Managing with Reserves: Modeling Uncertainty in Larval Dispersal for a Sea Urchin Fishery

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Abstract

The commercial fishery for the northern California red sea urchin, *Strongylocentrotus franciscanus*, began in 1985, peaked in 1989, and has declined steadily since that time. An alternative to traditional management is spatial management using no-take reserves that may improve the management of this and other fisheries. We formulated a size-structured metapopulation model with 24 patches and a dispersal matrix to address the key issue of larval linkages between reserve and fished patches. We explored four conceptual models of metapopulation connectivity including source-sink, limited distance, larval pool, and headlands dispersal models. These models indicated that the mode of dispersal led to potentially large differences in reserve performance. Larval pool models require little knowledge of spatial patterns in order to design an effective reserve network, while source-sink dynamics require a detailed understanding of larval dispersal if reserves are to be an effective means of fisheries management. Reserve networks can be optimized with knowledge of larval dispersal patterns; however, they are rarely known with certainty. A decision analysis used to evaluate alternative dispersal modes suggested a reserve system comprising approximately 25% of the total area can maintain catch in the red sea urchin fishery, buffering uncertainty in the pattern of larval replenishment and fishing mortality rate.

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Introduction

Marine reserves have been proposed as an alternative management strategy to arrest the decline in catch of the northern California red sea urchin fishery. Kalvass and Hendrix (1997) detail the fishery and its management, and point out the large reduction in biomass since the beginning of the fishery. While this decline is likely due to the "fishing up" effect, there is concern that the fishery may be recruitment overfished and will continue to decline. Here we attempt to address the question of spatially variable dispersal patterns in reserve design. The specific details of reserve placement are investigated in reference to knowledge of larval dispersal patterns and sources. Many factors contribute to the productivity of a particular location including growth, mortality, recruitment, and habitat features; however, we focus on a subset of simple, conceptual dispersal models to gain insight, and focus future attention on how reserves can be used in a fishery management context. We address reserve performance in terms of total catch versus percent area in reserves. We do not analyze other potential benefits of marine reserves, nor do we discuss other possible fishery management. These pose significant questions for future studies that can make use of the results obtained here.

Recent reviews of no-take marine reserves have pointed out the potential benefits to fisheries (Bohnsack 1990, Rowley 1994, Guénette et al. 1998, Murray et al. 1999). These benefits include reducing the likelihood of stock collapse (Quinn et al. 1993, Guénette and Pitcher 1999, Sladek-Nowlis and Roberts 1999), accelerating the rate of stock recovery and decreasing variability in annual catches (Sladek-Nowlis and Roberts 1999), serving as reference sites for collecting fishery-independent data (Allison et al. 1998), and preventing degradation of habitat caused by fishing (Allison et al. 1998, Dayton 1998).

One management goal of no-take reserves is to maintain sufficient reproductive capacity to provide recruits to adjacent fished areas. Consideration of the temporal and spatial nature of larval production, dispersal distance (Quinn et al. 1993, Botsford et al. 1994), and local oceanographic features (Carr and Reed 1993, Morgan and Botsford 1998) will influence the reserve siting decision. Previous authors have recommended a metapopulation approach to reserve networks with strategically placed reserves connecting metapopulations (Man et al. 1995, Stoner and Ray 1996, Roberts 1998). Reserve networks have also been proposed as a better way to protect source populations that produce larvae which recolonize fished, thus sink, locations (Pulliam 1988, Tuck and Possingham 2000). Here we define a metapopulation for a meroplanktonic species as a series of local, sedentary adult populations distributed along a coastline linked by larval dispersal (Botsford et al. 1994).

In the absence of fishing mortality, increases in the size and abundance of individuals in reserves has occurred (Roberts and Polunin 1991, Rowley 1994, Stoner and Ray 1996). Because larger individuals have a greater

per capita reproductive output than smaller individuals (e.g., Kalvass and Hendrix 1997 for the red sea urchin) reserves can increase the reproductive capacity of the population. Despite this evidence, there is still little documentation of reserves supplying benefits to adjacent fished areas (McClanahan and Kaunda-Arara 1996, Russ and Alcala 1996, Crowder et al. 2000), although theoretical studies predict fishery enhancement (Sladek-Nowlis and Roberts 1999).

Hastings and Botsford (1999) pointed out that an equivalence in yield to traditional management could be achieved with spatial management, but most modeling studies predict increased fishery yields under limited situations, most commonly when fishing pressure is unusually high. Greater enhancement occurs when larvae replenish nearby fished populations (Quinn et al. 1993, Holland and Brazee 1996, Guénette and Pitcher 1999, Sladek Nowlis and Roberts 1999). Although these models evaluated catch with regard to a variety of factors, none examined the specific spatial pattern of larval replenishment except Quinn et al. (1993). In this study, larvae were allowed to move to one or more adjacent patches. It was concluded that the distance between reserves should be less than the dispersal distance of the larvae.

The question of larval dispersal from a reserve location to a fished site is fundamental to the design and performance of a reserve network. Roberts (1997) estimated "transport envelopes" for larvae passively transported in prevailing currents of the Caribbean Sea, in an attempt to map linkages between populations. These maps allowed reefs to be identified as sources or sinks depending on the number of "upstream" or "downstream" populations. This study pointed to the need to address larval dispersal pathways in the design of reserve networks.

Although the duration of the larval stage is known for a variety of species, there is little else available to model larval dispersal pathways from adult spawning site to larval settlement site. Direct observations have been possible for a few species with relatively large larvae that disperse over relatively short distances (Davis and Butler 1989, Carlon and Olson 1993). Other studies have identified the physical mechanism underlying larval dispersal by sampling larval distributions in the plankton and recruitment over space and time concurrently with hydrographic measurements (Wing et al. 1995b, Hare and Cowen 1996, Miller and Emlet 1997). Studies have compared settlement variability over space on a variety of scales from meters to many kilometers (Sewell and Watson 1993, Wing et al. 1995a), although the relationship between settlement and recruitment to the fishery is often uncertain. Circulation models and satellite information on flow can also contribute to an understanding of the movement of planktonic larvae with specific physical and behavioral characteristics (Botsford et al. 1994, Keough and Black 1996, Polovina et al. 1999).

Because little is known of dispersal pathways, we are relegated to using models or likely transport paths to assess the effects of reserves on the metapopulation dynamics of meroplanktonic species. Carr and Reed (1993)

outlined conceptual larval replenishment models and qualitatively described their appropriateness to species with different life history characteristics. Adult populations can be linked in different ways based on the planktonic duration of larvae and regional circulation characteristics. The focus here is slightly different from that of Carr and Reed (1993) in that several dispersal models are evaluated in the context of the uncertainty of the dispersal pathway for one particular species, the red sea urchin. The models outlined by Carr and Reed (1993) form the basis of the current modeling, by serving as alternative states of nature covering a range of possible dispersal linkages. We include one additional model of dispersal based on ongoing research of sea urchin settlement and recruitment in northern California (Wing et al. 1995b, Morgan et al. 2000b). One important goal of this work is to make managers aware of the explicit assumptions regarding the pattern of larval dispersal and the effect this has on reserve performance and fishery yield. We attempt to generalize elements associated with understanding the pattern of larval dispersal to marine reserve design.

Methods

Metapopulation Model

Using a metapopulation model we evaluate the role of larval dispersal in maintaining meroplanktonic metapopulations in the face of fishing and reserves. The model consists of 24 independent size structured subpopulations linked in the larval stage by a dispersal matrix representing combinations of larval origins and destinations. Each subpopulation is modeled using von Bertalanffy growth with individual variability in asymptotic length. We use the red sea urchin as an example based on our familiarity with this species and a reasonable understanding of its life history. Parameter values representing typical growth and mortality of red sea urchin in northern California are used (Morgan et al. 2000a). We assume no adult movement between patches, constant annual fishing mortality, and no interannual recruitment variability due to environmental stochasticity. Because our interest is in the influence dispersal models have on spatial patterns of productivity, all growth and mortality parameters are the same for each subpopulation. A length-fecundity relationship, and size at sexual maturity for red sea urchins from Kalvass and Hendrix (1997) are used to model the production of larvae from each subpopulation.

Recruitment in the model incorporates Beverton-Holt density dependence between the larval and settlement stage of development. Post-settlement density dependence is likely influenced by the availability of protective spine-canopy habitat (Tegner and Dayton 1977). Thus density dependence is set such that successful settlement is dependent on the number of larvae attempting to settle and the amount of juvenile habitat available. The upper limit on carrying capacity is assumed to be the same for all sub-

populations and only the dispersal between subpopulations varies. Previous evaluation of the model by Botsford et al. (1999) derived values for the Beverton-Holt relationship, and we use those here. These values lead to model behavior in which the implementation of no-fishing reserves has an influence on catch (i.e., fishing at realistic rates reduces the number of settlers arriving at each site), but does not lead to local extinction.

We use equilibrium catch as the metric with which to compare the efficacy of no-fishing reserves. Catch after 100 years of constant fishing is calculated for each of four conceptually different larval dispersal models (Fig. 1). With no reserves catch is first calculated for each of the dispersal models to establish a baseline with which to evaluate reserves as a management tool. For fishing rates of $F = 0.5$, $F = 1$ and the rate which led to the highest maximum sustainable yield (MSY), we evaluated different reserve designs, including percent area and reserve position.

The first model, limited distance dispersal, is represented by a Guassian curve centered on the exporting site with different standard deviations corresponding to different dispersal widths, narrow contrasted with wide. Two different dispersal widths are evaluated (i.e., different standard deviations in the Gaussian function, S.D. = 0.1, 1.0). We make the assumption that all 24 sites are arrayed along a linear coastline, such that larvae are lost from subpopulations located on the edges. The second dispersal model considered is a source-sink scenario where one source population supplies larvae to itself and either three or five other populations equally, while sinks supply no larvae (i.e., "black hole sinks"). For the source-sink model we calculated catch based on knowledge of the location of larval sources, and also predicted catch based on the probability that one or more reserves placed randomly included a source location using the hyper-geometric distribution.

The third model, larval pool dispersal, is characterized by each subpopulation contributing larvae to a common pool based on the abundance of adult, and receiving $1/24$ of the larvae in the pool. In the case presented here, where carrying capacity, growth, and mortality are the same for all sites, the larval contributions from each subpopulation are identical, unless fishing occurs.

The final dispersal model, the headlands model, is based on field studies of larval settlement and recruitment in northern California (Wing et al. 1995a,b; Morgan et al. 2000b). This latter model makes no assumptions regarding the source location of larvae (all sites contribute), but the delivery pattern is unequal between locations, (i.e., each site receives different numbers of larvae from a common larval pool). It is based on results that suggest that during active upwelling larvae are transported southward and offshore, and retained in frontal zones and coastal eddies. Then, during relaxation of upwelling winds, current reversals transport invertebrate larvae northward to settle at predictable sites (Wing et al. 1995a,b; Morgan et al. 2000b). From these studies in northern California, areas immediately to the north of headlands are those that first come into contact with the

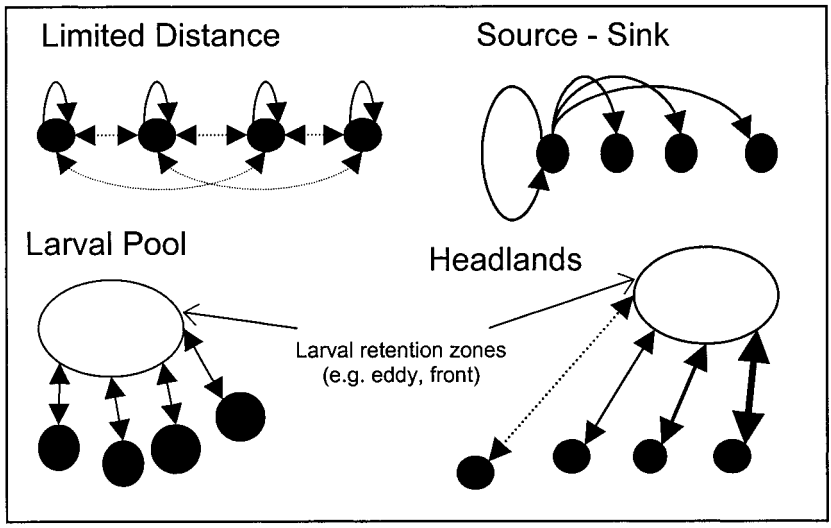

Figure 1. Conceptual models depicting possible larval linkages for a meroplanktonic metapopulation. Line weights represent different levels of transfer between patches. Dark circles represent individual patches.

poleward and onshore relaxation flow. As a result there is a gradient from south to north above headlands in the number of relaxation fronts that reach a site. We set up dispersal as a system with two separate headland cells, each with independent 12 patch metapopulations. For each 12-site set of cells, all sites contribute to the larval pool relative to the local abundance of adult sea urchins, but each site receives different numbers of larvae. Larval delivery for each site declines as a linear function from south to north within each set of 12 sites (Fig. 1).

Decision analysis was used to determine the optimal reserve configuration. The four dispersal models were considered as alternate states of nature with a probability of occurrence. We assigned the same probability of occurrence to each of the dispersal models assuming each was equally likely ($P = 0.25$). The weighted average catches for each fishing rate, reserve configuration and dispersal model were calculated to provide a basis for assessing the efficacy of marine reserves.

Results

Under equilibrium conditions, reserves enhanced catch when local populations were recruitment overfished. The fishing rate leading to MSY for our red sea urchin metapopulation varied depending on the dispersal matrix (Fig. 2). A fishing rate of $F = 0.2$ lead to MSY under larval pool models, but

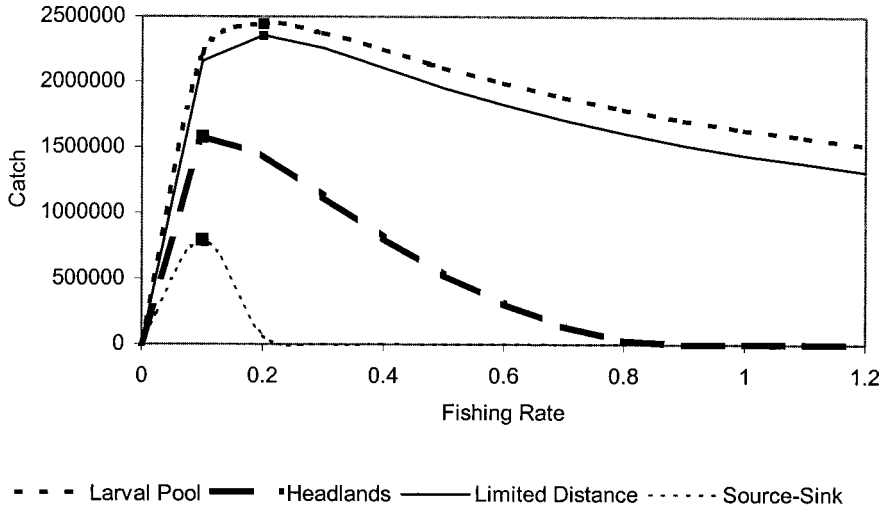

Figure 2. Maximum yield curves for different larval dispersal models with no reserves.

resulted in overfishing and a population collapse under the source-sink scenario. Furthermore there existed an equilibrium fishing value for larval pool and limited distance dispersal models over the range of values from $F = 0.1$ to 1.2, but under models with more restricted larval dispersal, catch led to extinction at lower fishing rates ($F = 0.2$ for source-sink, $F = 0.8$ for headlands). When specific larval dispersal patterns were included into the metapopulation model such that production across space was variable, different aspects of reserve design became important.

Limited Distance Dispersal

Maximum sustainable yield for two limited distance models with different dispersal widths occurred at a fishing rate of $F = 0.2$ (Fig. 2, Fig. 3). At F equal to MSY, reserves did not enhance catch for either of the dispersal widths. Dispersal width led to varying performance of the reserve systems at higher fishing rates. At a fishing rate, $F = 1$, with equally spaced reserves, the greatest yield occurred with four reserves (17%) for the wide dispersal width, and with six reserves (25%) for the narrow dispersal width (Fig. 3). Reserve spacing needed to be closer than the maximum dispersal distance of larvae. At $F = 0.5$ and $F = 1$, catch increased with the area in reserve up to an optimal value and then declined for both dispersal distances. Spacing was the critical parameter since each site was able to supply larvae when protected. When reserves were spaced optimally, narrow dispersal width led to slightly greater catch than wide dispersal width due

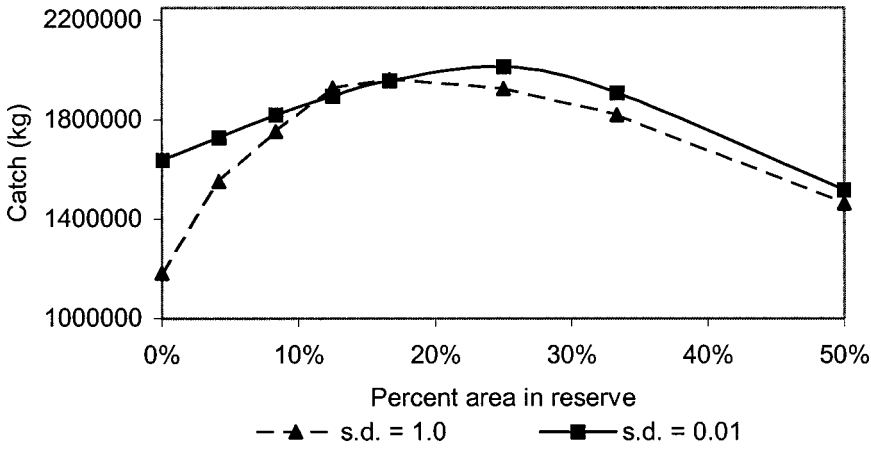

Figure 3. Catch with reserves for two different limited-distance dispersal width models for F=1 (S.D. refers to the standard deviation of the dispersal width).

to larvae from patches at the edges of the model boundary exiting the metapopulation system. The wider dispersal width had a greater loss of larvae. This result is partly an artifact of the way in which we modeled dispersal; i.e., without a reflecting boundary. However, the greater the dispersal width the greater the opportunity to rescue more distant fished populations. With only one or two reserves in place, reserves placed in the center of the range such that all larvae remained in the metapopulation were more effective than reserves positioned on the edge where larvae exited the system.

Source-Sink Dispersal

Maximum sustainable yield under source-sink conditions was much lower than for the other dispersal models (Fig. 2). Sinks in our model were "black-hole sinks" with no flow of larvae to the source population. This dispersal configuration resulted in a reduction in the number of successfully reproducing individuals by 75% in the case where one in four sites was a source. Catch under the source-sink model improved at MSY and when overfishing occurred, if source populations were protected (Fig. 4). Again, at F = MSY if reserves were not optimally placed (i.e., randomly), catch declined as reserve area was added, although the decline was slight. If high rates of fishing were allowed in source areas, the entire population rapidly collapsed. This placed a premium on locating reserves at source locations. The highest yields were obtained when all sources were protected, and sinks were heavily exploited (Fig. 4). This was true for F equal to MSY and at $F = 1$ (Fig. 4).

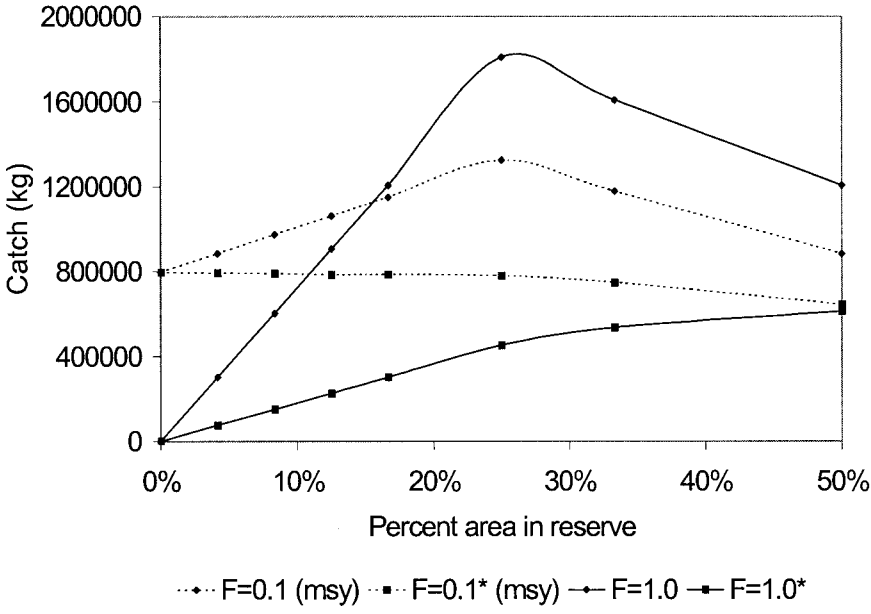

*Figure 4. Catch with reserves for source-sink dispersal, at two fishing rates. * Random placement without knowledge of source locations.*

In the more likely case where the source of larvae was unknown, we calculated the predicted catch based on the probability that one or more reserves placed randomly included a source location. At $F = 1$, catch increases with the number of reserves as the probability of locating a reserve by chance on a source location increases. Predicted catch increased with the number of reserves, up to 50% of the area in reserve for $F = 1$, but not for $F = 0.1$. Protecting sink populations never positively impacted yield.

Larval Pool Dispersal

Maximum sustainable yield occurred at a fishing rate of $F = 0.2$ with no reserves (Fig. 2). The amount of area to set aside in a reserve system was a function of the targeted fishing rate only. At $F = 0.5$, an increase in catch over the no reserve case was observed for percent reserve coverages of 4% (1 in 24) to 16.7% (4 in 24) with an optimum catch at 8.3% (2 in 24) (Fig. 5). With over 17% of the area in reserve catch declined with greater area in reserve. A similar pattern was observed for $F = 1$, except that notably, the increase in percentage catch was greater with reserves, although the optimum number of reserves was the same (16.7%). In contrast with the other dispersal models, the position of reserves had no influence, as all sites contribute and receive larvae equally.

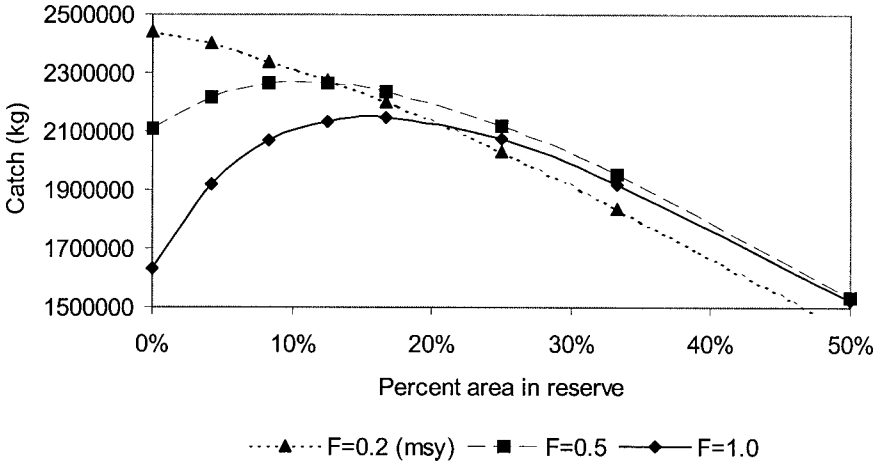

Figure 5. Catch with reserves for larval pool dispersal for three fishing rates.

Headlands Dispersal

Maximum sustainable yield without reserves occurred at a fishing rate of $F = 0.1$ (Fig. 2). At $F = 0.9$, the metapopulation was extinct at 100 years. When fishing rates exceeded MSY, reserves enhanced catch (Fig. 6). At $F = 0.5$, the optimal position and 25% of the area in reserve resulted in a nearly 60% increase over $F = 0.5$ and no reserves. For $F = 1$, the case was even more dramatic, as catch was not sustainable at $F = 1$ without at least one reserve.

With this dispersal model, the location of the reserves was important since no two patches were alike. When larvae were redistributed unequally from a common pool, spatial variability in recruitment lead to patches with different levels of biomass (Fig. 7). These results demonstrated not only that an increase in reserve area was needed with increased fishing mortality rates, but also that the position of the reserve could influence reserve performance. Although we did not detail all of the possible scenarios, these results suggested that as fishing rate increases the position of the reserve becomes more important. As an example, at $F = 1$ with one reserve, position alone accounted for a 15% difference in yield. While it was important to identify and protect the most productive sites at a fishing rate of $F = 1$, at a lower fishing mortality rate, $F = 0.5$, protecting the most productive patch resulted in a loss of yield, which was not made up for by transfer of larvae from this site. These more abundant populations with greater larval production, produced a higher standing biomass and thus had a greater contribution to the catch. Results (not shown) also indicated that, for $F = 0.5$, catch from three optimally placed reserves can exceed catch from four non-optimal reserves.

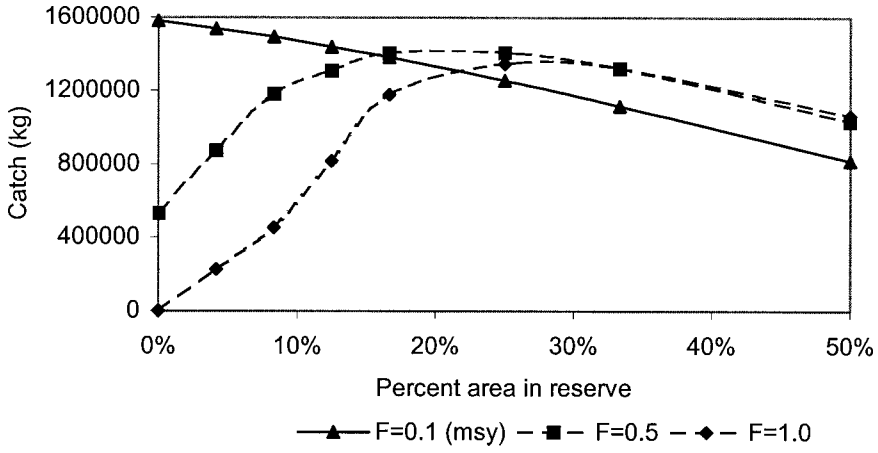

Figure 6. Catch with reserves for headlands dispersal at three fishing rates. Reserves placed to optimize catch.

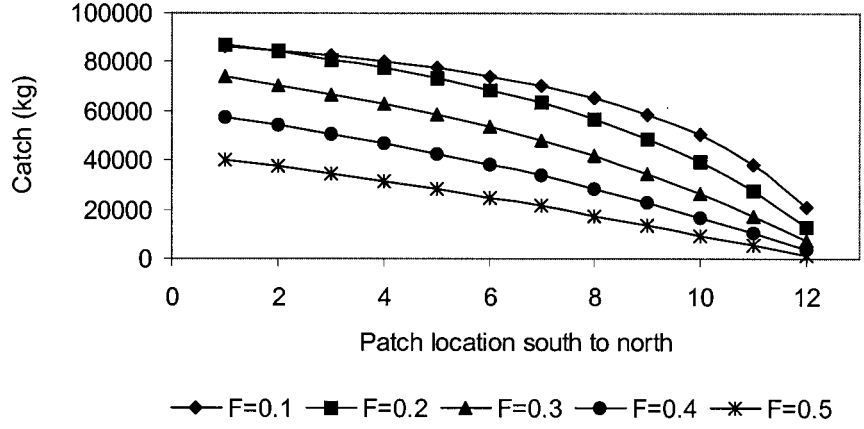

Figure 7. Catch for individual patches under headlands dispersal at various fishing rates without reserves. Areas with highest settlement sustain the greatest catch (e.g., site 1 vs. site 12).

Decision Analysis

Despite the widespread use of generic larval pool dispersal models, the present results suggest that they represent a best-case situation, and there is substantial evidence from field studies to suggest that they do not adequately describe larval dispersal patterns. Still, we are unable to adequately characterize the larval dispersal phase of the vast majority of species with any certainty. Therefore we assigned probabilities to the different dispersal models assuming each of the four was equally likely. The results of this averaging, when analyzed in the context of a fishing rate goal of MSY, indicated that the highest catch was obtained at $F = 0.1$, although $F = 0.2$ produced a very similar catch (Fig. 8). However, there was a drastic reduction in catch for higher fishing rates without a reserve ($F = 0.3$ and larger). At these higher fishing rates catch increased with greater area in reserve, and the loss of catch due to overfishing was much greater than the loss in catch due to removing areas from fishing. As the area in no-take reserve was increased, the variability in catch due to uncertain fishing rate was much narrower over the range of fishing rates, and this variability continued to decline up to approximately 25% of the area in reserve.

Discussion

Marine reserves are a robust management option for dealing with uncertainty in the mode of larval dispersal when fishing rate cannot be precisely determined or controlled (Fig. 8). With one reserve in our metapopulation (4% area) catch variability declined considerably, and landings increased substantially above the no reserve case for fishing rates above $F = 0.3$. Given the well-documented problems in assessing stocks and setting fishing rates (Walters and Maguire 1996), this result supports the use of marine reserves as a management tool. However, it should be noted that this result is based on a weighted average of four different dispersal models, which may have considerable error should one particular dispersal model be correct.

The role of larval dispersal is critical to the performance of a reserve system when knowledge of the underlying spatial patterns in dispersal patterns exist. Most modeling studies do not explicitly account for spatial variation in larval dispersal, assuming a generic, "larval pool" model of dispersal. Recently, evidence of substantial genetic heterogeneity in open marine populations has contradicted this larval pool assumption (Hedgecock 1994, Edmands et al. 1996, Moberg and Burton 2000). The present analysis shows that "larval pool" dispersal is the most optimistic scenario for catch enhancement through the use of marine reserves, and that other dispersal patterns can lead to very limited benefits or may even exacerbate conditions in poorly designed and implemented reserve systems. Calculations of maximum sustainable yield highlight this fact; MSY for one model can result in extinction if another dispersal model is in fact more appropriate (Fig. 2).

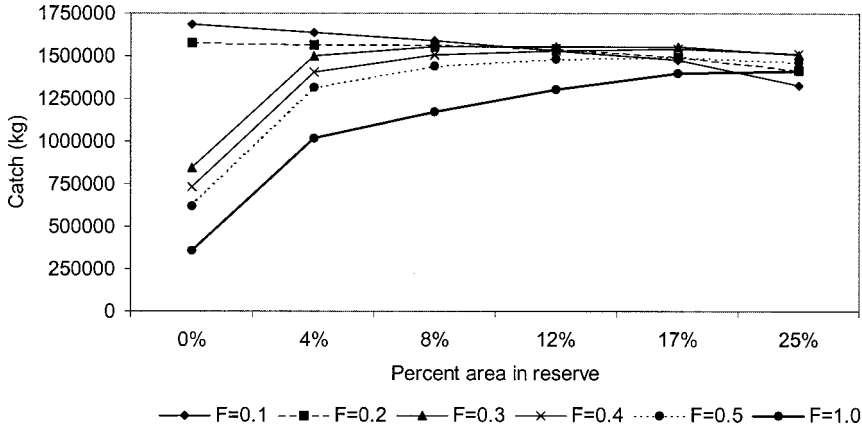

Figure 8. Decision analysis using average catch for each of the four dispersal models (equally weighted).

The appropriateness of the fishing rates used in this study in part relies on the present fishing rate in the northern California red sea urchin fishery. Morgan et al. (2000a) calculated fishing rates at 11 sites in 2 consecutive years and found a wide range of fishing mortality rates (0.12-1.87). Spatial and temporal variation in recruitment could bias these estimates in a positive direction (Morgan et al. 2000a); however, given this wide range of estimates, the values of F used in this study are likely conservative. The estimates of fishing mortality also indicate that in most cases fishing is well above the MSY calculated for all of the dispersal models. In light of this, a 25% total area reserve would benefit management of this population, although caveats to this recommendation must be noted. For example, in our modeled metapopulation all other sources of productivity are purposefully eliminated despite knowledge of spatial variation in growth and mortality rates (Morgan et al. 2000a).

The secondary question of where to place the reserves is unfortunately more difficult to ascertain. Although the headlands model appears to predominate in the years studied, evidence from red sea urchin size distributions in northern California indicates that occasionally recruitment events occurred over larger spatial scales (Morgan et al. 2000b). However, in light of the high estimated F (Morgan et al. 2000a), the pattern of recruitment (Wing et al. 1995a,b; Morgan et al. 2000b) and the modeling results presented here, locating reserves in productive areas to the north of headlands would be a good first step in implementing a reserve network.

Although it is generally perceived that no-fishing reserves require less management effort than traditional regulations, appropriate controls on fishing are still required with a reserve system in place. One of the signifi-

cant points of this and previous modeling studies (Beverton and Holt 1957, Holland and Brazee 1996, Guénette and Pitcher 1999) is that the size of a reserve system needs to be a function of the targeted fishing mortality rate. Other models have suggested reserves greater than 70% of the fishable area are needed to deal with uncertainties in management, and errors and bias in fishery management (Lauck et al. 1998).

This study also demonstrates that it is important to incorporate larval dispersal in management analysis of reserve design. These conceptual models point out different factors that will influence reserve design if a particular model is representative. Limited dispersal models suggest reserves on the edges of population ranges can be ineffective if larvae are lost to unfavorable patches, and that reserves spaced too widely cannot "rescue" distant patches. This result is consistent with ecologically realistic conditions in which short-lived planktonic larvae disperse relatively short distances compared to more long-lived larvae. Species with short-lived larvae would be better protected by smaller, closely spaced reserves, while species with longer-lived larvae need larger areas, but can withstand greater distances between reserves. This study agrees with earlier results that found spacing of reserves was a function of fishing rate and dispersal ability (Quinn et al. 1993). Limited distance dispersal requires appropriate spacing between reserves to ensure replenishment of fished areas between distant reserves.

We also note that a fishing rate set to $F = 0.2$, which is the MSY for the larval pool and limited distance dispersal models, results in extinction in the source-sink model, with the very same demographic parameters. Variation in spatial productivity due to differences in larval replenishment as well as the optimal size of the system can result in drastic differences in the performance of reserve systems. For example, if, as a tradeoff for closing areas to fishing, increases in fishing rate are allowed in remaining areas, precautions should be taken to protect source populations. A reserve design error that mistakes a source for a sink may exacerbate fishing conditions, leading to a more rapid stock collapse.

Further confounding the area required to offset fishing mortality is the shape and curvature of the stock-recruitment curve (Botsford et al. 1999, Parrish 1999) and density-dependent reproductive success. Yield in populations with strong density dependence may be disadvantaged by increased density inside reserves that leads to a reduction in per capita reproductive potential (Parrish 1999). Conversely, yield in species with broadcast spawning subject to Allee effects may be enhanced by reserves (Quinn et al. 1993, Botsford et al. 1999). Using a Beverton-Holt relationship Botsford et al. (1999) showed that changing the slope of this relationship at the origin could either increase or decrease yield as reserves were added to a fishery.

Previous authors have proposed using regional circulation patterns as criteria for designing reserve networks to maintain linkages between adult populations (Carr and Reed 1993, Morgan and Botsford 1998, Starr 1998). Here we present an analysis of the importance of larval dispersal patterns

on fishery yield. While maximizing larval export from reserves is an important goal for fishery management, few studies have evaluated the assumptions regarding this important life history period. Further studies of oceanographic features, such as frontal regions and coastal eddies, which accumulate larvae will likely improve our ability to successfully site reserves.

The analyses presented here for conceptual dispersal models appropriate to mesoscale metapopulation structure suggest that considerable research is necessary to adequately determine spatial patterns of productivity and correctly site reserves. The simple nature of these analyses, however, points to areas of concern with spatial management. First, mistakes in identifying either source or sink locations can have detrimental effects. Second, controls on fishing mortality still need to be in place, albeit with a greater buffer for uncertainty, if reserves are implemented. As with other management options, no-take reserves should be considered an additional tool in the effort to manage fisheries. Finally, if marine reserves are to be effective management solutions, then they must apply broadly to a range of species. The results of these analyses are appropriate to other meroplanktonic species, such as rockfish, but species that migrate as adults or shift distributions from one year to the next are not amenable to analyses herein.

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