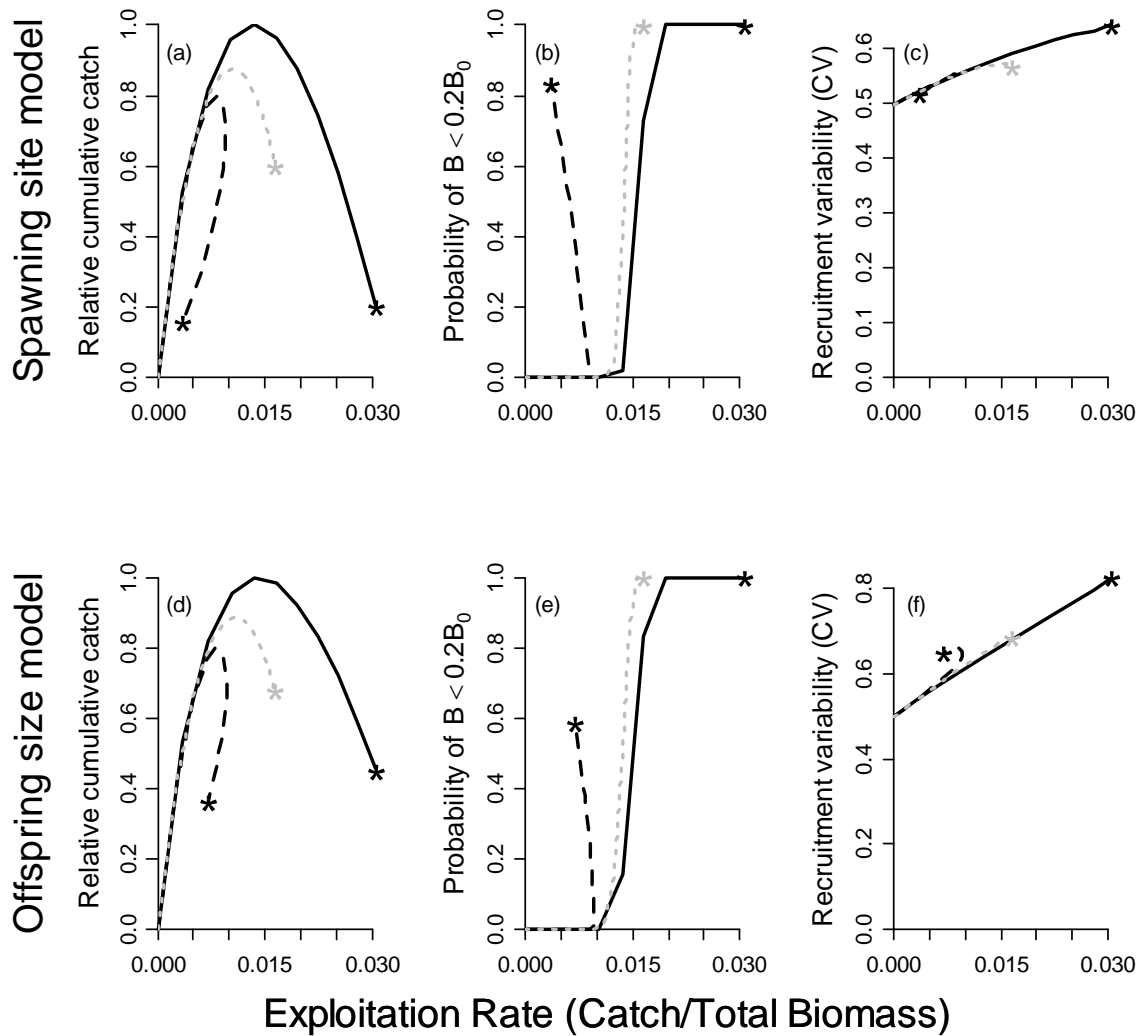


Figure 9. Relative long-term catch (a & d), probability of spawning stock biomass falling below 20% of unfished spawning stock biomass (b & e), and recruitment variability (c & f) over a range of exploitation rates (catch/total biomass) for the spawning site model (a-c) and the offspring size model (d-f). 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 $F = 0.2 \text{ yr}^{-1}$ (indicated with an asterisk).

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Appendix A. Chapter 1 Supplementary material

Operating model

The abundance, N , at age a in cell (i,j) at time $t+1$ is given by

$$(A.1) \quad N_{a,i,j,t+1} = \begin{cases} R_{i,j,t+1} & \text{if } a = 0 \\ \sum_i \sum_j (N_{a,\hat{i},\hat{j},t} e^{-M/2} - C_{a,\hat{i},\hat{j},t}) e^{-M/2} P_{i,j,\hat{i},\hat{j}} & \text{if } 1 \leq a \end{cases}$$

where $R_{i,j,t}$ is the number of recruits in cell (i,j) at time t , M the instantaneous rate of natural mortality, $N_{a,\hat{i},\hat{j},t}$ the abundance at age a and time t in cell (\hat{i}, \hat{j}) before movement, $C_{a,\hat{i},\hat{j},t}$ the catch at age a in cell (\hat{i}, \hat{j}) at time t , and $P_{i,j,\hat{i},\hat{j}}$ is the proportion of adults that move from cell (\hat{i}, \hat{j}) to cell (i,j) [see Equation (A.2)]. Adult movement is non-directional diffusion where σ_{Along}^2 and σ_{Aoff}^2 determine the extent of diffusion in the alongshore and inshore to offshore directions, respectively. The adult movement model is similar to the diffusion model used in Le Quesne and Codling (2009), but operates in two dimensions (alongshore and offshore), and there is no movement beyond the boundaries of the spatial grid.

$$(A.2) \quad P_{i,j,\hat{i},\hat{j}} = \frac{\exp\left(\frac{(\hat{i}-i)^2}{2\sigma_{\text{Along}}^2} + \frac{(\hat{j}-j)^2}{2\sigma_{\text{Aoff}}^2}\right)}{\sum_i \sum_j \exp\left(\frac{(\hat{i}-i)^2}{2\sigma_{\text{Along}}^2} + \frac{(\hat{j}-j)^2}{2\sigma_{\text{Aoff}}^2}\right)}.$$

Length, weight, maturity, and fecundity

Length at age (L_a) follows the von Bertalanffy growth curve, where L_{inf} is the asymptotic size, k determines the rate of growth, and τ_0 is the theoretical age at which an individual is of zero length; length-at-age is assumed to be constant over space:

$$(A.3) \quad L_a = L_{\text{inf}}(1 - e^{-k(a-\tau_0)}).$$

Weight-at-age (w_a) is an allometric function of length, where α is a scalar and β determines the rate of allometric growth:

$$(A.4) \quad w_a = \alpha L_a^\beta.$$

The maturity ogive (O_a) is a logistic function of length, where a_{50}^{mat} and a_{95}^{mat} represent the ages of females, which are the same as for males, at 50% and 95% maturity, respectively:

$$(A.5) \quad O_a = \frac{1}{1 + \exp\left(\frac{-\ln(19)(a - a_{50}^{\text{mat}})}{(a_{95}^{\text{mat}} - a_{50}^{\text{mat}})}\right)}.$$

Fecundity is a function of maturity and weight at age (w_a).

$$(A.6) \quad f_a = O_a w_a.$$

Spawning-stock biomass, B_t , is

$$(A.7) \quad B_t = \sum_a \sum_i \sum_j 0.5 N_{a,i,j,t} f_a.$$

Larval dispersal and recruitment

Recruitment follows the Beverton–Holt stock-recruitment curve with local post-dispersal density-dependent mortality [Equation (A.8)] or global density-dependent mortality [Equation (A.9)]. Steepness, h , is the proportion of the unfished number of recruits, $R0_{(i,j)}$, in spatial cell (i,j) produced when the number of eggs in cell (i,j) is 20% of the number of eggs in cell (i,j) , $\ddot{B}_{i,j,0}$, when the population is in an unfished state. Local and global process errors are applied to recruitment,

$\varepsilon_{R_{L_{i,j,t}}} \sim N(0, \sigma_{R_L}^2)$, $\varepsilon_{R_{G_t}} \sim N(0, \sigma_{R_G}^2)$ respectively:

$$(A.8) \quad R_{i,j,t+1} = R_0 Q_{i,j} \frac{4h \left(B_{i,j,t}^E / B_{i,j,0}^E \right)}{(1-h) + (5h-1) \left(B_{i,j,t}^E / B_{i,j,0}^E \right)} e^{(\varepsilon_{R_{L_{i,j,t}}} - \sigma_{R_L}^2/2)} e^{(\varepsilon_{R_{G_t}} - \sigma_{R_G}^2/2)}$$

or

$$(A.9) \quad R_{i,j,t+1} = R_0 Q_{i,j} \frac{4h \left(\sum_i \sum_j (B_{i,j,t}^E) / \sum_i \sum_j (B_{i,j,0}^E) \right)}{(1-h) + (5h-1) \left(\sum_i \sum_j (B_{i,j,t}^E) / \sum_i \sum_j (B_{i,j,0}^E) \right)} e^{(\varepsilon_{R_{L_{i,j,t}}} - \sigma_{R_L}^2/2)} e^{(\varepsilon_{R_{G_t}} - \sigma_{R_G}^2/2)}$$

where R_0 is the total number of recruits under unfished conditions, i.e. summed over all spatial cells, and $Q_{i,j}$ is the proportion of larvae that recruit to spatial cell (i,j) under unfished conditions. For scenarios with post-dispersal density-dependent mortality of larvae, $Q_{i,j} = 1$ for all (i,j) ; otherwise, if density-dependent mortality of larvae is global, $Q_{i,j}$ is characterized by the distance from a central cell of greatest concentration of larvae, $(\mu_{\text{along}}, \mu_{\text{off}})$, and standard deviations in each cardinal direction $(\sigma_{\text{north}}, \sigma_{\text{south}}, \sigma_{\text{east}}, \sigma_{\text{west}})$

following Equations (A.10)–(A.12). The indicator function $I_{i>\mu_{\text{along}}}$ is equal to 1 if cell

$i > \mu_{\text{along}}$, and 0 otherwise; likewise $I_{i>\mu_{\text{off}}}$ is 1 if cell $i > \mu_{\text{off}}$:

$$(A.10) \quad Q_{\text{along}_i} = \exp\left(\frac{(i - \mu_{\text{along}})^2}{\sigma_{\text{north}}^2}\right) I_{i>\mu_{\text{along}}} + \exp\left(\frac{(i - \mu_{\text{along}})^2}{\sigma_{\text{south}}^2}\right) (1 - I_{i>\mu_{\text{along}}})$$

$$(A.11) \quad Q_{\text{off}_j} = \exp\left(\frac{(j - \mu_{\text{off}})^2}{\sigma_{\text{east}}^2}\right) I_{i>\mu_{\text{off}}} + \exp\left(\frac{(j - \mu_{\text{off}})^2}{\sigma_{\text{west}}^2}\right) (1 - I_{i>\mu_{\text{off}}})$$

$$(A.12) \quad Q_{i,j} = Q_{\text{along}_i} Q_{\text{off}_j}.$$

The number of eggs in cell (i,j) at time t , $B_{i,j,t}^E$, is a function of abundance, N , and age-specific fecundity (f_a) after larval movement:

$$(A.13) \quad B_{i,j,t}^E = \sum_{\hat{i}} \sum_{\hat{j}} \left(\sum_a f_a N_{a,\hat{i},\hat{j},fem,t} \right) P_{i,j,\hat{i},\hat{j}}^l.$$

The matrix P^l describes larval dispersal [see Equation (A.14)]. Larval dispersal has a diffusion component where σ_{Lalong}^2 and σ_{Loff}^2 represent the extent of diffusion in the north–south and east–west directions, respectively:

$$(A.14) \quad P_{i,j,\hat{i},\hat{j}}^l = \frac{\exp\left(\frac{(\hat{i} - i)^2}{2\sigma_{\text{Lalong}}^2} + \frac{(\hat{j} - j)^2}{2\sigma_{\text{Loff}}^2}\right)}{\sum_i \sum_j \exp\left(\frac{(\hat{i} - i)^2}{2\sigma_{\text{Lalong}}^2} + \frac{(\hat{j} - j)^2}{2\sigma_{\text{Loff}}^2}\right)}.$$

Initial conditions

The OM is initialized using Equation A.15:

$$(A.15) \quad N_{a,i,j,0} = \begin{cases} R_0 Q_{i,j} & \text{if } a = 0 \\ \sum_{\hat{i}} \sum_j P_{i,j,\hat{i},j} N_{a-1,\hat{i},j,0} e^{-M} & \text{if } 1 \leq a \end{cases}$$

Fishery dynamics

The midyear exploitable biomass, X , is given by:

$$(A.16) \quad X_{i,j,t} = \sum_a N_{a,i,j,t} e^{-M/2} S_a w_a,$$

where age-specific selectivity, S_a , follows a logistic curve, and a_{50} and a_{95} represent the age at which 50% and 95% of fish are selected by the fishery, respectively:

$$(A.17) \quad S_a = \frac{1}{1 + \exp\left(\frac{-\ln(19)(a - a_{50})}{(a_{95} - a_{50})}\right)}.$$

Effort (E_t) is allocated among spatial cells in proportion to the distribution of exploitable biomass across spatial cells that are open to fishing, with variability in catchability among spatial cells, $q_{i,j} \sim N(0, \sigma_q^2)$, i.e.

$$(A.18) \quad E_{i,j,t} = \begin{cases} E_t \frac{\sum_s X_{i,j,t} e^{(q_{i,j} - \sigma_q^2/2)}}{\sum_i \sum_j X_{i,j,t} e^{(q_{i,j} - \sigma_q^2/2)}} & \text{for all cells } (i,j) \text{ open to fishing} \\ 0 & \text{otherwise} \end{cases}.$$

The catch is taken in the middle of the year. The catch at age for each spatial cell is

$$(A.19) \quad C_{a,i,j,t} = N_{a,i,j,t} e^{-M/2} S_a E_{i,j,t} e^{(q_{i,j} - \sigma_q^2/2)};$$

$$(A.20) \quad \dot{C}_t = \sum_a \sum_i \sum_j C_{a,i,j,t} w_a.$$

The catch per unit effort (cpue) in year t is

$$(A.21) \quad \text{cpue}_t = \frac{\dot{C}_t}{E_t}$$

Supplementary Tables (Appendix A, continued)

Table A1. Base-case parametrization.

Parameter	Base-case value
h	0.7
M	0.1 year ⁻¹
L_{inf}	30 cm
k	0.2 year ⁻¹
τ_0	0 years
α	0.001
β	3
L_{50}	3 years
L_{95}	5 years
a_{50}	3 years
a_{95}	6 years
σ_{R_L}	0.6
σ_{R_G}	0.6
Q_{ij}	1
σ_{survey}	0.2
$\sigma_{A_{\text{along}}}, \sigma_{A_{\text{off}}}$	0 cells
$\sigma_{L_{\text{along}}}, \sigma_{L_{\text{off}}}$	0 cells
$\sigma_{\text{north}}, \sigma_{\text{south}}$	Not used
$\sigma_{\text{east}}, \sigma_{\text{west}}$	Not used
$\mu_{\text{along}}, \mu_{\text{off}}$	Not used

Table A2. Performance measures for additional scenarios using optimal DRCRs and CERs, as for Table 3.

Description	Optimal x-intercept	Optimal slope	Optimal effort relative to optimal effort for the base case	Probability of $B < 0.25B_{MSY}$ after time-step 5	Average depletion in year 100	Average cpue in year 100 relative to cpue at MSY	Average catch in year 100 relative to MSY	Average interannual CV of catch (5%, 95% quantiles)	
Base case									
CER			1.00	0.00	0.45	0.90	0.76	0.22	(0.15, 0.29)
DRCR	0.42	1.05		0.28	0.44	0.86	0.72	0.62	(0.45, 0.82)
Initially at 10% of depletion at MSY									
CER			1.00	0.84	0.45	0.90	0.76	0.32	(0.23, 0.39)
DRCR	0.42	1.05		1.00	0.43	0.84	0.72	0.85	(0.68, 1.07)
Initially at 50% of depletion at MSY									
CER			1.09	0.00	0.43	0.81	0.76	0.16	(0.10, 0.23)
DRCR	0.42	0.84		0.00	0.44	0.86	0.78	0.46	(0.31, 0.64)
Initially at 100% of depletion at MSY									
CER			1.09	0.00	0.43	0.81	0.76	0.15	(0.08, 0.22)
DRCR	0.00	0.00		0.00	0.40	0.72	0.73	0.16	(0.09, 0.26)
Initially at 200% of depletion at MSY									
CER			1.09	0.00	0.43	0.81	0.76	0.20	(0.14, 0.29)
DRCR	0.42	0.42		0.00	0.44	0.86	0.77	0.38	(0.26, 0.52)
Steepness (h) = 0.3									
CER			0.36	0.58	0.25	0.28	0.39	0.15	(0.07, 0.25)
DRCR	0.00	0.00		0.96	0.14	0.02	0.06	0.71	(0.41, 1.02)
Steepness (h) = 0.5									
CER			0.64	0.04	0.47	0.84	0.74	0.27	(0.17, 0.36)
DRCR	0.42	0.63		0.74	0.42	0.68	0.58	0.96	(0.65, 1.34)
Steepness (h) = 0.9									
CER			1.55	0.02	0.40	0.84	0.77	0.18	(0.12, 0.25)
DRCR	0.37	2.53		0.06	0.40	0.86	0.80	0.73	(0.55, 0.95)
Natural mortality (M) = 0.05									
CER			0.64	0.00	0.42	0.83	0.74	0.23	(0.15, 0.30)
DRCR	0.37	1.89		0.84	0.41	0.78	0.79	1.16	(0.69, 1.77)
Natural mortality (M) = 0.20									
CER			1.73	0.08	0.46	0.92	0.78	0.23	(0.16, 0.31)
DRCR	0.42	1.05		0.24	0.43	0.82	0.73	0.51	(0.38, 0.65)
Natural mortality (M) = 0.40									
CER			3.27	0.34	0.46	0.97	0.79	0.27	(0.20, 0.36)
DRCR	0.47	0.84		0.34	0.44	0.91	0.76	0.47	(0.35, 0.60)
Spatial variability in catchability (σ_t) = 0.2									
CER			1.00	0.00	0.46	0.88	0.75	0.22	(0.15, 0.29)
DRCR	0.42	1.05		0.34	0.44	0.83	0.72	0.63	(0.44, 0.83)
Spatial variability in catchability (σ_t) = 0.4									
CER			1.09	0.00	0.45	0.77	0.71	0.23	(0.15, 0.30)
DRCR	0.42	1.05		0.40	0.44	0.74	0.71	0.66	(0.45, 0.91)

Table A3. Performance measures for additional scenarios using the max–min DRCR and CER, as for Table 4.

Description	Max–min x-intercept relative to optimal x-intercept	Max–min slope relative to optimal slope	Max–min effort relative to optimal effort	Probability of $B < 0.25B_{MSY}$ after time-step 5	Average depletion in year 100 relative to that for the optimal rule	Average cpue in year 100 relative to cpue for the optimal rule	Average catch in year 100 relative to that for the optimal rule	Average interannual CV of catch relative to that for the optimal rule
Base case								
CER			0.91	0.00	1.06	1.10	1.00	1.02
DRCR	1.75	0.20		0.16	1.70	2.27	0.78	0.59
Initially at 10% of depletion at MSY								
CER			0.91	0.80	1.06	1.10	1.00	1.01
DRCR	1.75	0.20		1.00	1.80	2.46	0.75	0.71
Initially at 50% of depletion at MSY								
CER			0.83	0.00	1.11	1.21	1.01	1.03
DRCR	1.75	0.25		0.00	1.68	2.22	0.71	0.61
Initially at 100% of depletion at MSY								
CER			0.83	0.00	1.11	1.21	1.01	0.93
DRCR	NA*	NA*		0.00	1.82	2.61	0.76	1.72
Initially at 200% of depletion at MSY								
CER			0.83	0.00	1.11	1.21	1.01	0.87
DRCR	1.75	0.50		0.00	1.65	2.18	0.72	0.62
Steepness (h) = 0.3								
CER			2.50	1.00	0.57	0.04	0.10	5.49
DRCR	NA*	NA*		0.92	2.95	37.35	0.11	2.03
Steepness (h) = 0.5								
CER			1.43	0.12	0.76	0.59	0.84	0.75
DRCR	1.75	0.33		0.50	2.02	2.91	0.66	0.59
Steepness (h) = 0.9								
CER			0.59	0.00	1.31	1.62	0.95	1.03
DRCR	2.00	0.08		0.04	1.78	2.50	0.66	0.32
Natural mortality (M) = 0.05								
CER			1.43	0.00	0.80	0.62	0.89	0.78
DRCR	2.00	0.11		0.34	1.95	2.80	0.51	0.36
Natural mortality (M) = 0.20								
CER			0.53	0.00	1.38	1.66	0.87	1.01
DRCR	1.75	0.20		0.24	1.65	2.19	0.82	0.65
Natural mortality (M) = 0.40								
CER			0.28	0.14	1.70	2.18	0.60	0.92
DRCR	1.56	0.25		0.34	1.52	1.89	0.84	0.71
Spatial variability in catchability (σ_q) = 0.2								
CER			0.91	0.00	1.06	1.10	1.00	1.02
DRCR	1.75	0.20		0.16	1.71	2.33	0.77	0.58
Spatial variability in catchability (σ_q) = 0.4								
CER			0.83	0.00	1.10	1.20	1.00	1.05
DRCR	1.75	0.20	NA	0.20	1.71	2.52	0.74	0.57

*The optimal DRCR was (x-intercept, slope) = (0, NA).

Appendix B: Chapter 2 operating model and supplementary tables

Operating Model

The abundance, N , at age a in cell (i,j) at time $t+1$ is given by

$$(B.1) \quad N_{a,i,j,t+1} = \begin{cases} R_{i,j,t+1} & \text{if } a = 0 \\ \sum_i \sum_j \left((N_{a,\hat{i},\hat{j},t} e^{-M/2} - C_{a,\hat{i},\hat{j},t}) e^{-M/2} P_{i,j,\hat{i},\hat{j}} \right) & \text{if } 1 \leq a < a_{plus} \\ \sum_i \sum_j \left((N_{a,\hat{i},\hat{j},t} e^{-M/2} - C_{a,\hat{i},\hat{j},t} + N_{a-1,\hat{i},\hat{j},t} e^{-M/2} - C_{a-1,\hat{i},\hat{j},t}) e^{-M/2} P_{i,j,\hat{i},\hat{j}} \right) & \text{if } a = a_{plus} \end{cases}$$

where $R_{i,j,t}$ is the number of recruits in cell (i,j) at time t , M the instantaneous rate of natural mortality, $N_{a,\hat{i},\hat{j},t}$ the abundance at age a and time t in cell (\hat{i}, \hat{j}) before movement, $C_{a,\hat{i},\hat{j},t}$ the catch at age a in cell (\hat{i}, \hat{j}) at time t , and $P_{i,j,\hat{i},\hat{j}}$ is the proportion of adults that move from cell (\hat{i}, \hat{j}) to cell (i,j) [see Equations (B.2 and B.3)]. The adult movement model operates in two dimensions (alongshore and offshore) and there is no movement beyond the boundaries of the spatial grid. Adult movement has a non-directional diffusion component where σ_{Aalong}^2 and σ_{Aoff}^2 determine the extent of diffusion in the alongshore and inshore to offshore directions, respectively. Adult advection occurs according to two quadratic functions, $f()$ and $g()$, for advection in the alongshore and offshore directions, respectively. A narrow quadratic function will result in higher rates of advection than a wide quadratic function. Parameters of the quadratic functions used in each movement scenario are listed in Table B1.

$$(B.2) \quad \hat{P}_{i,j,\hat{i},\hat{j}} = \exp\left(-\frac{(\hat{i}-i)^2}{2\sigma_{Aalong}^2} - \frac{(\hat{j}-j)^2}{2\sigma_{Aoff}^2}\right) \frac{f(i) g(j)}{f(\hat{i}) g(\hat{j})}$$

Normalizing Equation B.2 leads to $P_{i,j,\hat{i},\hat{j}}$ representing the proportion of individuals moving from spatial cell (\hat{i}, \hat{j}) that to cell (i, j) :

$$(B.3) \quad P_{i,j,\hat{i},\hat{j}} = \frac{\hat{P}_{i,j,\hat{i},\hat{j}}}{\sum_i \sum_j \hat{P}_{i,j,\hat{i},\hat{j}}}$$

Length, weight, maturity, and fecundity

Length-at-age at the start and middle of the year ($L_{a,beg}, L_{a,mid}$) follows the von Bertalanffy growth curve, where L_∞ is the asymptotic size, L_{min} is the theoretical length of an individual at age 0, and k determines the rate of growth; length-at-age is assumed to be constant over space:

$$(B.4) \quad L_a = L_\infty + L_{min} - L_\infty e^{-k(a)}$$

Lengths-at-age are divided into 2cm bins and binned lengths-at-age ($\hat{L}_a, \hat{L}_{a+0.5}$) are used to calculate weight-at-age in the start and middle of the year ($w_{a,beg}, w_{a,mid}$).

Weight-at-age is an allometric function of length, where α is a scalar and β determines the rate of allometric growth:

$$(B.5) \quad w_{a,beg} = \alpha \hat{L}_a^\beta; \quad w_{a,mid} = \alpha \hat{L}_{a+0.5}^\beta$$

The maturity ogive (O_a) is a logistic function of age, where a_{50}^{mat} and a_{95}^{mat} represent the ages of females, which are the same as for males, at 50% and 95% maturity, respectively:

$$(B.6) \quad O_a = \frac{1}{1 + \exp\left(\frac{-\ln(19)(a - a_{50}^{\text{mat}})}{(a_{95}^{\text{mat}} - a_{50}^{\text{mat}})}\right)}$$

Spawning-stock biomass, B_t , is a function of maturity and weight-at-age at the start of the year (O_a and $w_{a,beg}$, respectively):

$$(B.7) \quad B_t = \sum_a \sum_i \sum_j 0.5 N_{a,i,j,t} O_a w_{a,beg}$$

Larval dispersal and recruitment

Recruitment follows the Beverton–Holt stock-recruitment curve with global density-dependent mortality [Equation (B.8)], where R_0 is the total number of recruits under unfished conditions, i.e. summed over all spatial cells, and $Q_{i,j}$ is the proportion of larvae that recruit to spatial cell (i,j) under unfished conditions. Steepness, h , is the proportion of R_0 produced when the total SSB, B_t , is 20% of the SSB produced when the population is in an unfished state, B_0 . Local and global process errors are applied to recruitment,

$\varepsilon_{R_{L_{i,j,t}}} \sim N(0, \sigma_{R_L}^2)$, $\varepsilon_{R_{G_t}} \sim N(0, \sigma_{R_G}^2)$ respectively:

$$(B.8) \quad R_{i,j,t+1} = R_0 Q_{i,j} \frac{4h(B_t/B_0)}{(1-h) + (5h-1)(B_t/B_0)} e^{(\varepsilon_{R_{L_{i,j,t}}} - \sigma_{R_L}^2/2)} e^{(\varepsilon_{R_{G_t}} - \sigma_{R_G}^2/2)}$$

$Q_{i,j}$ is characterized by the distance from a central cell of greatest concentration of larvae, $(\mu_{\text{along}}, \mu_{\text{off}})$, and standard deviations in each cardinal direction

($\sigma_{\text{north}}, \sigma_{\text{south}}, \sigma_{\text{east}}, \sigma_{\text{west}}$) following Equations (B.9)–(B.10) and $Q_{i,j} = Q_{\text{along}_i} Q_{\text{off}_j}$. The indicator function $I_{i > \mu_{\text{along}}}$ is equal to 1 if cell $i > \mu_{\text{along}}$, and 0 otherwise; likewise $I_{i > \mu_{\text{off}}}$ is 1 if cell $i > \mu_{\text{off}}$:

$$(B.9) \quad Q_{\text{along}_i} = \exp\left(\frac{(i - \mu_{\text{along}})^2}{\sigma_{\text{north}}}\right) I_{i > \mu_{\text{along}}} + \exp\left(\frac{(i - \mu_{\text{along}})^2}{\sigma_{\text{south}}}\right) (1 - I_{i > \mu_{\text{along}}})$$

$$(B.10) \quad Q_{\text{off}_j} = \exp\left(\frac{(j - \mu_{\text{off}})^2}{\sigma_{\text{east}}}\right) I_{j > \mu_{\text{off}}} + \exp\left(\frac{(j - \mu_{\text{off}})^2}{\sigma_{\text{west}}}\right) (1 - I_{j > \mu_{\text{off}}})$$

Initial conditions

The OM is initialized using Equation B.11:

$$(B.11) \quad N_{a,i,j,0} = \begin{cases} R_0 Q_{i,j} & \text{if } a = 0 \\ \sum_{\hat{i}} \sum_{\hat{j}} P_{i,j,\hat{i},\hat{j}} N_{a-1,\hat{i},\hat{j},0} e^{-M} & \text{if } 1 \leq a < a_{\text{plus}} \\ \sum_{\hat{i}} \sum_{\hat{j}} P_{i,j,\hat{i},\hat{j}} N_{a-1,\hat{i},\hat{j},0} \frac{e^{-M}}{1 - e^{-M}} & \text{if } a = a_{\text{plus}} \end{cases}$$

Fishery dynamics

The midyear exploitable biomass, X , is given by:

$$(B.12) \quad X_{i,j,t} = \sum_a N_{a,i,j,t} e^{-M/2} S_a w_{a,\text{mid}},$$

where age-specific selectivity, S_a , follows a logistic curve, and a_{50} and a_{95} represent respectively the ages at which 50% and 95% of fish are selected by the fishery:

$$(B.13) \quad S_a = \frac{1}{1 + \exp\left(\frac{-\ln(19)(a - a_{50})}{(a_{95} - a_{50})}\right)}$$

Effort (E_t) is allocated among spatial cells in proportion to the distribution of exploitable biomass across spatial cells that are open to fishing, with variability in catchability among spatial cells, $\varepsilon_{i,j}^q \sim N(0, \sigma_q^2)$, i.e.

$$(B.14) \quad E_{i,j,t} = \begin{cases} E_t \frac{X_{i,j,t} e^{(\varepsilon_{i,j}^q - \sigma_q^2/2)}}{\sum_i \sum_j X_{i,j,t} e^{(\varepsilon_{i,j}^q - \sigma_q^2/2)}} & \text{for all cells } (i, j) \text{ open to fishing} \\ 0 & \text{otherwise} \end{cases}$$

The catch is taken in the middle of the year. The catch-at-age for each spatial cell is:

$$(B.15) \quad C_{a,i,j,t} = N_{a,i,j,t} e^{-M/2} S_a q E_{i,j,t};$$

$$(B.16) \quad \dot{C}_{i,j,t} = \sum_a C_{a,i,j,t} w_{a,mid}; \quad \dot{C}_t = \sum_a \sum_i \sum_j C_{a,i,j,t} w_{a,mid}$$

Supplementary Tables (Appendix B, continued)

Table B1. Parameter values for movement parameters

Parameter	Movement scenario		
	Alongshore diffusion	Sedentary	Alongshore advection
μ_{along}	10	10	1.5
μ_{off}	0.5	0.5	0.5
σ_{north}^2	100	10000	50
σ_{south}^2	100	10000	50
σ_{east}^2	0.5	10000	1
σ_{west}^2	0.5	10000	1
σ_{Aalong}^2	1.0	0.01	3.0
σ_{Aoff}^2	0.5	0.01	1.0
Points defining f()	(10,1), (17.5,1)	(10,1), (17.5,1)	(9,21), (17.5,41)
Points defining g()	(2.5,3), (4.5,0.001)	(2.5,1), (4.5,1)	(2.5,41), (4.5,81)

Table B2. Base-case parameterization of the operating model.

Parameter	Base-case value
h	0.75
M	0.2 year ⁻¹
L_{inf}	50 cm
k	0.2 year ⁻¹
L_{min}	0.001 years
α	0.001
β	3
L_{50}	4 years
L_{95}	8 years
a_{50}	5 years
a_{95}	8 years
σ_{R_L}	0
σ_{R_G}	0.42

Appendix C. Chapter 2 Statistical catch-at-age model (Stock Synthesis v3.22b)

Stock Synthesis v3.22b (SS) was used to conduct the assessments; a full technical description of the SS model can be found in Methot and Wetzel (in press). The population dynamics in SS match those of the operating model, with the exception of spatial dynamics. We conducted single area assessments (no spatial dynamics) and three–area assessments with estimation of movement parameters. While the OM was an 18x5 cell spatial grid with movement dynamics, the three–area assessment model was a 3x1 model and hence there were no spatial dynamics in the inshore-offshore direction. The spatial dynamics of SS include allocation of recruits to the three areas and adult movement between each of the areas. Aside from movement and recruitment allocation parameters, parameters were shared among areas (i.e. one recruitment deviation was estimated in each year, and one R_0 value and one selectivity curve were estimated in the base case scenario). A bias–adjustment correction was conducted (Methot and Wetzel, in press), using the function `SS_fitbiasramp()` in the `r4ss()` package written for R (Taylor et al., 2008).

The numbers of fish at age a in area j at time $t+1$, $N_{a,j,t+1}$, were:

$$(C.1) \quad N_{a,j,t+1} = \begin{cases} r_j N_{0,t+1} & \text{if } a = 0 \\ \sum_i m_{a,i,j} N_{a-1,i,t} e^{-(M+S_{a-1}F_{a-1,i,t})} & \text{if } 1 \leq a < x \\ \sum_i m_{a,i,j} \left(N_{a-1,i,t} e^{-(M+S_{a-1}F_{a-1,i,t})} + N_{a,i,t} e^{-(M+S_{a-1}F_{a-1,i,t})} \right) & \text{if } a = x \end{cases}$$

where r_j is the proportion of the recruits that recruit to area j (Equation C.4), $m_{a,i,j}$ is the proportion of individuals of age a that move from area i to area j in a given year, M is the instantaneous natural mortality rate, S_a is logistic selectivity-at-age, and $F_{a,i,t}$ is the instantaneous fishing mortality rate on fish of age a , area i , at time t .

SS adult movement model

SS estimates $\rho_{i,j}$, the rate of movement (in log-space) from area i to area j for individuals younger than age $a_{\min(i,j)}$ and $\zeta_{i,j}$, the rate of movement (in log-space) from area i to area j for individuals older than age $a_{\max(i,j)}$. The parameter $a_{\min(i,j)}$ was set to 0 and $a_{\max(i,j)}$ was equal to 1 for all areas (i,j) . The relative movement rate of an individual of age a from area i to area j , $\hat{m}(a,i,j)$, is:

$$(C.2) \quad \hat{m}_{a,i,j} = \begin{cases} \exp(\rho_{i,j}) & \text{if } a \leq a_{\min(i,j)} \\ \exp\left(\rho_{i,j} + (a - a_{\min(i,j)}) \frac{\zeta_{i,j} - \rho_{i,j}}{a_{\max(i,j)} - a_{\min(i,j)}}\right) & \text{if } a_{\min(i,j)} < a < a_{\max(i,j)} \\ \exp(\zeta_{i,j}) & \text{if } a \geq a_{\max(i,j)} \end{cases}$$

Normalizing such that $m_{a,i,j}$ is the proportion of individuals of age a originating in area i that move to area j :

$$(C.3) \quad m_{a,i,j} = \frac{\hat{m}_{a,i,j}}{\sum_j \hat{m}_{a,i,j}}$$

SS allocation of recruitment

Recruitment can occur to any of the three areas in the multi-area assessment. The recruitment rate for each area, θ_i , is specified in log-space and is relative to recruitment rates to the other areas such that the proportion of recruits in each area, r_i , is:

$$(C.4) \quad r_i = \frac{\exp(\theta_i)}{\sum_i \exp(\theta_i)} .$$

Appendix D. Bias induced when local recruitment variation exists

A set of simulations was conducted with local and global sources of recruitment variation in the OM. This resulted in consistent underestimation of SSB for the single assessment and three assessment configurations when adults were sedentary and no NTMR existed (Figure D.1, b & e), whereas no bias occurred for these scenarios when only global sources of recruitment variation were simulated in the OM (Chapter 2, Figure 3, b & e).

Local recruitment variability in the OM is set such that total recruitment variability is $\sigma_R = 0.6$ when global recruitment variability accounts for half of the total recruitment variability ($\sigma_{R_G} = 0.42$). This means that local recruitment variability is $\sigma_{R_L} = 1.87$ for the sedentary configuration because the effect of local recruitment variability becomes small as the number of spatial cells increases. A very high value for local recruitment variability means that occasionally catch rates can be very high within some spatial cells when fish that were produced in a favorable year in a particular spatial cell recruit to the fishery. The distribution of effort over space is proportional to the distribution of biomass over space in the OM. When there is a large recruitment event to the fishery in a particular spatial cell that results in its biomass being proportionally higher than biomass in other cells, a higher proportion of fishing effort will eventually occur in those cells. However, the biomass in these cells is composed of many young fish from the recruitment event. This means that the fishery catch-at-age data contains a higher proportion of young fish than are present in the population. Therefore, the assessment

underestimates spawning stock biomass because it assumes that the low proportion of older fish in the fishery catch-at-age data is a result of depletion due to fishing.

Figure D.2 shows several graphs that confirm this phenomenon. To eliminate the possibility that some negative bias was from issues in the phasing of estimated parameters or from not estimating recruitment deviations in initial years (years 1-33), we conducted a single-area assessment for the sedentary movement scenario with an alternative phasing configuration and with estimation of recruitment deviations starting in year 2 (Figure D.2a), which did not eliminate the negative bias in the estimation of SSB. Next, maintaining the assessment configuration used for Figure D.2a, we eliminated local recruitment variability in the OM for the sedentary movement scenario (as for the base case scenario; Figure D.2b), which also eliminated the negative bias in the estimated SSB (Figure D.2b), as happened for the base case scenario (Chapter 2, Figure 3b). Next, we conducted the single-area assessment for the sedentary movement scenario with local recruitment variability in the OM, but without spatial fishing fleet dynamics (fishing effort was uniform over space; Figure D.2c). As expected, when fishing fleets were unresponsive to local fluctuations in biomass, the fishery catch-at-age data mimicked the survey catch-at-age data, correctly representing the proportion of older fish in the population and hence there was no negative bias in SSB. Finally, we conducted a single-area assessment on the base case OM (with local recruitment variability and spatial fishing fleet dynamics), but set the effective sample size of catch-at-age data in the assessment to 1, which effectively removes the catch-at-age data by preventing it from influencing the estimation (Figure D.2d). SSB is unbiased without the influence of catch-at-age data (Figure D.2d), confirming that negative bias in SSB in Figure D.1b

was directly linked to the catch-at-age data. Finally, Figure D.3 shows an example realization of fishery and survey catch-at-age data for a scenario with local and global recruitment variation and spatial fishing fleet dynamics in the OM. Figure D.3 shows that the proportion of younger fish in the fishery catch-at-age data (particularly the proportion of ages 4 and 7 fish) is greater for the fishery catch-at-age data than for the survey catch-at-age data. The 3ASMT configuration applied to a sedentary movement scenario with no NTMR is almost identical to the single assessment configuration and the same phenomenon is the cause of negative bias in estimates of SSB in both cases.

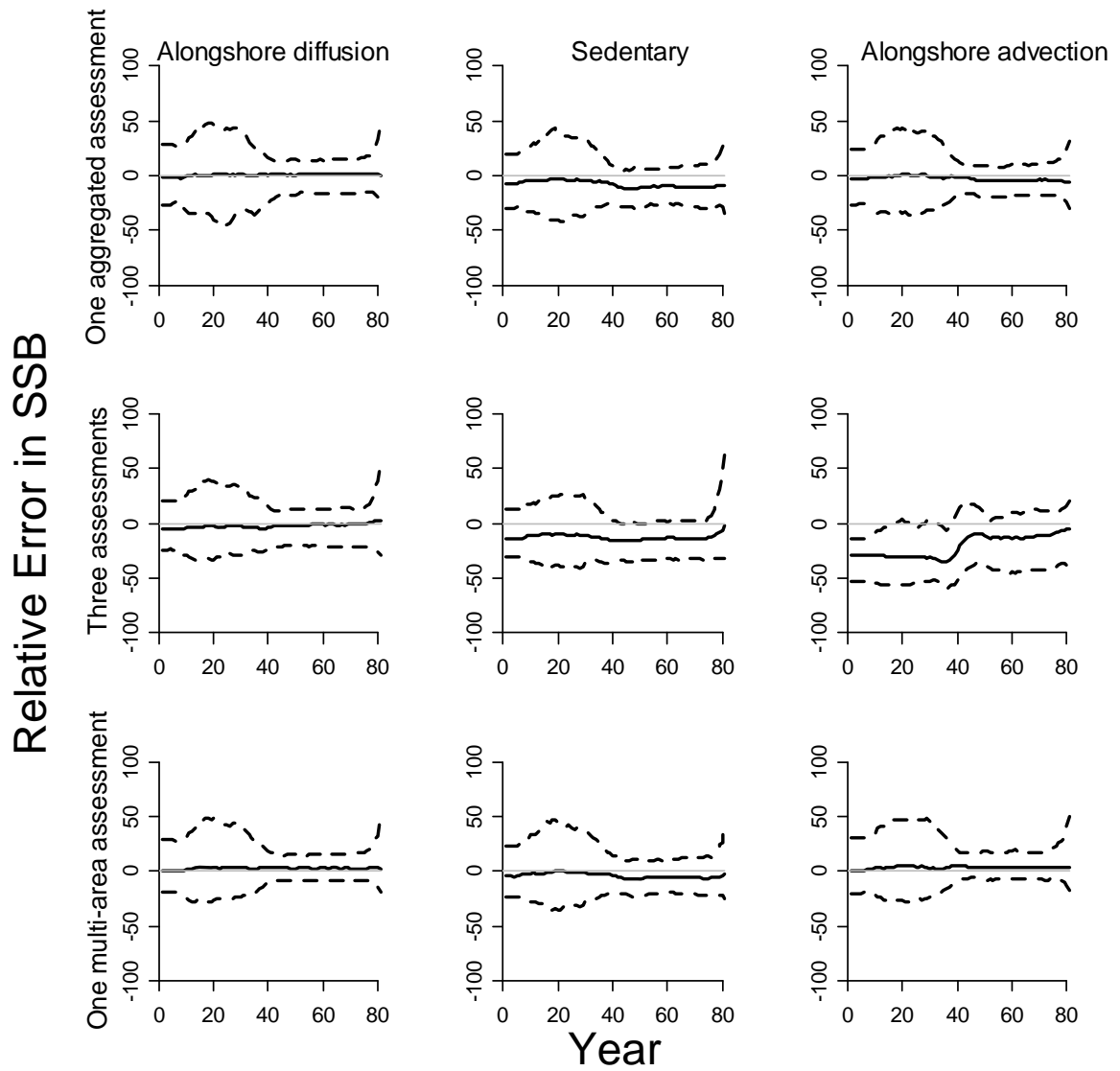


Figure D.1. As for Figure 3 (Chapter 2), but with local recruitment variation accounting for half of the total amount of variation in the OM.

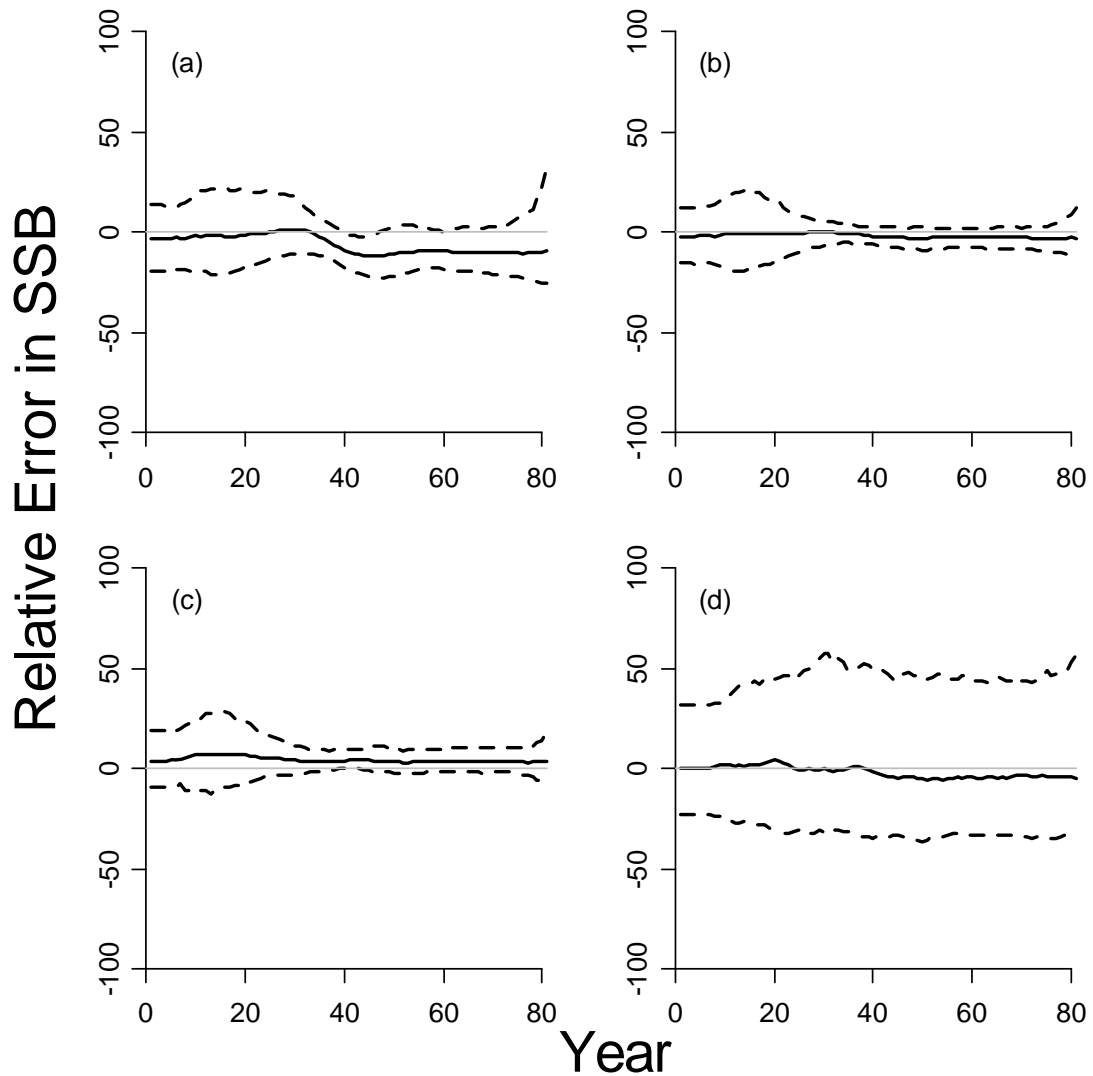


Figure D.2. Relative error in spawning stock biomass (SSB) over time no NTMR in the OM for the sedentary movement scenario. Scenarios differ from the base case scenario due to (a) local recruitment variation and recruitment deviations estimated beginning in year 2, (b) recruitment deviations beginning in year 2, (c) uniform distribution of fishing effort over space, local recruitment variation, and recruitment deviations beginning in year 2, and (d) local recruitment variation and effective sample size equal to 1. Solid black lines indicate the median relative error and dashed lines show the 90% quantiles of relative error. Horizontal grey lines indicate no relative error. When local recruitment variation is simulated it accounts for half of the total amount of recruitment variation in the OM.

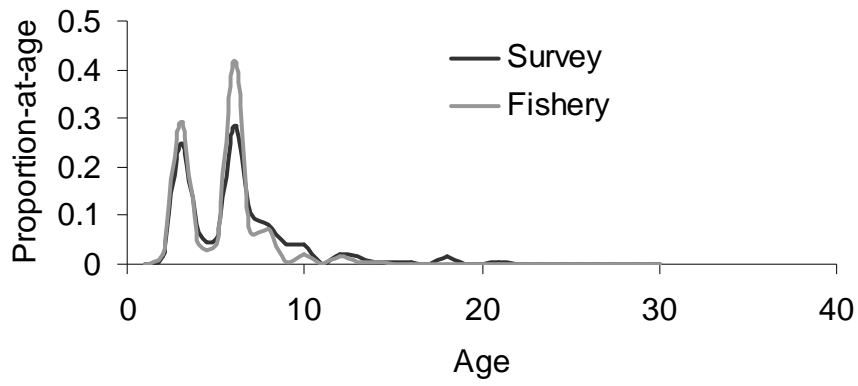


Figure D.3. Proportion of fish at each age in year 81 for the fishery (grey) and survey (black) data for one realization of the OM with local recruitment variability, spatial fishing fleet dynamics, using the alongshore diffusion movement scenario with no NTMR.

Appendix E. Chapter 3 Population Dynamics

The abundance, N , at age a in area j at time $t+1$ is given by

$$(E.1) \quad N_{a,j,t+1} = \begin{cases} R_{j,t+1} & \text{if } a = 1 \\ N_{a-1,j,t} \exp(-(M + S_{a-1,j}F)) & \text{if } 1 < a < a_{\max} \\ N_{a-1,j,t} \exp(-(M + S_{a-1,j}F)) + N_{a,j,t} \exp(-(M + S_{a,j}F)) & \text{if } a = a_{\max} \end{cases}$$

where $R_{j,t}$ is the number of recruits in area j at time t , M the instantaneous rate of natural mortality, F the instantaneous fishing mortality rate, $N_{a,j,t}$ the abundance in area j at age a and time t , and a_{\max} is the oldest age class in the model. Fishery selectivity in area j at age a , $S_{a,j}$, is 0 if area j is in a marine reserve and otherwise is asymptotic (S'_a).

$$(E.2) \quad S_{a,j} = \begin{cases} S'_a & \text{if } j \text{ is open to fishing} \\ 0 & \text{if } j \text{ is within a marine reserve} \end{cases}$$

Asymptotic selectivity follows a logistic curve:

$$(E.3) \quad S'_a = \left[1 + \exp\left(\frac{-\ln(19)(a - a_{50})}{(a_{95} - a_{50})}\right) \right]^{-1},$$

where a_{50} and a_{95} represent the age at which 50% and 95% of fish are selected by the fishery, respectively.

Length, weight, maturity, and fecundity

Length at age (L_a) follows the von Bertalanffy growth curve, where L_∞ is the asymptotic size, κ determines the rate of growth, and τ_0 is the theoretical age at which an individual is of zero length:

$$(E.4) \quad L_a = L_\infty (1 - e^{-\kappa(a-\tau_0)}).$$

Weight-at-age (w_a) is an allometric function of length, where α is a scalar and β determines the rate of allometric growth:

$$(E.5) \quad w_a = \alpha L_a^\beta.$$

The maturity ogive (O_a) is a logistic function of length, where a_{50}^{mat} and a_{95}^{mat} represent the ages of females at 50% and 95% maturity, respectively:

$$(E.6) \quad O_a = \left[1 + \exp\left(\frac{-\ln(19)(a - a_{50}^{\text{mat}})}{(a_{95}^{\text{mat}} - a_{50}^{\text{mat}})}\right) \right]^{-1}.$$

We assume a sex ratio of 1:1 for all ages in the model because there is no sex-specific survival. The spawning-stock biomass in area j at time t , $B_{j,t}$, is:

$$(E.7) \quad B_{j,t} = 0.5 \sum_a N_{a,j,t} O_a w_a.$$

Initial conditions

The model is initialized at equilibrium with respect to the fishing mortality rate F (Lawson and Hilborn, 1985).

$$(E.8) \quad N_{a,j} = \begin{cases} R_{j,\infty} & \text{if } a = 1 \\ N_{a-1,j} \exp(-(FS_{a-1,j} + M)) & \text{if } 1 < a < a_{\text{max}} \\ N_{a-1,j} \frac{\exp(-(FS_{a-1,j} + M))}{1 - \exp(-(FS_{a,j} + M))} & \text{if } a = a_{\text{max}} \end{cases}.$$

Pre-dispersal density-dependent mortality:

The number of eggs at equilibrium is a function of fecundity and numbers-at-age, but can also be seen as a function of equilibrium recruitment, $R_{j,\infty}$ (Lawson and Hilborn, 1985).

$$(E.9) \quad E_{j,\infty} = 0.5 \sum_a O_a w_a N_{a,j} = R_{j,\infty} Q_j,$$

where

$$(E.10) \quad Q_j = 0.5 \sum_{a=1}^{a_{\max}} O_a w_a q_{a,j} \quad \text{and}$$

$$(E.11) \quad q_{a,j} = \begin{cases} 1 & \text{if } a = 1 \\ \exp \sum_{k=1}^{a-1} (-(FS_{k,j} + M)) & \text{if } 1 < a < a_{\max} \\ \frac{\exp \sum_{k=1}^{a-1} (-(FS_{k,j} + M))}{1 - \exp(-(FS_{a_{\max},j} + M))} & \text{if } a = a_{\max} \end{cases}$$

Equilibrium recruitment in area j , $R_{j,\infty}$, is defined as:

$$(E.12) \quad R_{j,\infty} = \frac{4h(E_\infty/E_0)}{(1-h) + (5h-1)(E_\infty/E_0)} = \frac{4h(R_{j,\infty}Q_j/R_{j,0}Q_{j(F=0)})}{(1-h) + (5h-1)(R_{j,\infty}Q_j/R_{j,0}Q_{j(F=0)})}$$

Solving for $R_{j,\infty}$, equilibrium recruitment in area j is

$$(E.13) \quad R_{j,\infty} = \left(\frac{4hQ_j}{Q_{j(F=0)}} - (1-h) \right) \left(\frac{1}{5h-1} \right) \left(\frac{R_{j,0}Q_{j(F=0)}}{Q_j} \right).$$

A 500 year deterministic burn-in period is conducted to find the correct number of recruits in each area when there is larval movement and the model is initiated at an equilibrium with $F > 0$.

Larval movement dynamics

Some scenarios with a marine reserve include larval movement. The total number of recruits in area j in year $t+1$ summed over i spawning sites, $R'_{j,t+1}$, prior to larval movement is:

$$(E.14) \quad R'_{j,t+1} = \sum_i R'_{i,j,t+1} .$$

Larvae move between a marine reserve and a fished area according to a single movement rate, θ_{out} , which is the proportion of larvae that move from the marine reserve to the fished area in each time-step. The proportion of larvae that move from the fished area to the marine reserve, θ_{in} , is a function of the proportion of the total habitat within the marine reserve, ψ , and θ_{out} :

$$(E.15) \quad \theta_{in} = \frac{\psi \theta_{out}}{(1-\psi)} .$$

The number of recruits in the marine reserve (assuming area 1 is the marine reserve) is:

$$(E.16) \quad R_{1,t+1} = R'_{1,t+1} (1 - \theta_{out}) + \theta_{in} R'_{2,t+1}$$

The number of recruits in the fished area (area 2) after larval movement is:

$$(E.17) \quad R_{2,t+1} = R'_{2,t+1}(1 - \theta_{in}) + \theta_{out} R'_{1,t+1}.$$

Fishery dynamics

The catch is taken continuously throughout the year. The total catch biomass is:

$$(E.18) \quad C_t = \sum_a w_a \left(\sum_j \frac{S_{a,j} F}{S_{a,j} F + M} N_{a,j,t} (1 - e^{-(M + S_{a,j} F)}) \right).$$

CURRICULUM VITAE

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Master of Science, Aquatic and Fishery Sciences, University of Washington, Seattle, WA, May 2007. GPA: 3.92

- **Advisor:** Ray Hilborn
- **Thesis Title:** Space and the state of the fishery in models of no-take marine reserves.
- **Academic Honors and Awards:** Achievement Rewards for College Scientists (ARCS) Scholar (Sept. 2004 – May 2006), Claire L. and Evelyn S. Egtvedt Fellowship, H. Mason Keeler Endowment for Excellence, Shao-Wen Ling Memorial Scholarship, Samuel and Althea Stroum Scholarship.

Bachelor of Arts in Mathematics, The College of Wooster, Wooster, Ohio, May 2000. Minor: Spanish; Cumulative GPA: 3.57; Mathematics GPA: 3.70

- **Independent Thesis:** Statistical Topics in the Epidemiology of the Incubation Period of AIDS
- **Honors:** Cum laude, departmental honors in mathematics, honors on senior thesis, Women's Advisory Board Scholarship, honorary music scholarship in flute performance

Employment and Research Experience

Graduate Research Assistant, Aquatic and Fishery Sciences, University of Washington (September 2004-Present).

Research focus: Spatial modeling of fish population dynamics to investigate potential effects of no-take marine reserves on the performance of stock assessments, target fish abundance, catch, and CPUE. Exploration of potential management strategies that use information from no-take marine reserves as an alternative to historical catch data.

Relevant course work and experience: Stock assessment methods, non-linear minimization, maximum likelihood techniques, Bayesian analysis, meta-analysis, estimation of population parameters, theory of probability and statistics (graduate level courses in the Department of Statistics), testing of statistical methods, linear regression, mixed effects models, population viability analysis, management strategy evaluation, marine fish ecology.

Research Assistant II, Biological Oceanography, SAS Programmer, University of Maryland Center for Environmental Science, Horn Point Lab, Cambridge, MD. (Full Time, October 2001-September 2004)

Projects included assessment of spatial and seasonal variability of zooplankton in Chesapeake Bay, assessment of zooplankton and juvenile fish density in the Estuarine Turbidity Maximum in Chesapeake Bay.

Responsibilities: Preparation of papers and presentations; computer programming in SAS to clean, merge, convert spatial marine datasets from incompatible sources and formats; automate processes using SAS macro facility; perform statistical analyses; debug programs; assist others with programming, debugging; computer programming in Scriptor (Visual Basic based programming language for Golden Software's Surfer mapping software) to interpolate spatial data between data points using geostatistical methods and create maps of hydrographic, acoustic, and optical zooplankton data of Chesapeake Bay. Perform field work with optical and acoustic equipment, drive boats up to 25 ft. Identify zooplankton and perform laboratory experiments.

Research Assistant and SAS Programmer, The Urban Institute, Health Policy Center, Washington, DC. (Full Time, August 2000-October 2001)

Projects included analysis of disability policy, interaction between health and economic status in determining retirement dates, longitudinal analysis of residential transitions of older adults.

Responsibilities: computer programming in SAS and STATA using large, complex social science datasets such as Census and MCBS (Medicare Current Beneficiary Survey). Create longitudinal datasets by combining data from various sources and formats; automate processes using SAS macros, arrays, loops; perform mathematical and statistical functions using survival analysis techniques; analyze data for correctness, missing value problems; debug programs; assist others in programming, debugging.

Researcher, Utah State University Depts of Biology, Mathematics and Statistics, Logan, Utah. (NSF Research Experience for Undergraduates, June 1999 – September 1999); **Working paper title:** Effects of evolution on a predator-prey population dynamics model.

Selected Computer Knowledge

R, FORTRAN, Matlab, ADMB, SAS, Visual Basic for Excel and Surfer mapping, LaTeX, Maple, Mathematica, WinBugs.

Publications

- McGilliard, C.R.**, Punt, A.E., and Hilborn, R. 2011. Spatial structure induced by no-take marine reserves shapes population responses to catastrophes in simple mathematical models. *Ecological Applications*. 21(4): 1399–1409.
- McGilliard, C.R.**, Hilborn, R., MacCall, A., Punt, A.E., and Field, J. 2011. Can information from Marine Protected Areas be used to inform control rule-based management of small-scale, data-poor stocks? *ICES Journal of Marine Science*. 68(1): 201-211.

- Branch, T.A., Watson, R. Fulton, E.A., Jennings, S., **McGilliard, C.R.**, Pablico, G.T., Ricard, D., and Tracey, S.R. 2010. The trophic fingerprint of marine fisheries. *Nature*. 468: 431-435.
- Stewart, I.J., Wallace, J.R., and **McGilliard, C.** 2009. Status of the U.S. yelloweye rockfish resource in 2009. In *Status of the Pacific Coast Groundfish Fishery through 2009, Stock Assessment and Fishery Evaluation: Stock Assessments, STAR Panel Reports, and Rebuilding Analyses*. Pacific Fishery Management Council. Portland, OR. 431 p.
- Punt, A.E., **McGilliard, C.**, and R. Hilborn. 2008. Evaluation of the impact of Marine Protected Areas on stock assessment-based fisheries management. Final Report to Washington Sea Grant (109pp).
- McGilliard, C.R.**, Hilborn, R. 2008. Modeling no-take marine reserves in regulated fisheries: assessing the role of larval dispersal distance. *Can. J. Fish. Aquat. Sci.* 65: 2509-2523.
- Zhang, X., Roman, M.R., Kimmel, D., **McGilliard, C.**, and Boicourt, W. 2006. Spatial variability in plankton biomass and hydrographic variables along an axial transect in Chesapeake Bay. *J. of Geophys Res.*: 111(C05S11).
- Roman, M.R., Zhang, X., **McGilliard, C.**, and Boicourt, W. 2005. Seasonal and annual variability in the spatial patterns of plankton biomass in Chesapeake Bay. *Limnol. Oceanogr.*: 50(2): 480-492.
- Spillman, B., Liu, K., **McGilliard, C.** 2003. Trends in residential long term care: use of nursing homes and assisted living and characteristics of facilities and residents. Final report to the Office of the Assistant Secretary for Planning and Evaluation, US Dept of Health and Human Services.

Presentations

Oral Presentations at Conferences and Workshops

- McGilliard, C.** 2012. Accounting for marine reserves and fish movement in stock assessments. ICES/PICES Oceans of Change Early Career Scientist Conference, Mallorca, Spain.
- McGilliard, C.** 2012. Accounting for marine reserves using spatial stock assessments. Western Groundfish Conference, Seattle, WA.
- McGilliard, C.** 2011. How marine reserves could affect the performance of spatial and conventional stock assessments. AFS Annual Conference, Seattle, WA. (Abstr. 43-7).
- McGilliard, C.** 2011. Comparing the potential effectiveness of marine reserves and conventional management in the context of age-truncation effects. International Marine Conservation Congress, Victoria, B.C. (Abstr. FISH 25.6).
- McGilliard, C.** 2010. Using Marine Protected Areas to Inform Control Rule-Based Management of Data-Poor Stocks: Evaluating the Influence of Larval and Adult Movement. Fellowships in Population Dynamics and Marine Resource Economics 2010 Fellows Meeting, Seattle, WA.
- McGilliard, C.** 2009. Applying information from marine protected areas in control rules for the management of small-scale, data-poor stocks. Fellowships in Population Dynamics and Marine Resource Economics 2009 Fellows Meeting, Woods Hole, MA.
- McGilliard, C.**, Hilborn, R., MacCall, A., Punt, A.E., and Field, J. 2008. Invited talk: Can we use information from marine protected areas to inform management of small-scale, data-poor stocks? Managing Data-Poor Fisheries Workshop, California Department of Fish and Game, Berkeley, CA.

- McGilliard, C.,** Hilborn, R., MacCall, A., Punt, A.E., and Field, J. 2008. Can we use information from marine protected areas to inform management of small-scale, data-poor stocks? The Seventh William R. and Lenore Mote International Symposium in Fisheries Ecology, Sarasota, FL.
- McGilliard, C.** 2008. Evaluation of the Impact of Marine Protected Areas on Stock Assessment-based Fisheries Management. Fellowships in Population Dynamics and Marine Resource Economics 2010 Fellows Meeting, Honolulu, HI.
- McGilliard, C.,** and Punt, A.E. 2007. Effects of no-take marine reserves on persistence of populations experiencing catastrophic natural mortality events AFS Annual Conference. (Abstr. 1471)
- McGilliard, C.,** and Hilborn, R. 2006. Modeling no-take marine reserves in regulated fisheries: assessing the role of larval dispersal distance. AFS Annual Conference. (Abstr. 424)
- McGilliard, C.,** and Hilborn, R. 2006. Modeling MPAs in regulated fisheries: assessing the role of larval dispersal distance. NSF F3 Grant Working Meeting, University of California Santa Barbara.
- McGilliard, C.,** and Hilborn, R. 2005. A proposal for studying the effects of larval dispersal at the interface of Marine Protected Areas and traditional management regimes. NSF F3 Grant Working Meeting, University of California Santa Barbara.

Seminars

- McGilliard, C.** 2012. Utility and implications of no-take marine reserves in fishery management strategies. Ph.D. Defense Seminar; School of Aquatic and Fishery Sciences.
- McGilliard, C.** 2010. Can we use information from marine protected areas to inform management of small-scale, data-poor stocks? Quantitative Seminar, School of Aquatic and Fishery Sciences.
- McGilliard, C.** 2009. Can we use information from marine protected areas to inform management of small-scale, data-poor stocks? School of Aquatic and Fishery Sciences Graduate Student Symposium.
- Punt, A.E., **McGilliard, C.** 2008. Using Management Strategy Evaluation to Evaluate the Impact of Marine Protected Areas on Stock Assessment-based Fisheries Management. Quantitative Seminar, School of Aquatic and Fishery Sciences.
- Punt, A.E., **McGilliard, C.** 2008. Evaluation of the impact of marine protected areas on stock assessment-based fisheries management. NMFS-UW Stock Assessment Mini-workshop.
- McGilliard, C.** 2007. Space and the state of the fishery in models of no-take marine reserves. Thesis Defense Seminar; School of Aquatic and Fishery Sciences.
- McGilliard, C.** 2006. Marine Protected Areas used with effort limits: the role of larval biology and the older female. Quantitative Seminar, School of Aquatic and Fishery Sciences.
- McGilliard, C.,** and Hilborn, R. 2005. A proposal for studying the effects of larval dispersal at the interface of Marine Protected Areas and traditional management regimes. Quantitative Seminar, School of Aquatic and Fishery Sciences.

Posters

McGilliard, C., Hilborn, R., MacCall, A., Punt, A.E., and Field, J. 2010. Can information from Marine Protected Areas be used to inform control rule-based management of small-scale, data-poor stocks? National Stock Assessment Workshop, St. Petersburg, FL.

McGilliard, C. and Punt, A.E. 2008. Evaluation of the Impact of Marine Protected Areas on Stock Assessment based Fisheries Management. National Stock Assessment Workshop, Port Townsend, WA.

Selected Leadership Contributions

- Faculty search committee student representative, School of Aquatic and Fishery Sciences, University of Washington, Spring 2010.
- Participant in working group entitled “The Regional Fisheries Management Project,” NMFS Southwest Fisheries Science Center, Santa Cruz, CA, January 2010.
- Co-chair of the NMFS “Density Ratio Working Group,” simulating ramifications of integrating of information from MPAs into new fishery control rules; application of new methods through the development of a cooperative management program for California’s nearshore multi-species rockfish fisheries (January 2008 – February 2009).
- Participant in NMFS working group entitled “Science Integration of Marine Protected Areas and Fishery Management” (May 2005 – 2007).
- Chair of organization, departmental Graduate Student Symposium (Feb 9, 2007; Feb 10, 2006)
- Radio interview on salmon management. Alaska Public Radio Network, July 18, 2005.
http://publicbroadcasting.net/apti/news.newsmain?action=article&ARTICLE_ID=796775