

COMPARING DESIGNS OF MARINE RESERVES FOR FISHERIES AND FOR BIODIVERSITY

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Abstract. We compare and contrast the design of networks of marine reserves for two different, commonly stated goals: (1) maintaining high yield in fisheries and (2) conserving biodiversity, in an idealized setting using simple models. The models describe larval dispersal over a system of evenly spaced reserves of equal size, assuming sedentary adults. We initially demonstrate that, since populations in reserve systems can be sustained either by covering a minimal fraction of the coast with small reserves or by covering a smaller fraction of the coast with few large reserves, cost considerations dictate that the conservation goal would be best met by reserves as large as practically possible. In contrast, the fisheries goal of maximizing yield requires maximizing larval export outside of reserves, which we show means that reserves should be as small as practically possible. Meeting the fisheries goal is ultimately more costly because it suggests a larger area of the coastline should be in reserves, but it also improves on conservation goals by enhancing sustainability for species dispersing longer distances.

Key words: biodiversity; conservation; dispersal; fisheries; marine reserves; models.

INTRODUCTION

Marine reserves, or no-take zones, have been recently promoted as a means of managing marine populations for two different goals: preserving biodiversity (e.g., Agardy 1994), and managing fisheries (e.g., Holland and Brazee 1996) to produce the highest yields. There has been little effort to differentiate the benefits to each of these beneficiaries, and we know of no attempts to identify inherent differences in design. Most studies assume that because fisheries need to be sustained, reserves designed to maximize fisheries yield would also play a substantial role in maintaining biodiversity and vice versa. This problem is complicated by the varying life histories of marine organisms—adults can be sedentary or mobile, and larval dispersal can be over a wide range of distances, and is often poorly understood. Here we outline how various aspects of reserve design such as fraction of the coastline set aside and the size of reserves interact with life history characteristics such as dispersal distance to meet the two different goals of preserving biodiversity and increasing fishery yield. We do this for species with the kind of life history most likely to benefit from no-take zones: sedentary or nearly sedentary adults.

Initially, the two goals appear to be at cross purposes; in the case of biodiversity preservation, one might try to design reserves to minimize export of larvae from reserves, while the goal of maximizing yield might lead to the concept of maximizing export of larvae (Gue-

nette et al. 1998). It therefore appears that designing reserves will be a compromise, so the optimal solution is not obvious. Reserves or no-take zones for commercially important species certainly have benefits for other species in reducing incidental damage from harvesting (Allison et al. 1998), but this observation only begins to address the conflict in the design of reserves for the two goals of biodiversity and harvest management. For reserves designed to enhance or preserve fisheries, one baseline level of yield is that achieved by conventional management approaches based on control of effort or catch (Holland and Brazee 1996, Hastings and Botsford 1999, Sladek Nowlis and Roberts 1999). Reserve systems will always be judged relative to this alternative strategy, especially since other benefits of reserves are harder to quantify.

Our aim here is to examine carefully the solutions to the two different goals for reserve networks, with the aim of understanding how they are in conflict, and how they might both be best met within a single system of reserves. We have earlier focussed on two aspects of this problem separately—(1) the effect of reserves on maximum sustainable yield in the case of very widely dispersed larvae (ignoring aspects of reserve placement and size; Hastings and Botsford 1999) and (2) the effect of reserve design (size and spacing) on population persistence (Botsford et al. 2001)—but in neither of these studies did we consider the alternate goal.

As in our earlier work, and in much of the theoretical work on reserve design, we will use an abstract approach here, ignoring many of the complexities that would have to be taken into account when actually implementing a system of reserves. However, under-

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standing principles of reserve design in the simplest settings is an important first step that needs to be accomplished before including more realistic and site specific aspects of particular marine systems. We assume the simplest possible physical setting for our studies, assuming that the description of reserves in terms of location along shore is sufficient, so the problem becomes one-dimensional. We begin by examining at an effectively infinite coastline, ignoring the effects of range boundaries. We also ignore the role of advection, and assume a simple description of the dispersal phase. Finally, we ignore any year-to-year variability in the environment.

We also make a number of simplifying biological assumptions. As we noted, we assume that adults are sessile. We also assume that all the density dependence occurs only after dispersal, and that the density dependence depends only on the number of individuals settling. Our most important generality is that, other than these two assumptions, our results do not depend on the form of density dependence. This is important, since the form of density dependence is typically not known. We also take an explicit single species approach, ignoring the effects of any interactions between species. By using a deterministic model, we ignore any role of uncertainty or variability. Finally, detailed, explicit economic considerations are not included.

Despite the simplifications, we obtain results that are useful in providing initial intuition about the role of different goals for marine reserve design. We start by setting up a simplified model for reserve design. We then formalize the design goals for conservation and fisheries, and show that they apparently lead to different solutions. However, we then discuss how the fisheries approach could be compatible with some conservation goals.

MODELS

Our goal in this paper is to look in a quantitative fashion at this question within the context of simple deterministic models. Our model assumes sedentary adults, and that the pattern of larval movement and settlement is known. The key simplifying concept that underlies our approach is the approximation that the modeling of larval dispersal from point of release—between areas that are reserves and not reserves—can be largely separated from the population dynamics questions.

We begin with a general model that describes the larval dispersal phase of the life cycle. We assume that location along the coast is described by a single spatial variable, and ignore the effects of spatial and temporal environmental variability along this coast, as well as any effects due to the finite length of the coastline. A general description of the dynamics of a species with age structure and larval dispersal would be

$$n_1(t+1, x) = f\left(x, \left\{ \int g(y, n_1(t, y), n_2(t, y), \dots) k(x, y) dy \right\}\right) \quad (1)$$

$$n_j(t+1, x) = p_j n_{j-1}(t, x) \quad (2)$$

where $n_1(t+1, x)$ is the number of larvae per unit coastline that have dispersed to location x and survived the density-dependent phase of settling, $n_j(t+1, x)$ is the density function for the number of individuals of age j , p_j is the probability of survival from age $j-1$ to age j , $k(x, y)$ is the probability that a larvae released at location y arrives at location x , the function g describes the number of larvae released at y as a function of the individuals present at y , and the function f describes the density-dependent settling at location x .

Our analysis uses a number of simplifying assumptions, namely that dispersal depends only on the distance between release and settlement locations, $k(x, y) = k(|x - y|)$, and that the only density dependence occurs immediately after dispersal, so the function g reduces to just a constant times the sum of the adult age classes. The first assumption essentially amounts to ignoring alongshore advection, and assuming that along the coastline, there is no variation in dispersal pattern. We also assume that no reproduction takes place outside reserves, which we recognize is a simplification. However, this approach is a conservative one, and the results we present here should be viewed in that light.

This still leaves a complex problem because of the difficulty of describing the effects of dispersal over a system of marine reserves and the effects on overall population dynamics. Since very little is known empirically about the dispersal of meroplanktonic larvae, we use an approach to describing these dynamics that employs a slightly cruder description of the effects of dispersal than would result from an exact model. This approach was developed by Van Kirk and Lewis (1997) for the case of nonoverlapping generations. It essentially allows us to approximate the dynamics by expressing the density within each reserve or nonreserve area as the mean density in that area, rather than explicitly having to include the effects of varying density within each area. We do include the effect of the dispersal when determining the fraction of larvae produced in reserves that settle in reserves or settle outside. This approximation has been justified using both numerical and perturbation approaches (see Van Kirk and Lewis 1997 for details).

This approximation implies that we can describe the dynamics in terms of the mean larval density within reserves and do not have to explicitly keep track of the spatial distribution within reserves (see Fig. 1). Since we further assume an infinite coastline, we need only focus on the fraction of larvae that land inside (F) and outside ($1 - F$) reserves. We thus are able to include

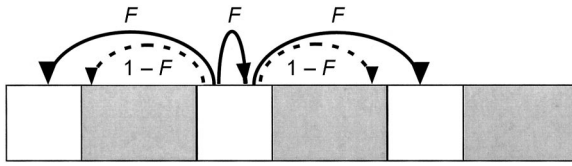


FIG. 1. Schematic representation of a network of marine reserves with reserves in white and fished areas in gray. In our analysis, we include the fraction of coastline in reserves, c , the fraction of larvae produced in reserves that are retained within reserves, F , and the fraction of larvae produced in reserves that are exported, $1 - F$.

the effects of spatial arrangement of reserves in a relatively simple formulation of population dynamics similar to our earlier work (Hastings and Botsford 1999). The difference between this and our earlier work is that here we do not assume that the density of larvae landing within reserves equals the fraction of coastline in reserves. The spatial arrangement of the reserves enters this model through F , the fraction of larvae settling within reserves, which becomes an additional control variable. We deal with the specifics of spatial arrangement (i.e., reserve width and spacing) only in terms of their effect on F , and obtain the relationship between F and spatial arrangement from our earlier work (Botsford et al. 2000), which is based on Van Kirk and Lewis (1997).

We assume that the density of organisms in the reserves is n_t^r , so the density of juveniles produced is thus cmn_t^r . The density of postdispersal juveniles therefore equals Fmn_t^r inside reserves, and $(1 - F)cmn_t^r/(1 - c)$ in the fished areas outside reserves. Thus, inside the reserves, the dynamics of the population is given by

$$n_{t+1}^r = f(Fmn_t^r) + an_t^r. \quad (3)$$

The key parameters in our model are c , the fraction of the coastline in reserves, and F , the fraction of larvae that settle inside the reserves. The per capita fecundity of adults is m . If we ignore alongshore advection, for most descriptions of larval movement the fraction of larvae produced inside reserves that settle inside reserves must be at least as large as the fraction of coastline in reserves, so $c < F < 1$. The value of F depends on the configuration of reserves (width and spacing) and the pattern of larval dispersal (Fig. 1). Note that the case $F = 1$ corresponds to no export of larvae from reserves, and the case $F = c$ corresponds to larvae that are uniformly dispersed.

We are now in a position to state the two problems of designing a reserve network for conservation and designing a reserve network for fishing in a formal fashion using the model formulation we have just developed. We can then ask how the two approaches differ.

USING RESERVES TO MAINTAIN BIODIVERSITY

One of the difficulties in attempting to conceive of design strategies for reserves for conservation is that, while several benefits can be quantified, there is seldom an obvious cost included. Here we will assume that the cost is proportional to the area or length of coastline placed in reserve, since that will presumably remove it from other uses whose benefits would be proportional to those same size measures. In our model then cost is proportional to c , the fraction of coastline placed in reserve.

The conservation problem is then to choose c so that F is at least the minimum value necessary for the species that need to be protected to persist. Furthermore, since cost is proportional to c , the optimum would be that value of c that provides the minimum required value of F . This becomes a question of reserve width and spacing which we have answered earlier (Botsford et al. 2000). There we used an approach based on the results of Van Kirk and Lewis and another ad hoc approach to compute F for a Laplacian dispersal kernel and equally spaced reserves of equal width (spacing s and width w). We indicated that the minimum value of F required for persistence was the same as the fraction of natural spawning biomass per recruit used to indicate overfishing in fisheries management (Sissenwine and Shepherd 1987, Clark 1993, Mace and Sissenwine 1993). We used a value of 0.35, though higher values have been suggested for some species—the choice for this value does not make a qualitative difference in our results. The value of c (fraction of coastline in reserves) for which F (fraction of natural recruitment maintained) exceeded the minimum value of 0.35 varied with reserve width. It was 0.35 (i.e., the same value) for small reserves relative to mean dispersal distance, but could be smaller than that value for larger reserves relative to mean dispersal distance (Fig. 2). For our

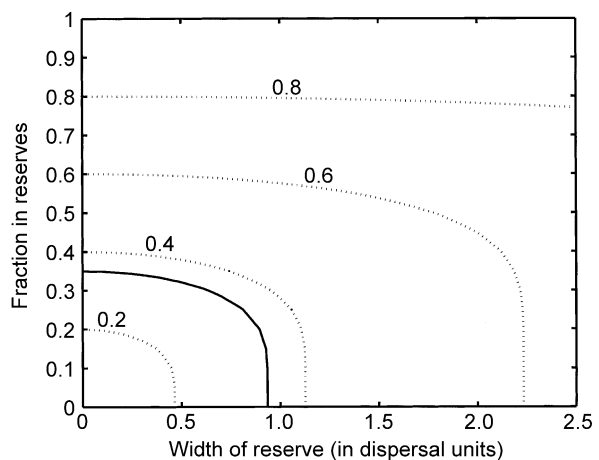


FIG. 2. Combinations of values of c and w (mean dispersal distance) that yielded a value of F of 0.35 (solid line), along with similar combinations for other values of F .

purposes here this result means that for any given mean dispersal distance, we can design a system of reserves that has either many small reserves covering 35% of the coastline or one large reserve, about nine-tenths of the mean dispersal distance in width, or any combination between these on the solid line in Fig. 2. (For different values of F , different values would need to be used.)

Note that phrasing this result in terms of dispersal distance means that, in terms of real distance measures (e.g., kilometers or miles), the optimal locus of points will vary both with the mean dispersal distance of the species of interest and the required fraction of natural settlement. This is important because when our goal is to preserve biodiversity we are interested in many species in each reserve, and species disperse over varying distances and have different life histories. However, we can resolve this problem by designing the reserve for the species with the largest required reserve size, and that design will always be more than adequate for species with lower requirements.

The solution to the conservation problem can then be obtained from the fact that the cost of reserves is proportional to the quantity c , the fraction of the coastline in reserves. The optimal solution is a single large reserve, the end of the solid line in Fig. 2 that is on the horizontal axis.

USING RESERVES TO MAXIMIZE FISHERY YIELD

We now turn to the problem of maximizing yield when by choice of both the spatial arrangement and size of reserves. For the maximum yield problem, we would first need to ensure that the population is sustained, which basically means that a high enough proportion of the larvae that are produced within reserves remain within reserves. Then one can adjust other factors to maximize the yield.

For our general model, Eq. 3, we recall that the density of larvae arriving is $(1 - F)c mn^r / (1 - c)$ in the fished areas outside reserves at the maximum yield. Hence, the sustainable yield can be found by choosing the fraction of coastline in reserves, c , to maximize the number of larvae that successfully settle outside the reserves:

$$Y_r = \max (1 - c)f[c[1 - F]mn^r / (1 - c)] \quad (4)$$

subject to the equilibrium condition from Eq. 3 that

$$n^r = f(Fmn^r) + an^r. \quad (5)$$

The maximum sustainable yield problem can then be stated as fix the level of larval retention within reserves, F , to preserve the species, and then adjust the fraction of coastline in reserves, c , to maximize yield. Note that stating the problem this way implies that as c is changed (conceptually), the width and spacing of reserves is also changed so that F remains constant (i.e., we stay on the solid line in Fig. 2). Changing the

level of larval retention would reduce reproduction per recruit to less than a sustainable level.

We would now like to know how different the answers to these problems are, and how the yield with reserves compares to the yield without reserves. Solving this problem is not straightforward in general, so we begin with a special case. If there are many small reserves, at least in the limit of infinitely many small reserves, we obtain the wide dispersal assumption, which is $F = c$. This is a problem we have solved previously, but we repeat the calculation here for completeness and because we need the results to examine the more general case. We previously showed (Hastings and Botsford 1999) that in this case, the optimal yield with reserves is the same as the optimal yield with conventional management approaches.

We rewrite the optimal yield computation in this special case to facilitate our exploration of the more complex problem. Letting $u = cn^r$, $p = 1 - c$, from Eq. 4, the maximum yield with $F = c$ is found to be

$$Y_r = \max pf(mu) \quad (6)$$

where from Eq. 5 we see that u satisfies

$$u = (1 - p)f(mu) + au. \quad (7)$$

Solving Eq. 7 for the right-hand side of Eq. 6, one sees that

$$Y_r = \max\{[f(mu) + au] - u\} \quad (8)$$

where u is the variable that can be chosen to maximize yield, which is the same maximum sustainable yield as in the conventional management models.

We now turn to the more general problem we posed above. We notice that F and c are really not independent, but that F depends on c and the configuration of the reserves, according to the results developed in Botsford et al. (2000). We now ask whether, from the viewpoint of yield, it would pay to reduce the size of the reserves while still maintaining the same level of larval retention within reserves, because then a larger area would be available for harvest. We again emphasize that we hold F , the fraction of larvae settling in reserves, constant while c is varied, by adjusting the spacing and width of reserves.

Thus, we start from our optimal solution with $c = F$, and ask what is the effect of varying c , while keeping F fixed. We begin with Eqs. 4 and 5 and note that since we assume that F is not changed, we can assume that n^r remains fixed. Thus, Eq. 5 is satisfied, and we can just examine the effect of changing c on the yield using Eq. 4, by computing dY_r/dc . Since F has been fixed, if we define the yield Y_F as a function of F and c ,

$$Y_F = (1 - c)f[c[1 - F]mn^r / (1 - c)] \quad (9)$$

we can simply compute dY_F/dc to find how the maximum yield depends on the fraction of coastline set aside for reserves. It will turn out we only need look at this

derivative at $c = F$. To facilitate calculation of this derivative, we define

$$z = c(1 - F)mn^r/(1 - c) \quad (10)$$

the argument of the density dependence function f in Eq. 9. Thus, Eq. 9 becomes

$$Y_F = (1 - c)f(z(c)). \quad (11)$$

We then calculate the derivative as

$$dY_F/dc = -f(z(c)) + (1 - c)(df/dz)(dz/dc). \quad (12)$$

Our first step in evaluating Eq. 12 is to calculate dz/dc from Eq. 10, using the fact that we noted above that the density of individuals within reserves is constant, so

$$dn^r/dc = 0. \quad (13)$$

We obtain

$$dz/dc = (1 - F)mn^r/(1 - c)^2. \quad (14)$$

We now explain how to calculate the term df/dz in Eq. 12, evaluated at $F = c$, and at the optimum choice of c obtained from Eq. 8 above. We note from Eq. 8 that the optimum choice for u is found from taking the derivative of $f(mu) + au - u$ and setting it equal to zero. (Recall that, knowing u , we can find c , as we argued above.) If we once again let z represent the argument of f , noting that at $F = c$ the argument of f in Eq. 8 equals that given in Eq. 10, at the optimum choice for u (from which we can find c):

$$\frac{d[f(z) + au - u]}{du} = 0 \quad (15)$$

where $z = mu$. So, evaluating the derivative Eq. 15, we get

$$(df/dz)m + a - 1 = 0. \quad (16)$$

Solving Eq. 16 for df/dz , we find

$$df/dz = (1 - a)/m. \quad (17)$$

In addition, solving for f in the equilibrium condition Eq. 7, we find that

$$f = n^r(1 - a). \quad (18)$$

Substituting Eqs. 14, 17, and 18 into Eq. 12, we now find that when $F = c$, and c is at the value that maximizes yield,

$$dY_F/dc = 0. \quad (20)$$

The import of this result is that fisheries yield is maximized when $c = F$, when the reserves are arranged so that export of larvae is at its maximum level possible. In contrast to the optimal design for conservation, the optimal design for fishery management is at the end of the solid line on Fig. 2 that lies on the vertical axis.

In terms of spatial arrangement, this implies that the reserves should be as small as possible. However, the

fact that this is a maximum not because of a constraint but because the derivative is zero, implies that the reduction in yield from reducing the fraction of area set aside in reserves from the optimum is very small at first.

DISCUSSION

It is important to emphasize that we are looking here only at species where adults are sessile, though this is the case where reserves are likely to be most useful (Botsford et al. 2003). The simple modeling approach exposes a possible conflict between fisheries goals and conservation goals for design of reserves. We based all our results here on the idea that altering the spacing and width of reserves changes the fraction of larvae that are retained within or exported from reserves (Botsford et al. 2000). The question then becomes what is the optimal arrangement and size of reserves.

The reserve configuration necessary for maintenance of biodiversity turns out to depend on dispersal distances and the minimum level of recruits required of the species we wish to preserve. We showed that the choice which, within a deterministic context, maintains the species with the smallest fraction of area set aside as a no-take zone is a single large reserve—large enough so that the single reserve is self-sustaining. The size of the reserve required is determined by the mean dispersal distance of the species and the recruitment level required.

For the issue of maximizing yield to a fishery, we demonstrated that the largest yield is obtained when reserves are as small as practically possible—so that the export of larvae from the reserves is maximized. This result is not unexpected, because in our previous work (Hastings and Botsford 1999), we showed that if the reserves are chosen so that export is as large as possible, the yield from a system of reserves (under our idealized assumptions) is equal to that from conventional management techniques. Thus, it is not surprising that this is in fact the largest yield possible even when the configuration (arrangement and size) of reserves is allowed to vary. We also show, however, that the yield is only slightly reduced as the arrangement of reserves moves away from this optimum. Thus, practical constraints, such as making reserves large enough to be enforced, and large enough so adults do not leave the reserves, will not significantly reduce yield.

How can one reconcile the apparently very different design optima for reserve networks to produce a single reserve network to meet both stated goals? Perhaps a reconciliation can be achieved that would lead to the design of a reserve network that would in fact meet the needs of both conservation and fisheries. Note that the optimal fisheries solution actually sets aside a larger fraction of the coastline than the optimal conservation solution, and hence would be more costly, but that the fisheries solution may be the best for conservation as

well. Note first that the broader reserve is specific to each species' characteristics, though one can simply choose the largest reserve required. The fisheries solution of many reserves should also preserve diversity, without regard to mean dispersal distances, if in fact a large enough (in fraction of the coast set aside) reserve network is used. When the reserve design is close to the vertical axis in Fig. 2, dispersal distance is less of an issue. To put this another way, a system of smaller reserves covering a greater fraction of the coast will protect a wider range of dispersal distances. In addition, the fisheries solution adds greatly to long term survival in a more realistic setting, since it ensures redundancy by suggesting that many reserves are best. Moreover, this redundancy would typically include more habitat types. Thus, the two goals of fisheries and conservation may not really be in conflict, if we recognize that fisheries approaches may be used to argue for a larger set aside area than purely conservation arguments could.

All of our results should be taken within the context of the simplifications and assumptions we have carefully outlined above. In particular, we only focus on the subset of marine species with mobile larvae and sessile adults, restrict the timing of density dependence, ignore the importance of range boundaries, interactions between species, and any details about the biological and physical environment. Many of the considerations we have ignored will further complicate the issues we discuss here, and these need urgently to be considered. We consider among the most important issues to tackle are the role of interactions among species (Beddington and Cooke 1982), the role of variability and uncertainty (Lauck et al. 1998), the role of life histories different from the ones we study here, the impact of adult movement, the role of more realistic descriptions of the physical environment (Richards et al. 1995), and the import of more realistic economic and policy aspects (Holland and Brazee 1996, Pezzey et al. 1998). In spite of these limitations, the more abstract approach we have taken here is an important first step in understanding the role and importance of reserves in marine systems, and perhaps may be the most suitable at the current state of uncertainty in parameters such as dispersal distance.

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