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Kaplan, David M

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# Alongshore advection and marine reserves: consequences for modeling and management

David M. Kaplan\*

Department of Wildlife, Fish, & Conservation Biology, University of California, Davis, California 95616, USA

**ABSTRACT:** The appropriate configuration of marine reserves for maximizing harvests or ensuring species persistence when there is uncertainty or variability in larval dispersal patterns is not completely understood. This is particularly true in environments with large alongshore advection rates, as the success of a system of marine reserves depends on connectivity through larval and/or adult dispersal between adjacent marine reserves. In this paper, the consequences of alongshore advection in the presence of marine reserves for a fish species with sedentary adults and widely dispersing larvae are examined. First, a uniform configuration of reserves with constant alongshore advection rate is considered. The highest overall catch and recruitment rates occur when the spacing between reserves is precisely tuned to the advection distance. When the alongshore advection distance is allowed to vary in time, catch and recruitment are considerably less sensitive to alongshore advection. At small diffusion distances, catch values differ from what would be predicted from the time-averaged larval dispersal pattern due to density-dependent post-settlement effects. It is important to include short time scale settlement variability in marine reserve models under these conditions. When the spacing between reserves is allowed to vary, the tuning of the system to particular advection distances is less precise. Configurations of marine reserves with a variety of spacings between reserves exhibited more uniform catch levels as a function of advection distance. This suggests that variability in the spacing between reserves is desirable for protecting a diverse group of species with different dispersal patterns.

**KEY WORDS:** Marine protected areas · Fisheries management · Population dynamics · Variable reserve-spacing · Advection variability

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## INTRODUCTION

Marine reserves, also known as marine protected areas and no-take areas, are an increasingly important management tool for many of the world's overexploited coastal fisheries. They possess certain advantages over traditional effort-based management methods, such as protecting entire ecosystems and potentially being easier to manage and enforce (e.g. Plan Development Team 1990, Dugan & Davis 1993, Bohnsack 1998). Furthermore, recent experimental and theoretical studies suggest that reserves benefit overfished populations through the export of adults and larvae to surrounding fished areas (Quinn et al. 1993, Attwood & Bennett 1994, Holland & Brazee 1996, Bohnsack 1998, Hastings

& Botsford 1999, Nowlis & Roberts 1999, McClanahan & Mangi 2000, Gell & Roberts 2003), although not all researchers agree on the need for reserves or the extent of the benefits they will provide (e.g. Lundberg & Jonzén 1999, Hilborn et al. 2004). In the present study, I use a numerical model to study the effects that alongshore advection of larvae and variability in the spacing between marine reserves have on a fish population along a linear coastline with a system of marine reserves.

Despite their potential advantages, marine reserves present challenges to managers and scientists as they create a spatially heterogeneous population with unknown or uncertain levels of connectivity between subpopulations. Spatial heterogeneity is not unique to

\*Email: dmkaplan@ucdavis.edu

systems of marine reserves. Terrestrial reserves also create heterogeneous environments. Nonetheless, results from terrestrial systems generally cannot be applied to marine systems because of differences in modes of dispersal between the 2 systems (Hockey & Branch 1994, Simberloff 2000, Carr et al. 2003). In terrestrial systems, dispersal usually occurs in the juvenile or adult phase and often takes place over a smaller spatial scale than in marine systems. Most marine species produce many small larvae that spend from several hours to several months in the plankton before settling into adult habitats (Strathmann 1990). During their time in the plankton, currents are capable of transporting larvae great distances, although larval behavior undoubtedly plays an important role in determining actual dispersal distances and final settlement locations (e.g. Mora & Sale 2002). As adults, many marine species, particularly those targeted for protection via marine reserves, are relatively sedentary and, therefore, dispersal is largely constrained to the larval phase. Because of the small size of most larvae, long time periods spent in the plankton, and complexity of the forces driving the transport and deposition of larvae to coastal habitats, experimentally determining larval dispersal patterns in marine systems is extremely difficult.

Given the difficulty of assessing larval dispersal patterns, as well as other aspects of the life history of many marine species, many researchers have turned to theoretical models for examining the potential effects of marine reserves on fish populations (e.g. Polacheck 1990, Quinn et al. 1993, Holland & Brazee 1996, Lauck et al. 1998, Hastings & Botsford 1999, Mangel 2000, Botsford et al. 2003, Gaines et al. 2003, Gerber et al. 2003). Although these models provide valuable insight into the effects of marine reserves on fish populations and serve as a baseline for future studies, most of them do not address the problem of larval dispersal in a realistic way (Gaines et al. 2003). Many models do not include a larval phase. Those models that do include larval dispersal generally make unjustified simplifying assumptions about the nature of larval dispersal, such as even redistribution of larvae to all subpopulations (pool dispersal; Hastings & Botsford 1999) or larval dispersal that is purely diffusive, i.e. symmetric around the point of larval origin and monotonically decreasing (e.g. Botsford et al. 2001, Kaplan & Botsford 2005). This level of abstraction is at times acceptable when one wishes to examine basic aspects of the model system with a limited set of parameters, but in many systems, alongshore advection is strong and/or highly variable. Recent work indicates that strong alongshore advection of larvae has important consequences for population persistence and fisheries yields (Gaylord & Gaines 2000, Gaines et al. 2003). A minimal parameterization

of larval dispersal requires the inclusion of both diffusive (random spread) and advective (net alongshore movement) processes (Largier 2003). In this paper, the consequences of temporal variability in the alongshore advection distance and variability in the spacing between reserves are examined in detail.

In real systems, larval dispersal is known to be highly variable in both time and space (e.g. Wing et al. 1998), suggesting that even a model of larval dispersal including advection and diffusion might not be sufficient. Larvae are thought to be transported by physical forces that vary on time scales of hours to weeks, producing variability in recruitment rates on similar time scales (Largier 2003). Furthermore, there is significant interannual variability in the strength of advective and diffusive currents. These distinct time scales of variability result in rather different pictures of settlement, depending on the temporal scales involved in the measurements (Largier 2003). At short time scales, recruitment appears extremely variable in time and space and has been related to changes in currents occurring shortly before settlement (e.g. Shanks 1986, Wing et al. 1998, Shanks et al. 2000). At longer time scales, spatial variability in dispersal is more regional than local, and temporal variability might be correlated with long time-scale physical processes, such as El Niño Southern Oscillation or the Pacific Decadal Oscillation (e.g. Wing et al. 2003). As a result of this variability, dispersal patterns depend significantly on the temporal scale involved.

Most modeling efforts to date have implicitly or explicitly assumed that dispersal variability on time scales smaller than some limit can be treated as increased diffusion and do not need to be directly addressed. Gaines et al. (2003) showed that variability in alongshore advection on a time scale of several years, modeled through occasional complete reversals of the advection direction, had a significant impact on population dynamics. Furthermore, the dynamics of the system with variable advection were significantly different than those of an equivalent system with increased diffusion. Gaines et al. (2003) suggested that averaging out variability on temporal scales shorter than several years might not significantly alter population dynamics, but that long-term variability is important for understanding population dynamics. In the present paper, this hypothesis is tested by comparing model results with yearly alongshore advection variability against models using long-term average dispersal patterns.

It has been suggested that one way to protect against uncertainty in dispersal patterns in real marine systems is to create a nonuniform distribution of reserves with variable spacing between them (Palumbi 2002). It is hoped that systems of reserves with variable spacing

will both provide protection to a wider class of marine life histories and be robust to temporal variability in dispersal patterns. The effects of variable spacing between marine reserves in the absence of alongshore advection were examined by Kaplan & Botsford (2005) who showed that the effects of variable reserve-spacing were quite limited for all but overfished populations. In this case, several closely spaced reserves provided added protection to long-distance dispersers by increasing the effective size of the reserve. This increase was at the expense of extreme spatial heterogeneity and collapse outside of reserves. Herein I expand on this work to include alongshore advection.

The paper is organized as follows: First, the model used in this study is described in detail. I examine the basic model of a fish population along an infinite linear coastline without alongshore advection variability or variable reserve-spacing. After this the maximum sustainable yields (MSY) for the model system with and without marine reserves are considered. Next, temporal variability in alongshore advection rates is included in the model and results are compared with expectations based on the long-term average dispersal pattern. Then, the spacing between reserves is allowed to vary and resulting changes in catch are examined. Finally, the consequences of the results for the design and study of systems of marine reserves are discussed.

## MODEL AND METHODS

The model used in this paper is a spatially-explicit, size- and age-structured model with a yearly time step similar to that used by Botsford et al. (1999), Lockwood et al. (2002) and Kaplan & Botsford (2005). It consists of 100 independent, size-structured subpopulations placed along a linear coastline connected via dispersal of larvae through a dispersal matrix. The length of coastline occupied by each subpopulation will be referred to as an SU (spatial unit) throughout. Because all distances are given in the same units, the actual units are arbitrary.

The distributions of adults in each subpopulation were subject to growth, natural and possibly fishing mortality, and reproduction. With the exception of fishing mortality, all population parameters affecting adults were identical in each subpopulation and were similar to those used by Botsford et al. (1999). Values were roughly based on those found for the red sea urchin *Strongylocentrotus franciscanus* along the coast of northern California (Morgan 1997). The red sea urchin is a slow-growing, benthic invertebrate that has widely dispersing larvae. It is known to be susceptible to overfishing and is considered to be a good candidate for management through the use of marine reserves

(Kalvass & Hendrix 1997, Botsford et al. 1999, Morgan et al. 1999). Although the population parameters used in the model are based on those for a particular species, the focus here is on those general trends that are not sensitive to changes in basic population parameters. The entire set of parameter values is in Table 1.

In the absence of fishing, the mean age of individuals in the model was 9.6 yr. Growth of individuals in each subpopulation was governed by a von Bertalanffy equation with Gaussian-distributed variability in maximum size (Smith et al. 1998). Beverton-Holt post-settlement density-dependence was included in the model (Beverton & Holt 1957). The value of the slope of the larvae-recruit curve at the origin,  $\alpha$ , was set so that the population collapsed when lifetime egg production (LEP) was less than 35 % of its unfished value (cf. Mace & Sissenwine 1993). This produced a collapse of the population at an instantaneous fishing rate of  $0.1 \text{ yr}^{-1}$  in the absence of marine reserves. Only individuals above a specific size were subject to fishing mortality. This fishing size limit was set to 60 mm, which is the size at which fish become sexually mature. Fishing rates in non-reserve subpopulations of  $0.08 \text{ yr}^{-1}$  (39 % of virgin LEP in fished areas; overfished without reserves) and  $0.14 \text{ yr}^{-1}$  (25 % of virgin LEP in fished

Table 1. Parameter values for population model. Italicized parameters: value varied between model runs; all others were held constant. SU: spatial units

Parameter name	Symbol	Value
<b>Recruitment</b>		
Slope of Beverton-Holt density-dependence	$\alpha$	0.0055
Recruit carrying capacity	C	12 000 000
<b>Growth</b>		
Maximum size	$L_{\infty}$	118 mm
SD of maximum size	$\sigma$	10 mm
Von Bertalanffy growth parameter	k	0.22
<b>Reproduction</b>		
Size of first reproduction		60 mm
Reproduction coefficient		5.47E-006
Reproduction exponent		3.45
<b>Mortality</b>		
Natural mortality rate	m	$0.08 \text{ yr}^{-1}$
Fishing size limit		60 mm
<i>Fishing mortality rate</i>	<i>f</i>	<i>0.08 and 0.14 yr<sup>-1</sup></i>
<b>Reserve configuration</b>		
Number of reserves		5
Reserve size		4
<i>Jitter</i>		<i>5, 10, 15 SU</i>
<b>Dispersal</b>		
<i>Diffusion distance</i>	<i>a</i>	<i>1–20 SU</i>
<i>Mean advection distance</i>	<i>D</i>	<i>0–30 SU</i>
<i>Standard deviation of advection distance</i>	$\sigma$	<i>1, 3, 5 &amp; 10 SU</i>

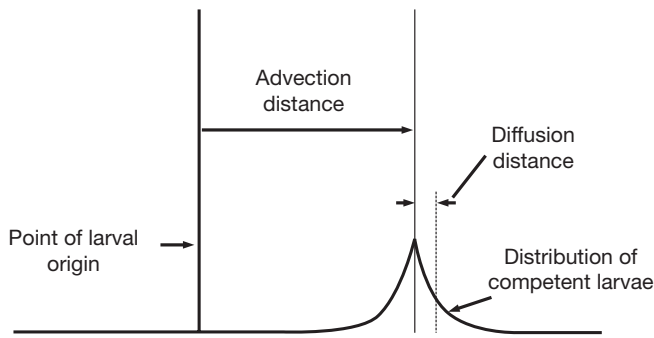


Fig. 1. Larval dispersal kernel used in model. Dispersal modeled as the sum of 2 processes, advection and diffusion. Advection consists of net alongshore movement of group of larvae from their common point of origin; diffusion is the spread of group of larvae originating from same location around center of distribution of larvae competent for settlement (process by which variability in spacing between reserves was introduced)

areas; collapse without reserves) were considered. The fishing mortality rate was identically zero inside reserves with knife-edge selection at the boundary. This implies that adults are sedentary and do not cross reserve boundaries. This is an acceptable approximation if one assumes that the scale of adult movements is much smaller than the average size of reserves (Nowlis & Roberts 1999). In addition, as the focus in the present study is on larval dispersal, adding adult movement would complicate the model and obscure the effects of dispersal.

A dispersal matrix related the density of pre-recruitment larvae along the coast to the final density of competent larvae that recruit into each subpopulation. Dispersal was described as the sum of 2 processes: (1) alongshore advection; (2) diffusion. The full dispersal kernel including advection and diffusion is shown graphically in Fig. 1. Alongshore advection was modeled as a net translation of all larvae down the coastline. The alongshore advection distance, i.e. the distance from the point of origin of the larvae to the center of the final larval distribution, was constant over space. Temporal variability in the advection distance was at times included in the model. In this case, for each year the advection distance was randomly selected from a Gaussian distribution with a given mean and SD. The mean alongshore advection distance,  $D$ , varied between model runs from 0 to 30, and the SD of the distribution of alongshore advection distances,  $\sigma$ , ranged from 0 to 10.

Diffusion of larvae around the alongshore advection distance was modeled using a Laplacian dispersal kernel of the form

$$p(|x - y|) = \frac{e^{-|x-y|/a}}{2a} \quad (1)$$

where  $p$  is the probability of a larvae starting at the origin and landing at the position  $x$ ,  $y$  is the alongshore advection distance, and  $a$  is a scaling parameter that is referred to in this paper as the diffusion distance. The diffusion distance is related to the SD of the Laplacian dispersal kernel,  $\sigma_d$ , by the formula

$$\sigma_d^2 = 2a^2 \quad (2)$$

The diffusion distance was constant over space and varied from 1 to 20 SU.

Circular boundary conditions were used, so larvae reaching one edge of the model system simply reappeared at the other edge. This essentially simulates an infinite coastline. I chose to use circular boundary conditions so as not to confound the effects of alongshore advection and reserve placement with edge effects due to finite habitat area.

All model runs had 5 reserves, each of which was 4 SU wide. Reserve positions were constant throughout each model run. Reserves could either be distributed uniformly along the coastline or with random variability in the spacing between reserves. The spacing between reserves was continuously perturbed from a uniform configuration by a process that will be referred to as 'jitter' (Kaplan & Botsford 2005; present Fig. 2). With no jitter, the system consisted of 5 uniformly spaced reserves. With jitter, the position of each reserve could deviate from that of a uniform distribution of reserves by up to a specified number of SU. Reserve size was maintained constant at 4 SU. Each reserve shifted independently of all other reserves. The number of SU shifted was randomly determined with equal probability for all values between zero and the specified jitter value. By increasing the amount of jitter, population dynamics for systems with increasingly variable reserve-spacing can be explored. I performed 20 model runs for each fishing rate, dispersal kernel and level of variability in reserve-spacing.

For each run of the model, the equilibrium state of the population was first approximated using a method developed by Kaplan et al. (in press). This technique recursively solves for the equilibrium values of recruitment based on the known LEP at each site (for a given

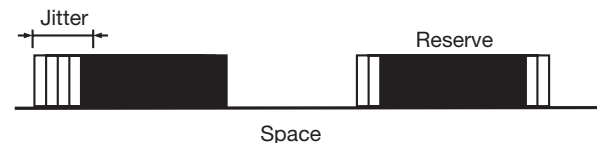


Fig. 2. Depiction of 'jitter' (i.e. process by which variability in spacing between reserves was introduced) in marine reserve design. Example shown has jitter of 5 spatial units (SU); each reserve is allowed to shift randomly by up to 5 SU; reserve size is held constant; 2 of the 5 possible reserve positions are shown

fishing rate) and the dispersal matrix. After approximating the equilibrium state, the full model was run for a short time to test goodness-of-fit. When temporal variability in the alongshore advection distance was included, the model was initially placed at the equilibrium state for the time-averaged dispersal matrix (see 'Results: Comparison with time-averaged dispersal pattern'). Then, the full model was run for an additional 100 yr. This procedure was repeated 20 times to estimate the mean and SD of catch and recruitment.

## RESULTS

### Constant alongshore advection

The effects of constant alongshore advection with a uniformly spaced system of marine reserves were investigated. The alongshore advection distance was varied from 0 to 20 SU. As boundary conditions were circular and the spacing between reserves was 20 SU,

the model system repeated itself every 20 SU. As a result, advection distances greater than 20 SU produced identical results to advection distances less than 20 SU. This configuration is highly unrealistic (although often used), as no real system will have exactly uniformly spaced reserves, nor will the advection rate be constant over time or space, but it serves as a useful basis for comparisons with time-varying advection distances and nonuniform reserve configurations.

For a uniform reserve configuration, an advection distance of 20 SU was the same as no advection at all, as larvae from one reserve simply landed in the next. Furthermore, catch and recruitment for advection distances greater than 10 SU were the mirror image of catch and recruitment for advection of less than 10 SU (Fig. 3). There was a small relative increase in catch and recruitment for advection distances near 10 SU for short diffusion distances. This was due to the fact that the second generation of offspring from adults living inside a reserve (i.e. the offspring of the offspring) will

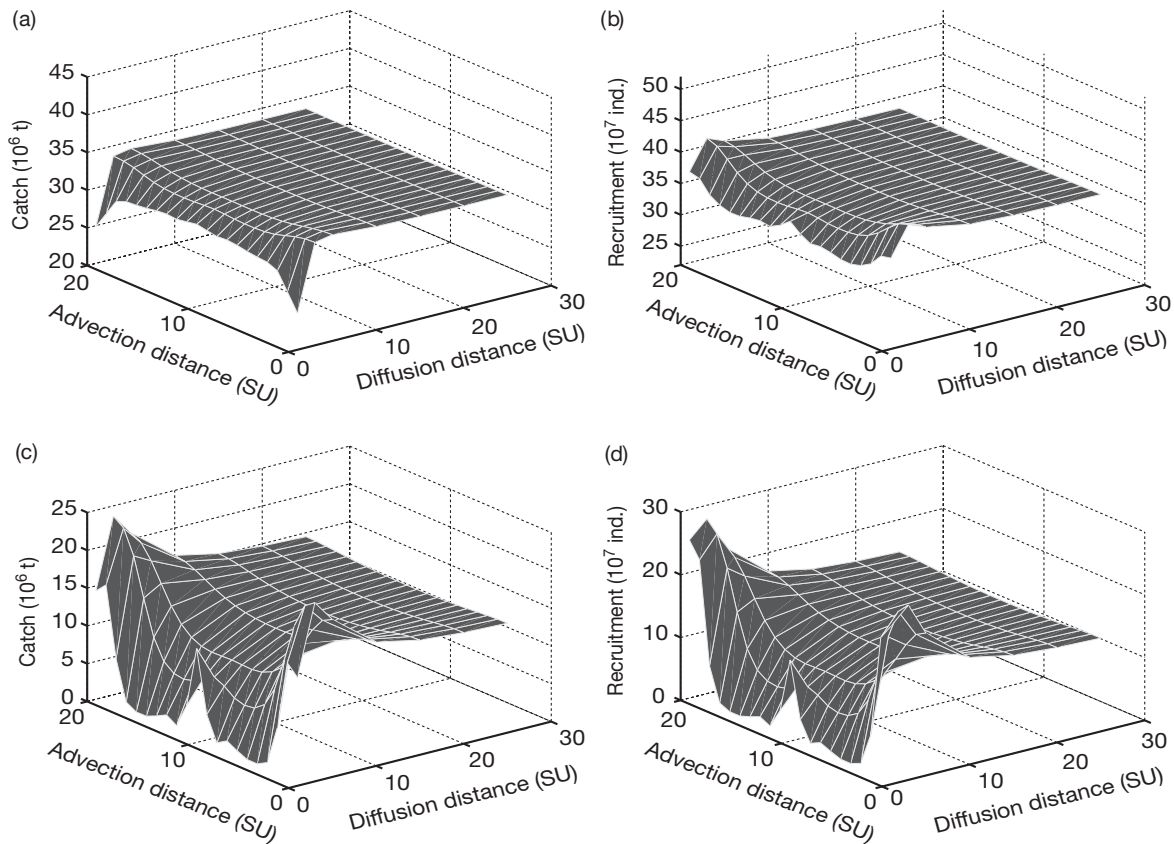


Fig. 3. Equilibrium values of (a,c) catch and (b,d) recruitment for system of 5 uniformly spaced reserves of 4 spatial units (SU) each as a function of larval diffusion distance and advection distance. Fishing rate outside reserves was  $0.08 \text{ yr}^{-1}$  in (a) and (b), and  $0.14 \text{ yr}^{-1}$  in (c) and (d). Results are symmetric around advection distance of 10 SU and are identical for all advection distances that are the same modulo 20. Note that although vertical scales in top and bottom graphs are not the same, ranges of the vertical scales are identical, so that levels of variability can be compared between graphs

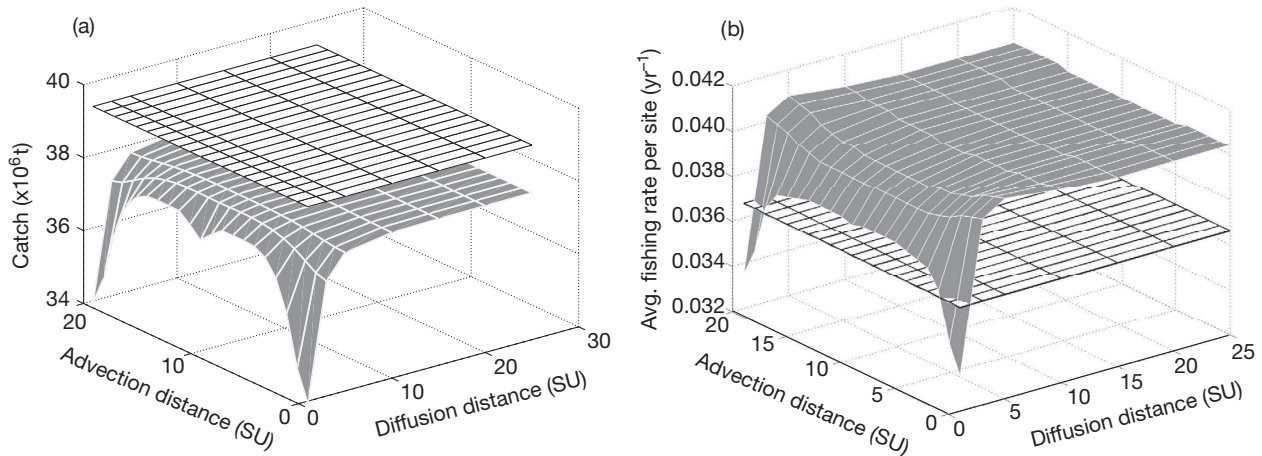


Fig. 4. (a) Maximum sustainable yield (MSY) and (b) average fishing rate over all sites at MSY as function of advection distance and diffusion distance. Horizontal open planes are MSY and associated fishing rate for system without reserves, gray planes are those for system with 5 uniformly-spaced reserves of 4 spatial units each (20% of habitat in reserves). Fishing rate in non-reserve sites at MSY (gray surface in b) has been multiplied by percent of sites not in reserves in order to represent comparable levels of overall effort with and without reserves

settle in the next reserve if diffusion distances are small and advection rates are roughly half the distance between reserves. Note that this increase would not occur if no recruits survived to reproduction outside of reserves. The increase near an advection distance of 10 SU disappeared for larger diffusion distances. All these results depend heavily on the fact that the system was spatially symmetric every 10 SU and that advection rates were constant over space and time.

Results for the high fishing rate ( $0.14 \text{ yr}^{-1}$ ) showed a much sharper dependence on advection and diffusion distance than results for the low fishing rate ( $0.08 \text{ yr}^{-1}$ ) (Fig. 3c,d vs. a,b). In particular, catch at the low fishing rate showed little response to advection distance at anything but the shortest diffusion distances. In all cases, catch showed a modest decline at very short diffusion and advection distances relative to somewhat larger dispersal distances due to the complete retention of larvae inside reserves when dispersal scales are very small. Sensitivity to advection distance decreased with increasing diffusion distance, as might be expected for dispersal patterns that are close to an even redistribution of larvae (i.e. pool dispersal). Catch and recruitment levels were intermediate for large diffusion distances relative to those for short diffusion distances.

For species with a short diffusion distance, recruitment decreased significantly as advection distance was increased from zero, particularly at the high fishing rate. Catch had a similar pattern, although it was very weak at the low fishing rate. At the high fishing rate, recruitment levels at intermediate advection distances (between 5 and 15 SU) reached levels that threatened persistence outside reserves. In the absence of advection, catch and recruitment decreased

as diffusion distance increased from 3 SU to larger values. With alongshore advection, catch and recruitment increased somewhat with diffusion distance for advection distances between 5 and 15 SU.

As dependence on advection distance was much stronger at the high fishing rate, I will focus on these results during the remainder of this paper. Furthermore, catch will be used as the principal indicator of population state, as catch and recruitment showed relatively similar patterns of variability with advection and diffusion distances.

### Comparison with conventional management

The primary goal of this paper was to compare equilibrium population levels with different reserves configurations and larval dispersal patterns without regard to how these results compare to those for effort-based management alone. A complete comparison of conventional management with management via a combination of effort controls and marine reserves is difficult, requiring a socio-economic analysis of the changes in the spatial distribution of effort that are likely to occur after reserves are introduced (e.g. Smith & Wilen 2003). As such, the analysis here is limited to comparisons of maximum sustainable yield (MSY) with and without reserves to determine what could occur under 'best management practices' with the 2 management schemes.

MSY levels for the system without reserves, which are independent of the larval dispersal pattern, were consistently higher than those for the system with 20% of the habitat in reserves (Fig. 4a). Lower levels of

overall effort were needed to achieve MSY with conventional management than with marine reserves (Fig. 4b), producing significantly higher levels of catch per unit effort (CPUE, not shown) for conventional management. Surprisingly, MSY and corresponding effort levels with marine reserves were relatively independent of the advection and diffusion distances, with the exception of extremely small diffusion distances. As noted by Kaplan & Botsford (2005), although MSY with reserves is lower than without reserves, the range of fishing rates that produce catch levels close to MSY is wider with reserves (data not shown). Results suggest that target effort levels with reserves will not be a strong function of the larval dispersal pattern and that there will be a considerable range of efforts levels that have reasonably high yields. Nevertheless, there are a number of factors not included in this analysis that could affect these results, such as fishermen's behavior (Smith & Wilen 2003), unexpectedly large maternal-age effects (Berkeley et al. 2004) and active habitat-selection or movement between reserve and non-reserve areas (Lundberg & Jonzén 1999).

### Advection variability

In the previous sections, advection and diffusion distances were held constant for each run of the model system. Temporal variability in dispersal patterns is often large in real systems. Here, one type of temporal variability in dispersal is examined by allowing alongshore advection to vary from year to year. In each year, the alongshore advection distance is selected from a fixed Gaussian distribution. First, the overall affect of this variability on the sensitivity of our system to the

mean alongshore advection distance will be considered; then, results will be compared to what would be expected from the long-term time-averaged dispersal pattern.

As the scale of advection distance variability is increased, the system becomes progressively less sensitive to the mean alongshore advection distance (Fig. 5). Average catch values tend towards values between maximum and minimum values for the system in the absence of advection variability. The greatest change occurs at small to intermediate diffusion distances and mean advection distances close to 0 or 20, for which advection variability leads to an overall drop in mean larval recruitment (Fig. 5c) and mean catch relative to the same system without advection variability. For intermediate mean advection distances (5 to 15 SU), significant variability in the alongshore advection distance leads to an increase in population levels (Fig. 5c). For large diffusion distances, there is little change in catch when advection variability is added to the model.

The variance among model runs of catch values increases as the scale of variability in the advection distance is increased. Variance is concentrated at short diffusion distances. Maximum variability occurs at the shortest diffusion distance (1 SU) for advection distances on the order of the size of an individual marine reserve (2 to 4 SU).

### Comparison with time-averaged dispersal pattern

If the effects of variability in the alongshore advection distance can be approximated by increased diffusion, then it would be expected that model results for the system with advection variability would be similar

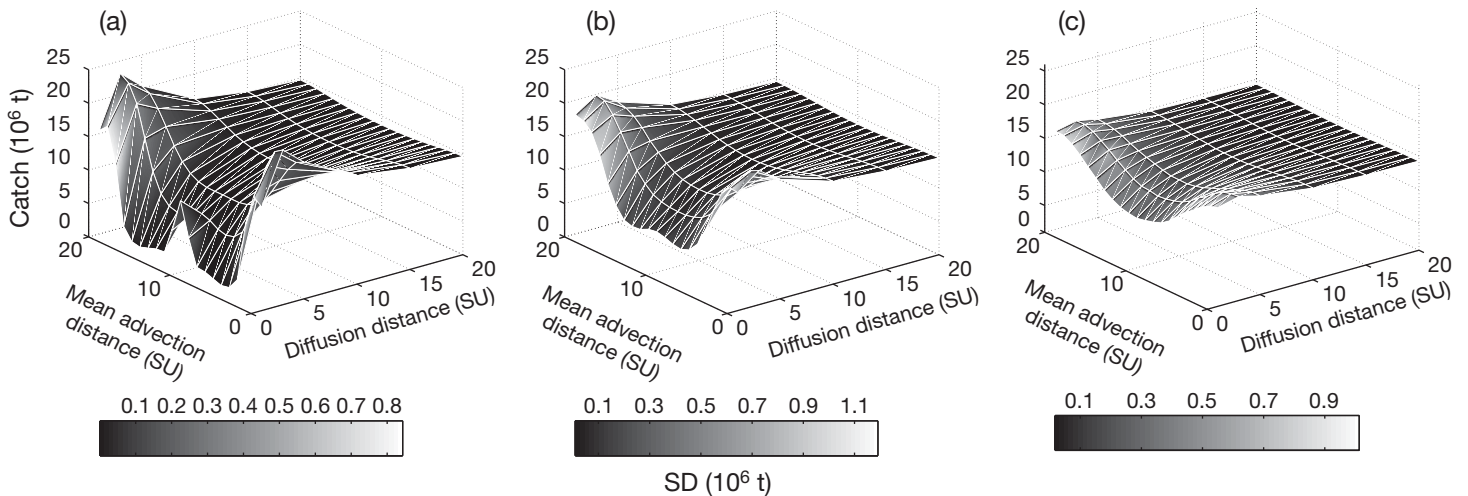


Fig. 5. Mean catch values as a function of larval dispersal distance and mean advection distance for advection variability scales of (a) 1, (b) 3 and (c) 5 spatial units. Fishing rate was  $0.14 \text{ yr}^{-1}$ . Scales indicate SD among model runs, with lighter grays indicating higher SD. Note that z-axis scales are identical for all 3 panels, but shading scales are different for each



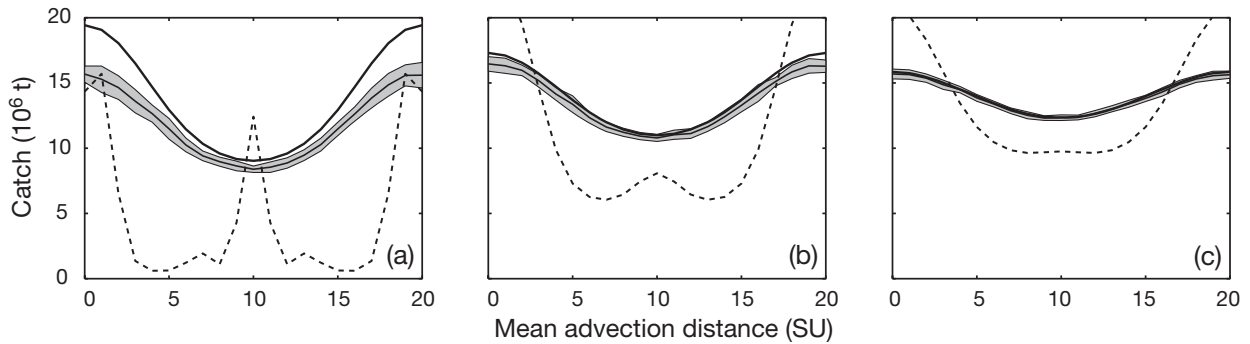


Fig. 6. Catch as a function of mean advection distance for an advection variability scale of 5 spatial units (SU), a fishing rate in non-reserve areas of  $0.14 \text{ yr}^{-1}$  and a diffusion distance of (a) 1, (b) 3 and (c) 5 SU. Dashed lines: catch in absence of advection variability; thin continuous lines and gray areas: mean  $\pm 1$  SD, respectively, for catches with real advection variability among model runs; thick continuous lines: catch for system with time-averaged larval dispersal kernel

to those for the system without advection variability using the time-averaged larval dispersal pattern. The long-term average distribution of larvae (when annual dispersal patterns are described by a distribution centered around the advection distance and interannual variability in the advection distance is modeled by a second distribution) is given by the convolution of the 2 distributions

$$\bar{p}(x) = \int_{-\infty}^{\infty} p_d(x, y) p_A(y) dy \quad (3)$$

where  $\bar{p}$  is the time-averaged dispersal kernel,  $p_d(x, y)$  is the probability of a larva originating at the origin settling at  $x$  given the advection distance is  $y$ , and  $p_A$  is the distribution of advection distances. In the present paper,  $p_d(x, y)$  is only a function of the difference between the advection distance and the point of settlement, so this expression can be simplified to

$$\bar{p}(x) = \int_{-\infty}^{\infty} p_d(|x - y|) p_A(y) dy \quad (4)$$

This equation expresses that the long-term average probability of a larva produced at the origin settling at Position  $x$  is given by the sum over advection distances of the probability of a larva settling at  $x$  for a specific advection distance weighted by the probability of that advection distance actually occurring.

If the 2 distributions involved are Gaussians, the solution to the integral in Eq. (4) is well known. The convolution of 2 Gaussians produces another Gaussian distribution, whose mean is the sum of the means of each of the 2 original distributions (in this case the mean alongshore advection distance) and whose variance is the sum of the 2 variances.

In the present paper, diffusion is modeled with a Laplacian distribution, while advection variability is modeled with a Gaussian distribution. The solution to

Eq. (4) is more complex in this case, but is straightforward (see Appendix 1 for details). The resulting distribution is a mix between a Laplacian and a Gaussian. At the limit where the scale of advection variability is much smaller than the diffusion distance, the distribution is Laplacian, while at the opposite limit it is Gaussian. In all cases, the mean of the distribution is the mean alongshore advection distance, and the variance of the final distribution is the sum of the variances of the original distributions.

Model results with advection variability were compared to results without advection variability and results from the system using the average larval dispersal pattern (Fig. 6). Catch with advection variability clearly differed significantly from results without any correction for advection variability. At large diffusion distances, catch with advection variability approached catch from the system using the time-averaged dispersal kernel (Fig. 6c). At diffusion distances smaller than the scale of advection variability (Fig. 5a,b), catch with advection variability was consistently lower than

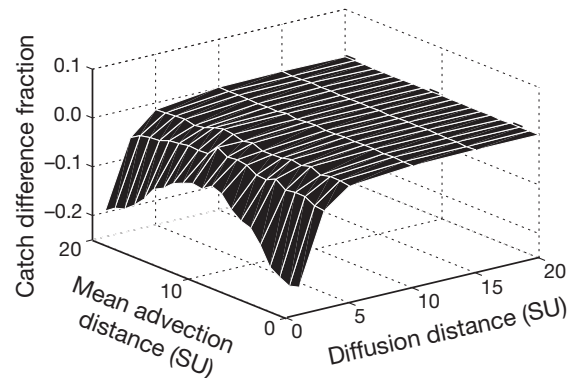


Fig. 7. Differences in mean catch between model with time-averaged dispersal kernel and model with real advection variability; differences for advection variability scale of 5 spatial units are shown. Differences have been normalized by catch results from time-averaged dispersal kernel

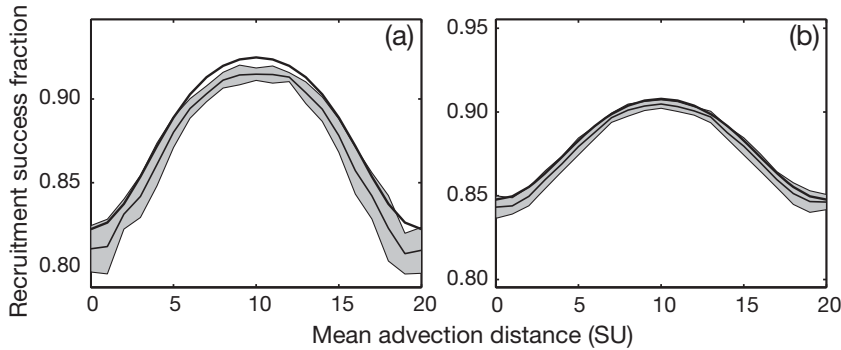


Fig. 8. Recruitment percentage for advection variability scale of 5 spatial units (SU) and diffusion distances of (a) 1 and (b) 3 SU. Recruitment percentage is number of recruits divided by number of settlers (i.e. potential recruits) and slope at origin of stock-recruitment relationship; i.e. number of recruits relative to what would be expected if stock-recruitment relationship were linear. Thin lines and gray areas: mean  $\pm$  1 SD, respectively, for runs with real advection variability; thick continuous lines are from model runs using time-averaged dispersal kernel

results from the average dispersal kernel for all mean alongshore advection distances. Catch with advection variability was particularly low relative to results from the average dispersal pattern at mean alongshore advection distances near 0 or 20 SU (Figs. 6a & 7).

The differences between the system with advection variability and the system using the average dispersal pattern were associated with differences in recruitment success (Fig. 8). Recruitment success refers to the percentage of potential settlers that actually recruit into the adult population. Recruitment success was lower for the system with advection variability at small diffusion distances (Fig. 8a), despite the fact that more larvae overall were being produced at equilibrium in the system using the average dispersal pattern, contrary to what would be expected from density-dependent post-settlement effects (i.e. recruitment success should drop as the number of settlers increases).

### Variable reserve-spacing

In real systems of marine reserves, the spacing between reserves is unlikely to be perfectly uniform. Furthermore, it has been suggested that variability in the spacing between marine reserves might be essential to creating a system of reserves that protects a group of species with diverse life histories and is robust to fluctuations in oceanographic conditions (Palumbi 2002). Variability in reserve-spacing in systems without alongshore advection of larvae was found to have little

effect on persistence and catch, except in cases of severe overfishing (Kaplan & Botsford 2005). Here I expand on these results to include alongshore advection.

Initially, a single example of a configuration of marine reserves with variability in the spacing between reserves was considered (Fig. 9b). For advection distances between 0 and 5 SU, catch differed little between runs with spacing variability and without (Fig. 9c,d). For larger alongshore advection distances, catch showed marked differences between the uniform and variably-spaced configurations of marine reserves. With variable reserve-spacing, catch never reached the maximum values that

occurred at short advection distances. On the other hand, catch was generally not as low as the lowest values with a uniform configuration of reserves. In general, catch was somewhat higher with reserve variability than without for intermediate advection distances, i.e. those distances most detrimentally affected by alongshore advection.

When averaged over several reserve configurations with a given level of variability in the spacing among reserves, variable spacing had the effect of reducing the dependence of catch on the alongshore advection distance for advection distances greater than the size of an individual reserve (4 SU in this case; Fig. 10). As spacing variability was increased, average catch values became more homogeneous as a function of advection

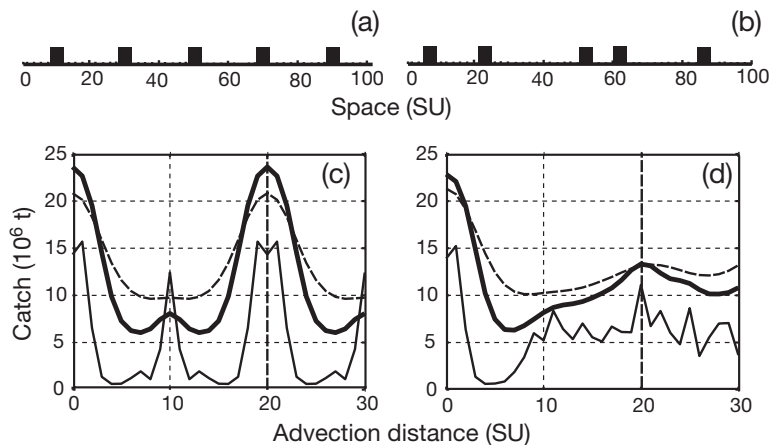


Fig. 9. Catch for systems of reserves with and without variable spacing between reserves. (a,b) Reserve configurations (reserve areas in black) corresponding to catch values in (c) and (d), respectively. (a) Uniform configuration of reserves; (b) reserve configuration that yielded catch values closest to mean catch values for all reserve configurations (see Fig. 10c). In (c) and (d), catch for diffusion distances of (—) 1 spatial units (SU), (—) 3 SU, and (---) 5 SU

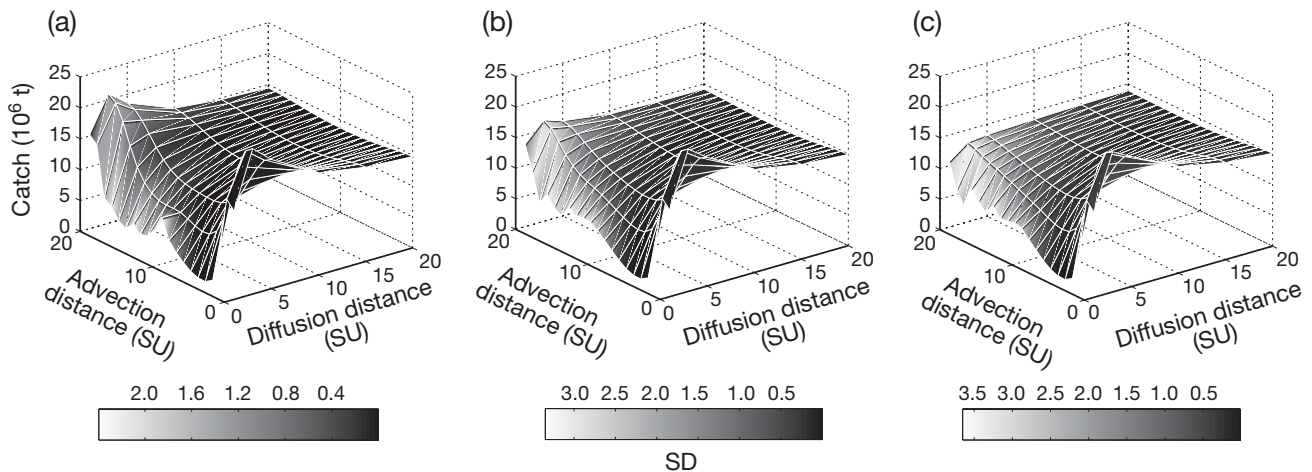


Fig. 10. Catch as a function of diffusion distance and advection distance averaged over all runs at jitter levels of (a) 5, (b) 10 and (c) 15 spatial units. Scales indicate SD among model runs, with lighter grays indicating greater variability. Note that shading scales differ between graphs

distance, particularly for short diffusion distances. On average, the difference between catch values with reserve-spacing variability and without was positive for most intermediate advection distances, and represented as much as a 50% increase in catch relative to a system of uniformly spaced reserves. Nonetheless, the variability among model runs was significant, and reserve configurations exist that have catch and recruitment values below those of a uniform configuration of reserves for particular advection and/or diffusion distances. Furthermore, catch for species with advection distances slightly larger than the reserve size (5 to 8 SU) was little affected by spacing variability. Population sizes for these advection distances only increased when several reserves were placed extremely close to each other, a configuration that was not possible with

the type of spacing variability included in this paper, and that is unlikely to be practical in real systems.

The reserve configuration in Fig. 9b produced the most uniform catch levels as a function of advection distance among all reserve configurations tested, as measured by the difference with respect to the average catch values shown in Fig. 10c. Examination of several configurations that produced relatively constant levels of catch for different advection and diffusion distances revealed that these configurations had a variety of spacings between pairs of reserves (e.g. the configuration in Fig. 9b has spacings of 16, 29, 10, 24 and 21 SU). However, this uniformity in total catch should not be confused with a population that is uniform over space. Despite similar total catch levels, catch and recruitment vary greatly over space as a function of advection and diffusion distance, and recruitment shows a notable increase in areas that are the recipients of larvae produced inside reserves (Fig. 11).

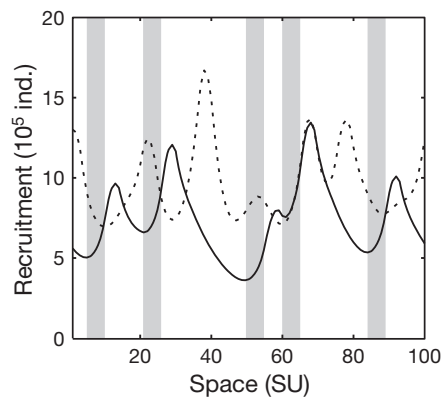


Fig. 11. Spatial patterns of recruitment for fishing rate of  $0.14 \text{ yr}^{-1}$  in non-reserve areas, a diffusion distance of 3 spatial units (SU) and advection distances of (—) 5 SU and (---) 15 SU. Configuration of reserves, indicated by the gray areas, as in Fig. 9b

## DISCUSSION

The results in this paper for catch with constant alongshore advection are consistent with those of Gaines et al. (2003) for a system of marine reserves on a finite coastline. In the regime where diffusive forces are relatively strong compared to advective forces, catch is independent of the alongshore advection distance. In this case, sufficient numbers of larvae generally reach reserve areas, either through diffusion from nearby reserves or by local retention due to weak alongshore advection. Reserve areas are able to maintain populations outside reserves through larval export, although at times population size is quite small

(a fishing rate of  $0.14 \text{ yr}^{-1}$ ). In the opposite case, where diffusion distances are smaller than alongshore advection distances, alongshore advection has a considerable effect on catch and the overall state of the population. For diffusion distances less than the reserve size and advection distances greater than the size of a single reserve, but smaller than the separation between reserves, the majority of larvae produced inside reserves are swept out of reserve areas and into fished areas. This produces a general decline in the fish population inside reserves and a subsequent decline outside reserves due to overfishing and weak input of larvae from reserves.

When temporal variability in the alongshore advection distance is added to the system, there is a general decrease in the dependence of the system on alongshore advection distance. Results for diffusion distances greater than the scale of variability in advection distance are consistent with those from the time-averaged larval distribution, indicating that one can safely approximate variability in alongshore advection by increased diffusion under these conditions.

For diffusion distances less than the advection variability scale, catch is lower with advection variability than it is for the time-averaged larval distribution. This decrease is due to the density-dependence included in the model. If a large number of larvae arrive in a single year to a particular site, only a relatively small fraction of those individuals will actually recruit to the site because of post-settlement density-dependence. For short diffusion distances, the distribution of larvae is highly peaked. When the majority of larvae is produced in a relatively small area, as occurs at high fishing rates with small reserves, a relatively large number of larvae settle at just a few sites. This produces a strong density-dependent effect at those sites. Temporal variability in the alongshore advection distance does nothing to ameliorate the negative effects of density-dependence. The effect of using a time-averaged larval distribution in the model is, in any given year, to

spread out the distribution of larvae. This reduces density-dependent effects and allows a greater percentage of larvae to recruit into the adult population. This increase in percent settlement might be a small in a single year, but averaged over long time periods it produces higher recruitment and catch when the time-averaged dispersal kernel is used.

This process is graphically demonstrated in Fig. 12, where it has been greatly exaggerated for effect. The original larval distribution is highly peaked relative to the time-averaged larval distribution (Fig. 12a). At low recruitment levels, density-dependent effects do little to change this, and roughly equal numbers of larvae recruit into the system whether the time-averaged distribution or the original larval distribution is used. At high recruitment levels, density-dependent effects are much stronger for the original larval distribution than for the time-averaged distribution, resulting in lower net recruitment for the model when the original distribution is used. This explains why the decrease in catch and recruitment was greatest for small mean advection distances. Under these conditions, most larvae are retained inside reserves, and population levels inside reserves reach (high) saturation levels. Density-dependent effects are large due to the large number of larvae produced in reserves, causing a notable decline in settlement percentage.

Overall, density-dependent recruitment produces a system that is less sensitive to the mean alongshore advection distance than would be predicted from the average larval distribution, but also produces lower population levels. If one wishes to produce a model that correctly predicts population behavior based on experimentally-determined parameters, then it is necessary to include temporal variability in this model. On the other hand, if one only wishes to produce a model that correctly predicts the behavior of the population without the complications of including temporal variability, then annual variability in alongshore advection can be roughly approximated by increasing diffusion

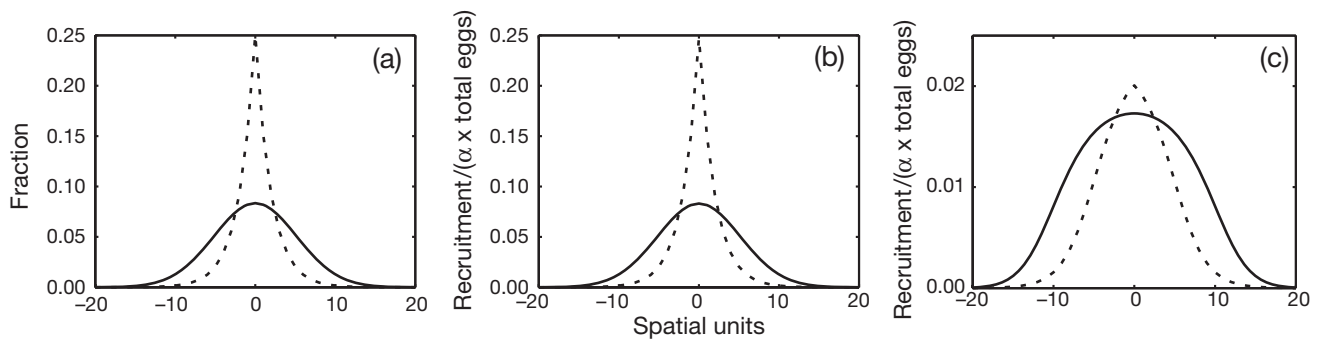


Fig. 12. Density-dependent recruitment effects. (a) (---) Distribution of larvae for a single year and (—) time-averaged larval distribution. (b,c) Recruitment relative to that for a linear stock-recruitment relationship for low and high recruitment levels, respectively, for (---) yearly and (—) time-averaged larval distributions.  $\alpha$ : slope of the Beverton-Holt density-dependence at the origin

distances to a level above that of the time-averaged dispersal pattern and decreasing reproductive output.

It should be noted that these effects are connected to the type of density-dependence included in the model used here. Density-dependence in the model was related only to the density of settlers. As a result, even variability on time scales shorter than the life-span of adults can have important effects on population dynamics. If density-dependence were related to the density of adults at a site instead of larval density, as could occur in space-occupying species such as mussels and barnacles, these effects might not be present. As adult density is essentially an integral over many years of recruitment, it is less sensitive to time-varying recruitment levels and will produce less variability in density-dependent effects. Despite this, Gaines et al. (2003) did find that density-dependence related to the adult population could be important when there is advection variability, but the mechanism was different from that discussed herein. In their study, periodic complete reversal of the advection direction produced regular cycles in population size that did not diminish in amplitude with time. These cycles produced variations in the strength of density-dependence that affected the population in ways that are not captured by the average dispersal pattern.

Including variability in the spacing between reserves produces systems that show lower levels of variability in catch as a function of alongshore advection distance, particularly for short diffusion distances. In general, systems with variability in the spacing between reserves perform better than a uniform distribution of reserves under the most difficult conditions (intermediate advection distances, small diffusion distances). This suggests that variability in reserve-spacing could be beneficial in creating systems of reserves that equally protect a wide variety of species with different dispersal distances and larval period durations. Nonetheless, variability in catch levels for different reserve configurations is relatively large and there is no *a priori* guarantee that a configuration of reserves with variable spacing will perform better than an equivalent system with uniformly spaced reserves. Furthermore, catch for advection distances slightly larger than the reserve size only improves when 2 or more reserves are adjacent to each other, indicating that only a system of larger reserves will protect species whose larvae are consistently transported from the reserves to adjacent areas. When either the diffusion distance or the spatial scale of temporal variability in alongshore advection is large compared to the size of an individual reserve, the model system is relatively insensitive to the mean alongshore advection distance. Changing the spacing between reserves under these conditions is unlikely to significantly alter the resulting population levels.

In real systems, alongshore advection, diffusion and variability in alongshore advection are probably not completely independent. It is unlikely that real systems will have extremely large advection distances coupled with small diffusion distances, suggesting that the effects of alongshore advection could be somewhat less than those in our model. Furthermore, a number of recent studies have shown that larval retention is quite common, suggesting that advection and diffusion distances might be smaller than was once thought (Todd 1998, Warner et al. 2000, Mora & Sale 2002). Nonetheless, it is conceivable that in systems with strong, coherent alongshore flows (such as those that occur in many upwelling systems) advective forces will be large and important. In such situations, or when there is considerable uncertainty in the dispersal patterns of the relevant marine species, variability in the spacing between reserves is likely to reduce the dependence of catch and recruitment on a particular advection distance and better protect a diverse group of species.

In conclusion, in the present paper, the effects of alongshore advection, advection variability and variability in the spacing between reserves on a species with dispersing larvae and sedentary adults have been examined. When advective forces dominate larval transport patterns, population levels of overfished species depend strongly on the connectivity between adjacent reserves through larval dispersal. Systems of marine reserves should be created that ensure that a significant proportion of larvae produced in reserves end up settling in reserve areas. Excessive export of larvae to non-reserve areas can be detrimental to the health of a system of marine reserves by negating the additional protection to adults that these reserves provide. If little is known about the dispersal patterns of important species, managers should include variability in the spacing between reserves to increase the probability that there will be sufficient connectivity between pairs of adjacent reserves to maintain a diverse group of species. Variable spacing will not reduce the spatial heterogeneity in population levels inherent in the use of marine reserves, and is likely to affect species with distinct dispersal potentials differently. Such spatial heterogeneity does, however, suggest that systems of marine reserves can be used to understand dispersal patterns, as higher recruitment levels should occur downstream of reserve areas and increased population levels should result when the spacing between reserves is close to the alongshore advection distance. Despite the importance of alongshore larval transport for overfished species, the fishing effort level producing MSY depends primarily on the area in the reserves and not the precise larval dispersal pattern. This suggests that management via a combination of marine reserves and effort controls is possible, even in systems where little is known about larval transport patterns.

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#### Appendix 1. Solution to Eq. (4)

Time-averaged dispersal kernel derived when advection distance varies in time according to a Gaussian distribution, while larval diffusion has a Laplacian distribution. Distributions for both processes are

$$p_A(y) = \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(y-D)^2}{2\sigma^2}} \quad (\text{A1})$$

$$p_d(|x-y|) = \frac{e^{-|x-y|/a}}{2a}$$

where  $D$  is average advection distance,  $\sigma$  is SD of advection distance distribution, and  $a$  is diffusion distance. In Eq. (A1),  $y$  represents the advection distance at a particular time and  $p_d(x,y)$  the larval dispersal kernel in that year. SD of the Laplacian distribution is given by

$$\sigma_d^2 = 2a^2 \quad (\text{A2})$$

The time-averaged larval dispersal kernel  $\bar{p}(x)$  is given by the convolution of these 2 distributions:

$$\bar{p}(x) = \int_{-\infty}^{\infty} p_d(x-y) p_A(y) dy$$

$$\bar{p}(x) = \int_{-\infty}^{\infty} \frac{e^{-|x-y|/a}}{2a} \frac{1}{\sigma\sqrt{2\pi}} e^{-\frac{(y-D)^2}{2\sigma^2}} dy$$

$$\bar{p}(x) = \frac{1}{2a\sigma\sqrt{2\pi}} \left[ \int_{-\infty}^x e^{-|y-x|/a} e^{-\frac{(y-D)^2}{2\sigma^2}} dy + \int_x^{\infty} e^{(x-y)/a} e^{-\frac{(y-D)^2}{2\sigma^2}} dy \right] \quad (\text{A3})$$

$$\bar{p}(x) = \frac{1}{2a\sigma\sqrt{2\pi}} \left[ \int_{-\infty}^x e^{(y-x)/a} e^{-\frac{(y-D)^2}{2\sigma^2}} dy + \int_{-\infty}^{-x} e^{(y+x)/a} e^{-\frac{(y-D)^2}{2\sigma^2}} dy \right]$$

$$\bar{p}(x) = \frac{e^{\sigma^2/2a^2}}{2a\sigma\sqrt{2\pi}} \left[ e^{-(x-D)/a} \int_{-\infty}^{(x-D)/\sigma - \sigma/a} e^{-\frac{z^2}{2\sigma^2}} dz + e^{(x-D)/a} \int_{-\infty}^{-(x-D)/\sigma - \sigma/a} e^{-\frac{z^2}{2\sigma^2}} dz \right]$$

The final line in Eq. (A3) cannot be explicitly evaluated, but the integrals are familiar gamma functions:

$$\bar{p}(x) = \frac{e^{\sigma^2/2a^2}}{2a} [e^{-(x-D)/a} \Gamma((x-D)/\sigma - \sigma/a) + e^{(x-D)/a} \Gamma(-(x-D)/\sigma - \sigma/a)] \quad (\text{A4})$$

Careful calculation shows that the expectation value of  $x$  is  $D$  and that variance of  $x$  is  $\sigma^2 + 2a^2$ , as one would expect. Distribution is approximately Laplacian for  $\sigma \ll a$ , and approximately Gaussian for  $a \ll \sigma$ .

The same sets of steps can be used to show that convolution of a pair of Laplacian distributions is

$$\bar{p}(x) = \frac{b^2}{b^2 - a^2} \frac{e^{-|x-D|/b}}{2b} + \frac{a^2}{a^2 - b^2} \frac{e^{-|x-D|/a}}{2a} \quad (\text{A5})$$

where  $a$  and  $b$  are scaling factors for diffusion distribution and temporal variability in advection distance, respectively, and  $D$  is as before