

# UC Davis

## UC Davis Previously Published Works

### Title

Effects of variability in spacing of coastal marine reserves on fisheries yield and sustainability

### Permalink

<https://escholarship.org/uc/item/75p6q8t0>

### Journal

Canadian Journal of Fisheries and Aquatic Sciences, 62(4)

### ISSN

0706-652X

### Authors

Kaplan, David M  
Botsford, L W

### Publication Date

2005-04-01

Peer reviewed

# Effects of variability in spacing of coastal marine reserves on fisheries yield and sustainability

David M. Kaplan and Louis W. Botsford

**Abstract:** The size and configuration of marine reserves best suited to reaching fisheries and conservation goals are poorly understood. It has been suggested that variable spacing between reserves is essential to the success of a system of marine reserves. We used numerical models to examine the effect of variable spacing on the efficacy of marine reserves for managing a fish species with sedentary adults and planktonic larvae. Variability in reserve spacing affected catch and recruitment relative to values for a uniform configuration of reserves only for populations near collapse even in the presence of a system of reserves. For species with low fishing rates or large marine reserves, variability in spacing had only a minor effect. At high fishing rates and small reserve sizes, variable reserve placement had a positive local effect on catch and recruitment when several reserves fell close to each other. These configurations led to uneven spatial distributions with greater catch and recruitment in areas with a higher concentration of reserves. Variable reserve spacing can offer additional protection to overfished populations along certain sections of the coastline, but concern for spatial homogeneity will argue for a uniform distribution of reserves covering an adequate proportion of the entire coastline.

**Résumé :** On connaît mal les tailles et les configurations des réserves marines requises pour atteindre les objectifs de la pêche commerciale et de la conservation. Il a été suggéré qu'un espacement variable entre les réserves est essentiel au succès d'un réseau de réserves marines. Nous avons utilisé des modèles numériques pour étudier les effets de l'espacement variable sur l'efficacité des réserves marines pour l'aménagement d'une espèce de poisson à adultes sédentaires et à larves planctoniques. La variabilité de l'espacement des réserves affecte les captures et le recrutement différemment d'une configuration uniforme de réserves, seulement chez les populations s'approchant de l'effondrement malgré la présence d'un système de réserves. Chez les espèces affectées par de faibles taux de pêche ou situées près de grandes réserves, le placement variable n'a qu'un effet mineur. Aux taux de pêche élevés et en présence de petites réserves, le placement variable des réserves a un effet local positif sur les récoltes et le recrutement lorsque plusieurs réserves se retrouvent près l'une de l'autre. Ces configurations mènent à des répartitions spatiales inégales avec des récoltes et un recrutement élevés dans les régions à plus fortes concentrations de réserves. L'espacement variable des réserves peut ajouter une protection supplémentaire aux populations surexploitées dans certains secteurs de la côte, mais le souci d'une homogénéité spatiale militera pour une répartition uniforme des réserves couvrant ainsi une proportion adéquate de toute la côte.

[Traduit par la Rédaction]

## Introduction

Although protected areas have been common practice in terrestrial systems since the beginning of the twentieth century, it is only recently that there has been an intense effort in many parts of the world to institute systems of coastal marine reserves for conservation and fisheries management. It has been suggested that reserves are a more efficient way to manage certain marine resources than traditional effort-based management (e.g., Plan Development Team 1990; Dugan and Davis 1993; Bohnsack 1998). The design of systems of marine reserves provides unique challenges different from those seen in terrestrial systems (Hockey and Branch

1994; Simberloff 2000; Carr et al. 2003). This is primarily due to the predominance of marine species with sedentary adult phases and widely dispersing larval phases. Moreover, marine reserves have to satisfy two often-competing measures of performance: for conservation, ecosystem sustainability is the primary goal, while for fisheries, high catch and sustainability of harvested species are desired.

There is a growing body of literature that addresses spatial aspects of marine reserve design. Some have focused on developing rules for choosing configurations that maximize biodiversity, maximize habitat heterogeneity, and (or) include vulnerable habitats, life stages, or species within reserves (e.g., Hockey and Branch 1997; Leslie et al. 2003; Roberts et al. 2003). While these reserve-siting schemes are needed to create reserves with the appropriate selection of desired habitats, species, and ecosystems, they do not specify the combination of reserve locations, sizes, and spacings necessary for species sustainability and high fisheries yields. These issues have been addressed primarily through modeling efforts that identify the factors that are important for determining the size and configuration of marine reserves (see Gerber et al. 2003 and references therein). Here, we

Received 22 October 2003. Accepted 4 December 2004.  
Published on the NRC Research Press Web site at  
<http://cjfas.nrc.ca> on 11 May 2005.  
J17811

**D.M. Kaplan<sup>1</sup> and L.W. Botsford.** Department of Wildlife,  
Fish and Conservation Biology, University of California,  
Davis, CA 95616, USA.

<sup>1</sup>Corresponding author (e-mail: [dmkaplan@ucdavis.edu](mailto:dmkaplan@ucdavis.edu)).

build on this literature by examining the effect that variability in the spacing of reserves along a linear coastline has on the sustainability and yield of a coastal marine species with a planktonic larval phase and sedentary adults. Species that have this type of life history include most benthic invertebrates, most rockfish, and some reef fish. These are among the species most threatened by overfishing, and they are the most likely to benefit from the implementation of marine reserves.

One factor that has been identified as important for determining the size and spacing of reserves required for persistence is larval dispersal distance. Botsford et al. (2001) created a population model for a species with sedentary adults and dispersing larvae with a system of uniformly spaced marine reserves, complete removal of adults outside reserves by fishing, and Laplacian dispersal patterns. They showed that a species persists in any single reserve that is at least as large as the species' average dispersal distance. Furthermore, species with any dispersal distance would be sustained by a system of marine reserves that covered at least a minimum fraction of the entire coastline. In their model, that minimum fraction is the same as the fraction of natural (unfished) lifetime egg production required for a population to persist, which is often taken to be 35% (cf. Mace and Sissenwine 1993). These results have been extended to combinations of reserves and fishing removal rates that provide sustainability along noninfinite coastlines (D.R. Lockwood et al., Center for Population Biology, Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA 95616, USA, unpublished data). Actual dispersal distances of relevant species are poorly known. It has been shown that they vary greatly between species (Grantham et al. 2003; Kinlan and Gaines 2003; Shanks et al. 2003), although recent empirical results indicate that local retention of larvae might be much more common than once thought (e.g., Todd 1998; Warner et al. 2000; Mora and Sale 2002).

The above-mentioned results that assess reserve configurations (i.e., Botsford et al. 2001; Gaines et al. 2003; D.R. Lockwood et al., Center for Population Biology, Department of Wildlife, Fish and Conservation Biology, University of California, Davis, CA 95616, USA, unpublished data) are based on idealized, evenly spaced systems of reserves applied to fish populations with sessile adults. However, as a practical matter, it is unlikely that a uniform distribution of marine reserves will be implemented in the real world. Furthermore, some have suggested that nonevenly spaced reserves could better protect fish populations with a variety of dispersal distances (e.g., Palumbi 2002). For these two reasons, there has been considerable interest recently in the consequences for fisheries yield and marine conservation of creating systems of reserves with nonuniform spacing. In this paper, we address the issue of variability in reserve spacing through a spatially explicit numerical model of marine populations.

The rest of this paper is organized as follows. We begin by describing the model that we used to examine the effects of variable reserve spacing on fish populations. Then, we briefly describe the effect of marine reserves on fish populations in the absence of random reserve placement. We follow that by presenting results on sustainability and catch with random reserve placement. Finally, we summarize the results

and place them in the larger context of marine reserve design in the discussion.

## Methods

We studied the effects of random reserve placement using a spatially explicit, size- and age-structured model with a monthly time step, similar to that used in Botsford et al. (1999) and Lockwood et al. (2002). It consisted 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 a "spatial unit" throughout this paper. Because dispersal distance is given in the same units, the actual units are arbitrary.

Adults in each subpopulation were subject to growth, natural and possibly fishing mortality, and size-dependent reproduction. With the exception of fishing mortality, all population parameters affecting adults were identical in each subpopulation and were similar to those used in Botsford et al. (1999). Values were 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 and Hendrix 1997; Botsford et al. 1999; Morgan et al. 1999). Although the population parameters used in the model are species specific, we focus here on those general trends that are robust to changes in parameter values. The results presented here are applicable to a wide class of marine species with relatively sedentary adults, including most benthic and intertidal invertebrates, as well as rockfish and some coral reef fish. The entire set of parameter values is provided in Table 1.

Growth of individuals in each subpopulation was governed by a von Bertalanffy equation with Gaussian distributed variability in maximum size (Ricker 1975; Smith et al. 1998). Individuals in the model were allowed to live for a maximum of 30 years. In the absence of fishing, mean age of individuals in the model was 9.6 years. Beverton–Holt postsettlement density dependence of juveniles was included in the model (Beverton and Holt 1957). The value of  $a$ , the slope of the larvae–recruit curve at the origin, was set so that the population collapsed (i.e., population size eventually went to zero) when lifetime egg production was less than 35% of its unfished value. Thirty-five percent lifetime egg production was chosen as a convenient and oft-quoted reference point. The exact value used is not crucial for the results discussed here. This value produced collapse of the population at a fishing rate of  $0.11 \cdot \text{year}^{-1}$  in the absence of marine reserves. Fishing mortality rate was identically zero inside reserves with knife-edge selection at the boundaries. This implies that adults are sedentary and do not cross reserve boundaries, an acceptable approximation as long as the spatial scale of adult movement is considerably smaller than the size of reserves (Nowlis and Roberts 1999).

A dispersal matrix related the density of presettlement larvae along the coast to the final density of competent larvae that settle into each subpopulation. A Laplacian dispersal kernel was used, which exponentially decays with distance

**Table 1.** Parameter values for the population model.

Parameter name	Symbol	Value
Recruitment		
Slope of Beverton–Holt density dependence	$a$	0.006 62
Juvenile carrying capacity	$C$	12 000 000
Growth		
Maximum size	$L_{\infty}$	118 mm
Standard deviation of maximum size	$\sigma$	10 mm
von Bertalanffy growth parameter	$k$	0.22
Reproduction		
Size of first reproduction		60 mm
Reproduction coefficient	$a$	$5.47 \times 10^{-6}$
Reproduction exponent	$b$	3.45
Mortality		
Natural mortality rate	$m$	$0.08 \cdot \text{year}^{-1}$
Fishing size limit		60 mm
Fishing mortality rate	$f$	$0.05\text{--}0.2 \cdot \text{year}^{-1}$
Reserve configuration		
Number of reserves		4
Reserve size		<i>5 or 10 spatial units</i>
Dispersal		
Dispersal distance		<i>1–25 spatial units</i>

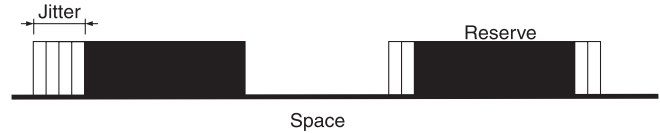
**Note:** Italics indicate parameter values that varied between model runs. All others were held constant.

in both alongshore directions. The average distance that settling larvae were from the point of reproduction, here referred to as the “dispersal distance”, was constant over space and varied from 1 to 25 spatial units. We also considered the case of a larval pool, where larvae are evenly redistributed across subpopulations. This is essentially equivalent to an infinite dispersal distance. 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. We chose to use circular boundary conditions so as not to confound the effects of reserve placement with edge effects due to finite habitat length.

For each run of the model, the system was started at equilibrium in the absence of fishing and marine reserves. Then, fishing and marine reserves were introduced and the model was run for an additional 100 years. After that, because the system approached equilibrium very slowly, model results were fit by least-squares to an exponential decay to obtain final equilibrium values of catch and recruitment.

Two types of variability in reserve spacing were considered. In the first type, which we call the “jitter” case, reserve placement was continuously perturbed from the uniform configuration (Fig. 1). With no jitter, the system consisted of four uniformly spaced reserves. With jitter, each reserve could shift position by up to a specified number of spatial units while maintaining reserve size constant. Each reserve shifted independently of all other reserves. The number of spatial units shifted by an individual reserve was randomly determined with equal probability for all values between zero and the specified jitter value. By increasing the amount of jitter, we were able to explore population dynamics for systems with increasingly variable reserve spacing. In the

**Fig. 1.** Depiction of “jitter” in marine reserve design. Reserves are indicated by solid boxes. Possible alternate positions for the reserves are shown by open boxes. The example shown has a jitter of four spatial units. Each reserve is allowed to appear randomly in one of five positions. Reserve size is held constant. The figure demonstrates two of the five possible reserve positions.



second type of variability in reserve spacing, the placement of reserves was completely random, with the condition that reserves be nonoverlapping. These two configurations will be presented together, with the totally random case being considered an extreme case of jitter. Ten model runs were performed for each fishing rate, reserve size, and level of variability in reserve spacing. These runs were then compared with a model with the same fishing rate and reserve size but a uniformly spaced configuration of reserves.

## Results

### Uniform reserve placement

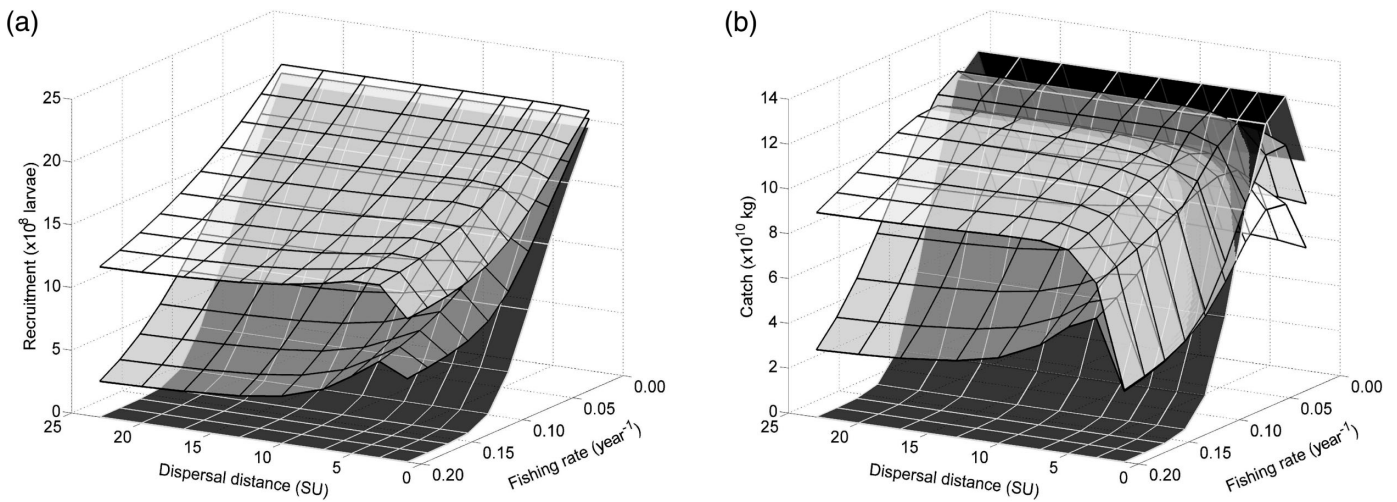
We first summarize the results for the case of uniform reserve placement, against which random reserve placement is compared. Without reserves, the system collapses at a fishing rate of approximately  $0.11 \cdot \text{year}^{-1}$  and dispersal distance has no effect on population dynamics (Fig. 2). Maximal sustainable yield in the absence of reserves occurs at a fishing rate of  $0.05 \cdot \text{year}^{-1}$ . When reserves are added, the fishing rate in nonreserve subpopulations at which maximal sustainable yield occurs increases with the size of the marine reserves introduced (Fig. 2b). The maximal sustainable yield is greatest in the absence of reserves, although the range of fishing rates for which catch is relatively high is wider when the system includes marine reserves.

With reserves, maximal sustainable yield also depends on dispersal distance, with the greatest yields being produced at intermediate dispersal distances (relative to the size of the reserves, 5 or 10 spatial units in our model; Fig. 2b). Extremely short-distance dispersers show both lower yields (Fig. 2b) and lower recruitment (Fig. 2a), relative to species with larger dispersal distances, owing to poor export outside of reserve areas, while long-distance dispersers have intermediate to low levels of recruitment and catch. The effect of dispersal distance is strong: minimum recruitment levels in the model with reserves of five spatial units each and a fishing rate of  $0.2 \cdot \text{year}^{-1}$  represent about 50% of the maximum level.

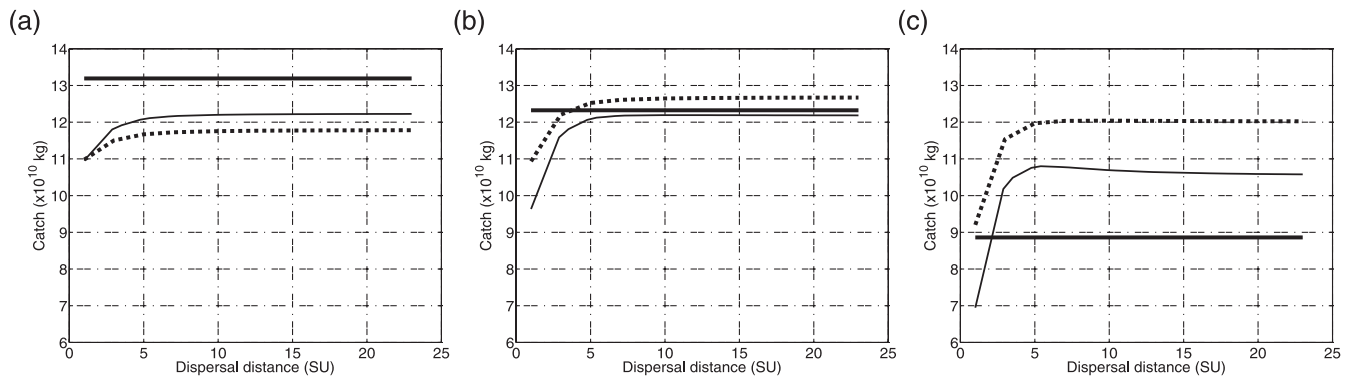
Although the focus of this paper is on the population state after reserves are created, the results in Fig. 2 can be used to make a comparison between management with reserves and effort-based management alone. Two possible scenarios for the redistribution of fishing effort after reserves are created are removal of fishing effort by marine reserves and conservation of total fishing effort before and after reserves are created. Reserves reduce catch relative to effort-based management alone at low prereserve fishing mortality rates (Fig. 3a) but increase catch at high prereserve fishing mortality rates (Fig. 3c), as noted by several other authors (e.g., Bohnsack 1998; Hastings and Botsford 1999; Nowlis and



**Fig. 2.** Equilibrium values of (a) recruitment and (b) catch for a system of uniformly spaced reserves as a function of dispersal distance (spatial units (SU)) and fishing rate. The darkest surface is the result for the population without any reserves, the medium-gray surface is for a system with four reserves of five spatial units each (20% coverage by reserves), and the lightest surface is for a system of four reserves of 10 spatial units each (40% coverage by reserves).



**Fig. 3.** Equilibrium catch levels as a function of dispersal distance (spatial units (SU)) for prereseve fishing mortality rates of (a) 0.04-year<sup>-1</sup>, (b) 0.06-year<sup>-1</sup>, and (c) 0.08-year<sup>-1</sup>. The thick solid lines are for the system in the absence of marine reserves. The broken lines are for a system of four uniformly spaced reserves of five spatial units each (20% of total habitat in reserves) when total fishing effort is not conserved (i.e., the fishing mortality rate in nonreserve areas is the same as the prereseve fishing mortality rate). The thin solid lines are for an identical system of marine reserves when total fishing effort is conserved (i.e., the fishing mortality rate in nonreserve areas is the prereseve fishing mortality rate divided by the fraction of the total area not in reserves).



Roberts 1999). Conservation of total fishing effort generally reduces the absolute difference between yield with reserves and without. In particular, at high prereseve fishing rates, the potential gains when reserves are created are reduced if effort is conserved (Fig. 3c). On the other hand, for prereseve fishing rates above 0.11-year<sup>-1</sup> (not shown), the population without reserves went to extinction, while systems with reserves persisted until quite high fishing rates even if total fishing effort was conserved.

In the following analysis of the effects of random reserve placement, we will refer to the fishing mortality rate in nonreserve areas without reference to how it relates to the prereseve fishing rate, as our focus is on comparing systems with different spatial configurations of marine reserves.

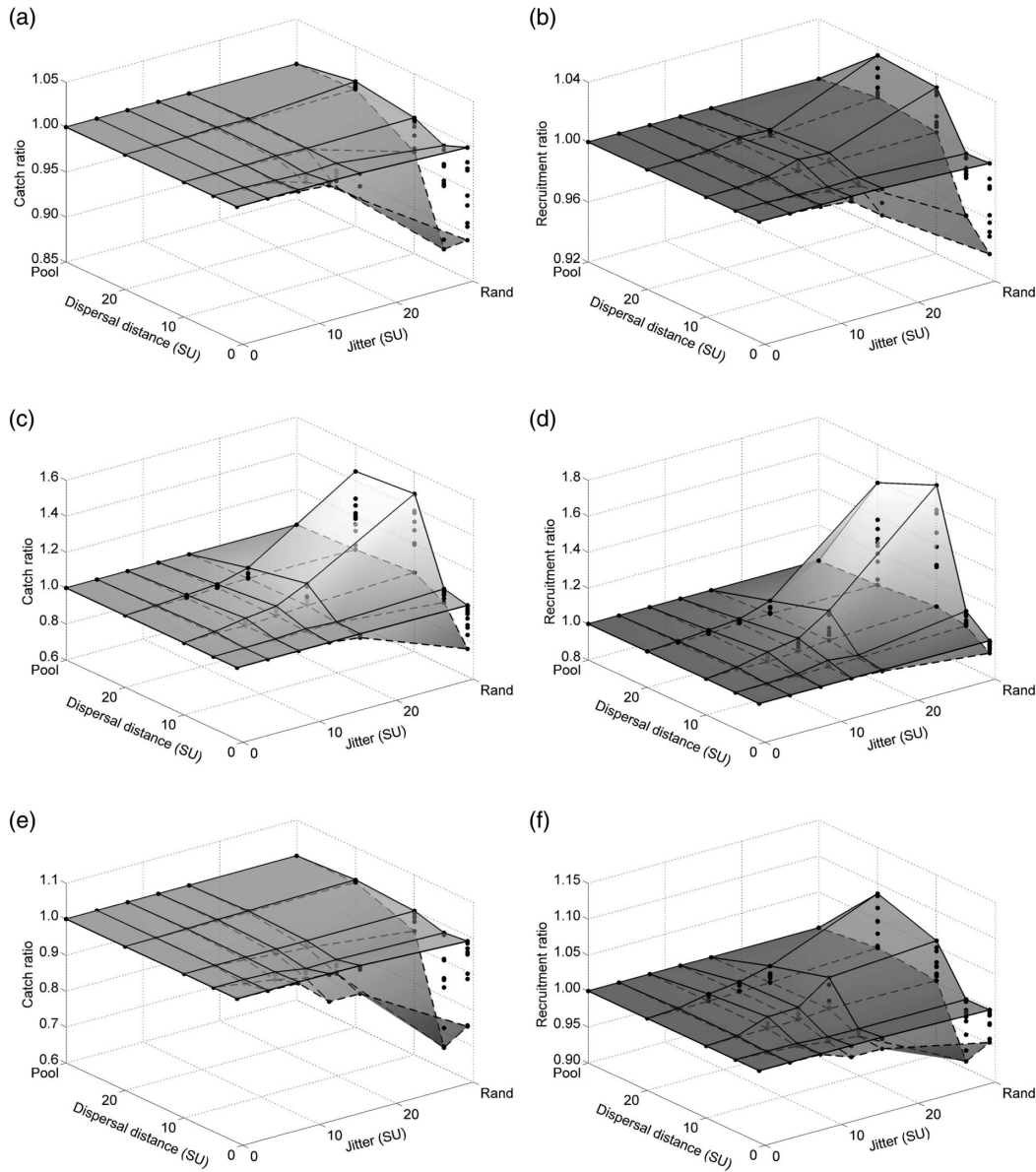
#### Random reserve placement

We tested the effect of random reserve placement on the model with fishing rates in nonreserve areas of 0.05, 0.1,

and 0.2-year<sup>-1</sup> and four reserves of 5 or 10 spatial units each (20% or 40% of total area in reserves). Over most values of dispersal distance and jitter, the effect on recruitment and catch was relatively small (Fig. 4), particularly when viewed in the context of the variation caused by dispersal distance, which significantly affected both catch and recruitment (Fig. 2). In the vast majority of runs, jitter and random reserve placement resulted in less than a 5% change in catch and recruitment relative to the system with uniformly spaced reserves. In the most extreme cases of random reserve placement examined, recruitment increased by about 75% over the same system with uniformly spaced reserves, and catch increased by 45%.

Three principal trends are evident in the results: (i) the effect of variable reserve spacing on recruitment and yield was greatest in the least persistent cases (note that scales on the vertical axes vary), (ii) the effect tended to be positive for longer dispersal distances and negative for shorter dispersal

**Fig. 4.** Equilibrium catch and recruitment for a variety of fishing rates as a function of dispersal distance and “jitter” (spatial units (SU)). Results have been normalized by the value for a uniform distribution of reserves for each dispersal distance. Surfaces are maximum and minimum values for each set of 10 runs, with individual runs indicated by circles. “Rand” indicates runs that had a completely random distribution of reserves. “Pool” indicates that larvae were dispersed uniformly to all subpopulations, the equivalent of an infinite dispersal distance. (a) Catch for a fishing mortality rate ( $f$ ) of  $0.1 \cdot \text{year}^{-1}$  and reserve size (RS) of five spatial units; (b) recruitment for  $f = 0.1$  and RS = 5; (c) catch for  $f = 0.2$  and RS = 5; (d) recruitment for  $f = 0.2$  and RS = 5; (e) catch for  $f = 0.2$  and RS = 10; (f) recruitment for  $f = 0.2$  and RS = 10. Note that the vertical scale is different in each panel.

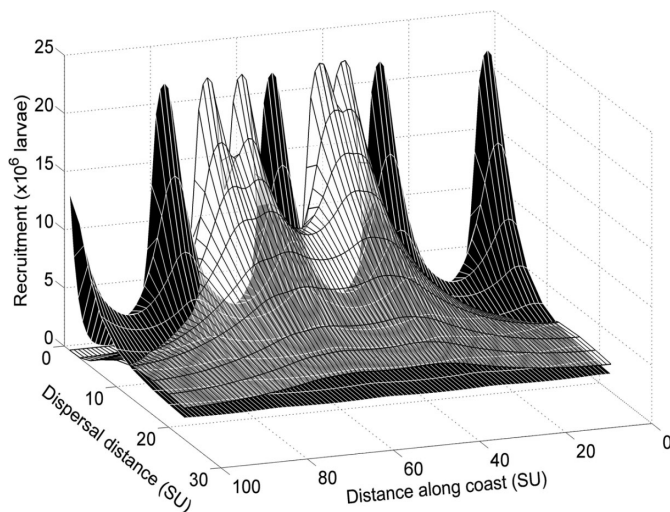


distances, and (iii) the effect on recruitment was generally positive, but the effect on catch was positive only in the least persistent case. With regard to the first trend, variable reserve spacing produced higher values of catch and recruitment than a uniform configuration of reserves when the fishing rate was high (Figs. 4a and 4b versus 4c and 4d) or reserve size was low (Figs. 4e and 4f versus 4c and 4d), both of which tend to move the system towards collapse (Fig. 2). This effect is most evident in the system with reserves of five spatial units each and a fishing rate of  $0.2 \cdot \text{year}^{-1}$  (Figs. 4c and 4d). In this case, recruitment was as much as

75% higher with random reserve placement. Note, however, that at a fishing rate of  $0.2 \cdot \text{year}^{-1}$  and mean dispersal distance of 10–20 spatial units, this is 75% of a fairly low recruitment rate.

With regard to the second trend, for species with dispersal distances less than five spatial units, random reserve placement reduced both catch and recruitment in all cases. For longer dispersal distances, variability in reserve spacing generally increased recruitment but only increased catch when the fishing rate was  $0.2 \cdot \text{year}^{-1}$  and the reserve size was five spatial units, the case closest to collapse. At extremely long

**Fig. 5.** Spatial pattern of equilibrium values for recruitment as a function of dispersal distance (spatial units (SU)) for uniform and nonuniform distributions of marine reserves at a fishing rate of  $0.2\text{-year}^{-1}$ . The solid surface is recruitment for a system that has four evenly spaced reserves, while the open surface is for a system that has four unevenly spaced reserves. Each of the reserves is five spatial units wide. The nonuniform distribution is the configuration of reserves that resulted in the highest values of catch and recruitment for that fishing rate and reserve size. Note that recruitment for the uneven distribution of reserves remains nonzero in the center of the domain even for large dispersal distances but collapses along the edges where there are no reserves. Recruitment for the even distribution of reserves collapses for all but the smallest dispersal distances.



dispersal distances (the “pool” case, the upper left-hand margin of each plot), spatial configuration is no longer relevant to population dynamics.

### Configurations producing extreme values

We examined in greater detail those reserve configurations that produced significant changes in catch and (or) recruitment for a reserve size of five spatial units and fishing rate of  $0.2\text{-year}^{-1}$ . These parameter values were chosen because they are illustrative of species that are not well protected by a single reserve for intermediate to large dispersal distances because of larval dispersal outside the reserve and overfishing, a case that is likely to be of interest in real marine reserves given the relatively long dispersal distances of some important species (Kinlan and Gaines 2003; Shanks et al. 2003), the size restrictions placed on potential marine reserves, and the heavily fished state of many of the world’s fisheries (Botsford et al. 1997; Hutchings 2000).

Under these conditions, a nonuniform distribution of reserves had higher levels of both catch and recruitment than a uniform distribution in cases where reserves of the system randomly happened to be concentrated along a relatively short piece of coastline (e.g., Fig. 5). Recruitment would have collapsed for anything but the smallest dispersal distances in the corresponding system with a uniform distribution of reserves, but several closely spaced reserves maintained high recruitment levels in and around the reserves even for large dispersal distances. The nonuniform distribution of reserves, however, had extremely low levels of recruitment

along those parts of the coastline that had few reserves, particularly at short dispersal distances.

## Discussion

Variable spacing between marine reserves has a relatively minor effect on catch and recruitment of larvae in populations that would be far from collapse with a uniform distribution of marine reserves, i.e., those with low fishing rates and (or) large reserves. Both jitter and completely random reserve designs tended to perform poorly when compared with a uniform distribution of marine reserves for persistent populations, although the effect was quite small. This small decrease in catch and recruitment is attributable to saturation of larval settlement inside marine reserves. Postsettlement density dependence places a maximum on the number of larvae that can settle successfully in a subpopulation each year. Potential settlers above this maximum do not increase the number of successfully settling larvae. As a result, in persistent populations, larvae that disperse from one reserve to another reserve do not contribute to the adult population and it is beneficial to export as many larvae as possible from reserves to fished areas. With a decaying dispersal pattern, this is achieved by a uniform distribution of reserves.

In populations that are not persistent or are near collapse with uniformly spaced reserves (high fishing rates and dispersal distances greater than reserve size), variable spacing of reserves can increase local population density relative to the uniform case. The effect can be quite large. In collapsing populations, small changes in protection of an area along the coastline can make the population locally persistent and thereby produce large changes in the overall population (when compared with the low recruitment levels produced by overfished populations). For high fishing rates and a system of small reserves, species with dispersal distances larger than the reserve size are not sufficiently protected to ensure persistence with a uniform distribution of reserves (Botsford et al. 2001). By instituting variable spacing in a system of marine reserves, some reserves naturally fall close together and protect more than 35% of the reproductive output in that local area, producing a network of reserves that is locally self-sustaining for intermediate distance dispersers. This saves the population from complete collapse and produces higher catches and recruitment in and around the reserves. Nevertheless, in this scenario, large areas of coastline have no marine reserves and necessarily the population collapses in those areas.

These results suggest that varying the spacing of marine reserves along the coastline could have a benefit for those species that are most threatened by overfishing. If there is concern that reserves will not cover an adequate percentage of the entire coastline to ensure persistence for all species, a higher percentage of the coastline could be covered over a limited area. However, that would be at the expense of the fraction covered in other areas. Furthermore, nonuniform reserve spacing produces an uneven distribution of catch and is unlikely to please anyone but fisherman living near the area of higher reserve density. The political ramifications of this uneven distribution could potentially outweigh any benefit derived from an uneven distribution of reserves.



Our results are consistent with the results for a uniform distribution of reserves (Botsford et al. 2001). If a single reserve protects all species with dispersal distances less than the size of the reserve, then varying the reserve spacing should only be a benefit to those species with longer dispersal distances. Furthermore, even those species with dispersal distances larger than the reserve size can only receive a significant benefit from variability in reserve spacing if the uniform system of reserves does not cover a sufficient percentage of the coastline to protect all species along the entire coastline.

There are a number of other factors that are potentially relevant to the design of marine reserves for sustainability and yield of fish populations that have not been treated in this study. The functional relationship between size and reproductive output was not varied and overcompensatory density dependence was not considered. Although these factors are important to the issue of whether effort-based management or management with marine reserves is likely to produce the highest yields (Parrish 1999; Berkeley et al. 2004), they are unlikely to significantly alter trends in catch as a function of the spacing between reserves. Furthermore, we have not attempted a complete treatment of how fishing effort might be redistributed after the creation of marine reserves. This process is quite complex and case specific (Beverton and Holt 1957; Wilen et al. 2002; Smith and Wilen 2003). Our results indicate that the potential gains due to the creation of marine reserves for overfished species are likely to be reduced when total effort is conserved. Exactly how fishing effort is redistributed will change the difference between catch from conventional management and catch with reserves, but will not alter our conclusions regarding variable spacing between reserves. Variable spacing can only have an effect if the final fishing rate in nonreserve areas produces a system that is overfished even with marine reserves.

Larval dispersal in our model was symmetric around the point of larval origin and uniformly decreasing with distance. Alongshore advection of larvae was not included in the model. It has been shown that alongshore larval advection can have a significant impact on the efficacy of a system of marine reserves (Gaines et al. 2003). On the other hand, a number of recent studies indicate that larval retention and concentration are relatively common (Todd 1998; Warner et al. 2000; Mora and Sale 2002), even in upwelling-dominated systems where one would normally expect strong alongshore currents (Graham and Largier 1997; Wing et al. 1998). Significant retention suggests that advection distances are likely to be smaller than was once thought and alongshore advection might not play an important role in population dynamics. Nonetheless, one must apply the results in this paper with caution when there exists the possibility of strong alongshore advection.

We also did not consider more complex two-dimensional patterns of larval dispersal, as might be found along convoluted coastlines and groups of islands, for example. These conditions will change the connectivity between adult subpopulations and therefore could have important consequences for the design of systems of marine reserves. Given the complexity of possible two-dimensional configurations of dispersal patterns and marine reserve designs, we have

limited ourselves here to a linear coastline. We speculate that the trends found here regarding variability in reserve spacing would not differ significantly if two-dimensional reserve configurations were considered.

Adult movement and "spillover" from reserve boundaries were not included in our model. This is a reasonable approximation if the size of reserves is considerably larger than the spatial scale of adult movement (Nowlis and Roberts 1999), as one would expect for species with low mobility (e.g., many marine invertebrates) and (or) small territorial ranges (e.g., most rockfish). If adults are migratory or have large territories, reserves will only offer them protection for the percentage of the time they spend inside reserves. In this case, the distinction between reserve and fishing areas is much less clear. The results of our model would only be applicable to the extent that reserves provide a real decrease in local fishing pressure.

All habitats in our model were considered equally suitable for settlement of larvae and adult survival in the absence of fishing. Here, it is assumed that the scale of habitat variability is smaller than an individual spatial unit and that all spatial units have roughly an equivalent percentage of habitable terrain. One might expect to satisfy these conditions for sufficiently large sections of the coastline in the middle of a species' range. Species domain boundaries, large areas of unsuitable terrain, and large-scale variability in terrain habitability will undoubtedly complicate population dynamics, but it is likely that several closely spaced reserves will continue to locally benefit overfished species along that section of the coastline.

Ultimately, the actual distribution of marine reserves will be determined by a mixture of science and political feasibility. It is unlikely that an extremely nonuniform distribution of reserves could be implemented because of the short-term negative effects on local fishermen of closing sections of the coastline to fishing in areas where reserve density is high. To lessen the impact on any one group of fishermen, it is probable that reserves will tend to be approximately uniformly spaced along the coast. This study indicates that small divergences from uniform reserve spacing are unlikely to have a large positive or negative impact on population size. However, there is one case in which an uneven distribution of reserves may actually be acceptable to stakeholders. There has been some discussion of partial implementation of a system of reserves as a way of demonstrating their benefits as they are "phased in". Our results indicate that if the purpose of placing only a small fraction of the coast in reserves were to demonstrate the benefits of marine reserves, then that fraction should be concentrated in an area on the order of the dispersal distance of the species to be protected rather than distributed evenly along the coast.

## Acknowledgments

This work was supported by NSF grant OCE-9711448 and by California Sea Grants R/F 179. We would like to thank Christine N. Meynard and Michael R. O'Farrell for their helpful suggestions and comments. We would also like to thank both reviewers whose comments greatly improved this paper.



## References

- Berkeley, S.A., Hixon, M.A., Larson, R.J., and Love, M.S. 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries*, **29**: 23–32.
- Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. Facsimile reprint (1993). *In* Fish & fisheries series. Vol. 11. Chapman & Hall, London, UK.
- Bohnsack, J.A. 1998. Application of marine reserves to reef fisheries management. *Aust. J. Ecol.* **23**: 298–304.
- Botsford, L.W., Castilla, J.C., and Peterson, C. 1997. The management of fisheries and marine ecosystems. *Science (Wash., D.C.)*, **277**: 509–515.
- Botsford, L.W., Morgan, L.E., Lockwood, D.R., and Wilen, J.E. 1999. Marine reserves and management of the northern California red sea urchin fishery. *CalCOFI Reports*, **40**: 87–93.
- Botsford, L.W., Hastings, A., and Gaines, S.D. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distance. *Ecol. Lett.* **4**: 144–150.
- Carr, M.H., Neigel, J.E., Estes, J.A., Andelman, S., Warner, R.R., and Largier, J.L. 2003. Comparing marine and terrestrial ecosystems: implications for the design of coastal marine reserves. *Ecol. Appl.* **13**: S90–S107.
- Dugan, J.E., and Davis, G.E. 1993. Applications of marine refugia to coastal fisheries management. *Can. J. Fish. Aquat. Sci.* **50**: 2029–2042.
- Gaines, S.D., Gaylord, B., and Largier, J.L. 2003. Avoiding current oversights in marine reserve design. *Ecol. Appl.* **13**: S32–S46.
- Gaylord, B., and Gaines, S.D. 2000. Temperature or transport? Range limits in marine species mediated solely by flow. *Am. Nat.* **155**: 769–789.
- Gerber, L.R., Botsford, L.W., Hastings, A., Possingham, H.P., Gaines, S.D., Palumbi, S.R., and Andelman, S. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. *Ecol. Appl.* **13**: S47–S64.
- Graham, W.M., and Largier, J.L. 1997. Upwelling shadows as near-shore retention sites: the example of northern Monterey Bay. *Cont. Shelf Res.* **17**: 509–532.
- Grantham, B.A., Eckert, G.L., and Shanks, A.L. 2003. Dispersal potential of marine invertebrates in diverse habitats. *Ecol. Appl.* **13**: S108–S116.
- Hastings, A., and Botsford, L.W. 1999. Equivalence in yield from marine reserves and traditional fisheries management. *Science (Wash., D.C.)*, **284**: 1537–1538.
- Hockey, P.A.R., and Branch, G.M. 1994. Conserving marine biodiversity on the African coast: implications of a terrestrial perspective. *Aquat. Conserv., Mar. Freshw. Ecosyst.* **4**: 345–362.
- Hockey, P.A.R., and Branch, G.M. 1997. Criteria, objectives and methodology for evaluating marine protected areas in South Africa. *S. Afr. J. Mar. Sci.* **18**: 369–383.
- Hutchings, J.A. 2000. Collapse and recovery of marine fishes. *Nature (Lond.)*, **406**: 882–885.
- Kalvass, P.E., and Hendrix, J.M. 1997. The California red sea urchin, *Strongylocentrotus franciscanus*, fishery: catch, effort, and management trends. *Mar. Fish. Rev.* **59**: 1–17.
- Kinlan, B.P., and Gaines, S.D. 2003. Propagule dispersal in marine and terrestrial environments: a community perspective. *Ecology*, **84**: 2007–2020.
- Leslie, H., Ruckelshaus, M., Ball, I.R., Andelman, S., and Possingham, H.P. 2003. Using siting algorithms in the design of marine reserve networks. *Ecol. Appl.* **13**: S185–S198.
- Lockwood, D.R., Hastings, A., and Botsford, L.W. 2002. The effects of dispersal patterns on marine reserves: Does the tail wag the dog? *Theor. Popul. Biol.* **61**: 297–309.
- Mace, P.M., and Sissenwine, M.P. 1993. How much spawning per recruit is enough? *Can. Spec. Publ. Fish. Aquat. Sci. No. 120*. pp. 101–118.
- Mora, C., and Sale, P.F. 2002. Are populations of coral reef fish open or closed? *Trends Ecol. Evol.* **17**: 422–428.
- Morgan, L.E. 1997. Spatial variation in the population dynamics of the red sea urchin, *Strongylocentrotus franciscanus*, in northern California. Ph.D. Diss., University of California, Davis, Calif.
- Morgan, L.E., Botsford, L.W., Lundquist, C.J., and Quinn, J.F. 1999. The potential of no-take reserves to sustain the red sea urchin (*Strongylocentrotus franciscanus*) fishery in northern California. *Bull. Tohoku Natl. Fish. Res. Inst.* **62**: 83–94.
- Nowlis, J.S., and Roberts, C.M. 1999. Fisheries benefits and optimal design of marine reserves. *Fish. Bull.* **97**: 604–616.
- Palumbi, S.R. 2002. Marine reserves: a tool for ecosystem management and conservation. Pew Oceans Commission, Arlington, Va.
- Parrish, R. 1999. Marine reserves for fisheries management: Why not? *Calif. Coop. Ocean. Fish. Investig. Rep.* **40**: 77–86.
- Plan Development Team. 1990. The potential of marine fishery reserves for reef fish management in the U.S. Southern Atlantic. NOAA Technical Memorandum NMFS-SEFC-261.
- Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries and Marine Service, Ottawa, Canada.
- Roberts, C.M., Andelman, S., Branch, G., Bustamante, R.H., Castilla, J.C., Dugan, J., Halpern, B.S., Lafferty, K.D., Leslie, H., Lubchenco, J., McArdle, D., Possingham, H.P., Ruckelshaus, M., and Warner, R.R. 2003. Ecological criteria for evaluating candidate sites for marine reserves. *Ecol. Appl.* **13**: S199–S214.
- Shanks, A.L., Grantham, B.A., and Carr, M.H. 2003. Propagule dispersal distance and the size and spacing of marine reserves. *Ecol. Appl.* **13**: S159–S169.
- Simberloff, D. 2000. No reserve is an island: marine reserves and nonindigenous species. *Bull. Mar. Sci.* **66**: 567–580.
- Smith, B.D., Botsford, L.W., and Wing, S.R. 1998. Estimation of growth and mortality parameters from size frequency distributions lacking age patterns: the red sea urchin (*Strongylocentrotus franciscanus*) as an example. *Can. J. Fish. Aquat. Sci.* **55**: 1236–1247.
- Smith, M.D., and Wilen, J.E. 2003. Economic impacts of marine reserves: the importance of spatial behavior. *J. Environ. Econ. Manag.* **46**: 183–206.
- Todd, C.D. 1998. Larval supply and recruitment of benthic invertebrates: Do larvae always disperse as much as we believe? *Hydrobiologia*, **376**: 1–21.
- Warner, R.R., Swearer, S.E., and Caselle, J.E. 2000. Larval accumulation and retention: implications for the design of marine reserves and essential fish habitat. *Bull. Mar. Sci.* **66**: 821–830.
- Wilen, J.E., Smith, M.D., Lockwood, D., and Botsford, L.W. 2002. Avoiding surprises: incorporating fisherman behavior into management models. *Bull. Mar. Sci.* **70**: 553–575.
- Wing, S.R., Botsford, L.W., Ralston, S.V., and Largier, J.L. 1998. Meroplanktonic distribution and circulation in a coastal retention zone of the northern California upwelling system. *Limnol. Oceanogr.* **43**: 1710–1721.