AVOIDING CURRENT OVERSIGHTS IN MARINE RESERVE DESIGN

Steven D. Gaines,[1] Brian Gaylord,[1] and John L. Largier[2]

[1]*Department of Ecology, Evolution, and Marine Biology and Marine Science Institute, University of California, Santa Barbara, California 93106 USA*
[2]*Marine Life Research Group, Scripps Institution of Oceanography, University of California–San Diego, La Jolla, California 92093-0209 USA*

Abstract. The pun in the above title reflects two points. First, marine life cycles commonly include a dispersive juvenile stage that is moved about by ocean currents. This stage often is the predominant, or only, means of dispersal that connects spatially disjunct populations. As a consequence, details of dispersal likely play a critical role in determining the effectiveness of marine reserves as a management and conservation tool. Curiously, however (and this is the second point of the title), although dozens of models for marine reserves now exist, few actually account explicitly for larval dispersal. Moreover, those that do include dispersal, do so almost exclusively by considering it to be a nondirectional spreading process (diffusion), ignoring the effects of directional transport by currents (advection). Here we develop a population dynamical model for marine organisms with relatively sedentary adults whose larvae are transported in a simple flow field with both diffusive spreading and directional characteristics. We find that advection can play a dominant role in determining the effectiveness of different reserve configurations. Two of the most important consequences are: (1) with strong currents, multiple reserves can be markedly more effective than single reserves of equivalent total size; and (2) in the presence of strong currents, reserves can significantly outperform traditional, effort-based management strategies in terms of fisheries yield, and do so with less risk. These results suggest that successful reserve design may require considerable new efforts to examine explicitly the role of dispersal of young.

Key words: advection; extinction; fishery yield; larval dispersal; marine reserves; model; ocean currents; persistence; population dynamics.

INTRODUCTION

The protection of marine species by the establishment of marine reserves has become an area of intense political and scientific activity (Carr and Reed 1993, Holland and Brazee 1996, Sladek-Nowlis and Roberts 1997, Allison et al. 1998, Hastings and Botsford 1999). Two broad classes of goals drive this effort: (1) conservation of populations, habitats, and biodiversity in the face of a wide range of threats from human activities, and (2) the management of biological marine resources that are extracted from the sea. While many other issues also shape the debate over the need, benefits, and optimal design of marine reserves (e.g., tourism, recreation, scientific research, and education; see Roberts et al. 2003), conservation and fisheries management play dominant roles.

Although a conceptual framework for meeting either of these two goals is still emerging, one factor is clearly crucial: connectivity, the exchange of individuals among sites. In the case of fisheries management, reserves are of no benefit to yields unless there is export of individuals from a reserve to unprotected areas that can be harvested (Polacheck 1990, DeMartini 1993). The export can be of adults, spilling across the reserve boundary (Russ and Alcala 1996), or of young (larvae or other reproductive stages) spawned from adults in the reserve that ultimately recruit to fished populations outside the reserve (Tremblay et al. 1994, Murawski et al. 2000). Similarly, in the case of biodiversity preservation, several aspects of reserve success depend on the extent of connectivity between the reserve and other locations. One is the recruitment of young into the reserve. Even if there are dramatic increases in the survival of residents within the reserve, there can be no long-term conservation benefit unless subsequent recruitment also occurs to the reserve. Such recruits could come from local retention/return of young produced within the reserve itself (Swearer et al. 1999, Warner et al. 2000), or from immigration of young produced by adults residing elsewhere (including those in other reserves). The latter situation is particularly important for reestablishing populations that have gone locally extinct.

A large number of models now explore consequences of marine reserves (see reviews by Botsford 1997, Gerber et al. 2003), most from the perspective of fisheries yields rather than species conservation (but see Botsford et al. 2001). However, despite the clear relationship between larval export/recruitment, and fishery

sustainability or species persistence, few existing models consider larval dispersal explicitly. Indeed, most existing models do not even include the larval stage in the life cycle (most are cohort models; see Gerber et al. 2003), largely because of a limited understanding of where marine larvae go while they are developing in the plankton.

In the few modeling studies that do incorporate the entire life cycle, larval movement is typically represented by one of three simple abstractions: (1) larval pool models, where larvae produced by all adults enter a common pool and are then redistributed uniformly among all local populations; (2) stepping-stone models, where adults live in discrete populations and larvae disperse to adjacent populations; and (3) pure diffusion models, where larval dispersal is modeled as a simple (typically spatially symmetrical) diffusion process among populations distributed along a coastline.

These simple abstractions of the dispersal process are good starting points, but they also share important limitations that could affect model dynamics, limitations that may not be exhibited by natural systems. First, the modal dispersal distance is typically zero in these abstractions, which means that many larvae do not disperse at all. This enhances the return of larvae to source populations, increasing the likelihood that a reserve can be self sustaining and not dependent on recruitment of larvae from unprotected regions. Second, the opposite effect also occurs. A number of models make all sites potential sources of larvae for all other sites. This may artificially inflate levels of exchange among populations that are in reality unconnected, allowing even isolated locations to be recolonized quickly by young from any other site. Third, dispersal is symmetrical around the parental population. Larvae are just as likely to disperse in one direction as another, a feature that ignores potential directional bias in real ocean currents. This last simplification discounts the importance of position along a shoreline, whereas in the real world, ''upstream'' and ''downstream'' sites may exhibit different probabilities of receiving larvae from other locations (Cowen 1985, Gaylord and Gaines 2000, Largier 2003). Such asymmetry could have dramatically different consequences for outcomes of various reserve geometries.

Although more complicated Lagrangian models of ocean circulation are emerging that may hold the capacity to describe specific trajectories of larval dispersal (e.g., Tremblay et al. 1994, Hare et al. 1999, Cowen et al. 2000) and may be useful in more detailed studies of reserve designs for particular locations (e.g., see Stockhausen et al. 2000), we believe considerable insight can be gained from an intermediate step. To this end, we develop a simple two-part conceptual framework for examining the role of ocean currents on reserve effectiveness. First, we give a brief overview of a population model for a marine species with larvae dispersing in a simplified flow field. We use this model to explore the influence of different patterns of larval dispersal on the dynamics of marine populations. Second, we expand the model to examine the effects of different reserve configurations on population dynamics. We explore issues relevant to both conservation (e.g., effects on population size and persistence) and fisheries management (e.g., yield). These theoretical treatments do not provide a complete examination of the influence of ocean circulation and larval dispersal on reserve design, but are intended instead to provide a contextual framework that we hope will spur new ideas/hypotheses to be explored in future studies.

A MODEL OF A BENTHIC POPULATION WITH DISPERSING LARVAE

We begin with a modification of a model originally developed by Roughgarden, Gaines, and Possingham (1988), and Possingham and Roughgarden (1990). This model describes the population dynamics of a species with relatively sedentary adults and dispersing larvae. The adult population is arrayed along a coastline that is bathed by an alongshore current. We ignore all spatial variation in the quality of adult habitat (e.g., essential fish habitat as discussed in Dayton et al. 2000 and modeled by Mangel 2000 and St. Mary et al. 2000). Adults release larvae into nearshore currents where they develop and are dispersed. The concentrations of larvae in the coastal ocean are defined using a simplified two-dimensional advection-diffusion equation:

$$\frac{\partial L}{\partial t} = K \left[\frac{\partial^2 L}{\partial x^2} + \frac{\partial^2 L}{\partial y^2} \right] - u \frac{\partial L}{\partial x} - v \frac{\partial L}{\partial y} - \lambda L \quad (1)$$

where L is the larval concentration per unit area of ocean, K is the eddy diffusivity, a measure of the strength of horizontal mixing, u and v are the cross-shore and alongshore velocity (mean current), respectively, and λ is the per capita larval mortality rate. Spatial coordinates x and y indicate cross-shore and alongshore position in the sea, respectively. We assume that parameters K and λ are constant in space and time, even though this will not be strictly true in nature. Appropriate values of $u, v,$ and K depend greatly on the scales of interest (see Largier 2003), in this case population scales.

The first two terms (bracketed) on the right-hand side of Eq. 1 represent changes in larval concentration due to eddy diffusion (i.e., changes in larval distributions due to random and isotropic flow fluctuations around the mean). This dispersion is nondirectional and acts to smooth out larval concentration gradients, but invokes critical implicit assumptions that may have subtle but important consequences. The third and fourth terms account for advection or displacement of larval concentration gradients (i.e., changes due to mean alongshore and cross-shore currents). The final term describes larval mortality. This two-dimensional for-

mulation approximates larvae as being uniformly distributed within a single depth layer (e.g., in the surface mixed layer of the ocean), a standard first-order simplification, but one which can be affected by up/down-welling, larval behavior, and variation in vertical mixing.

We assume that adults are sessile and follow dynamics described by

$$\frac{\partial B}{\partial t} = cFL_{\text{shore}} - \mu B \qquad (2)$$

where B is the density of adults per unit length of coastline, c is a larval settlement coefficient, F is the amount of free space available per unit length of shore, and μ is the adult mortality rate. L_{shore} is the concentration of larvae at the shore and $F = A - aB$, where A is the total area of suitable habitat per unit length of coastline and a is the age-averaged area occupied by an adult. Thus the rate of change of adult density is set by relative rates of density-dependent larval settlement and density-independent adult mortality.

The larval and adult phases are linked along the shoreline ($x = 0$) where larvae enter and exit the off-shore pool. This flux of larvae into and out of the plankton is described by

$$K\left(\frac{\partial L}{\partial x}\right)_{\text{shore}} = mB - cFL_{\text{shore}} \qquad (3)$$

where m is the per-capita larval birth rate. The first and second terms on the right-hand side represent larval release by and larval settlement into the benthic population, respectively; the difference between them quantifies the larval flux across the plane of the shoreline.

Eqs. 1–3 were originally used (Roughgarden et al. 1988, Possingham and Roughgarden 1990, Alexander and Roughgarden 1996, Connolly and Roughgarden 1998) with K, λ, c, μ, and m all held constant in both space and time. Unfortunately, such an implementation unrealistically ignores two key life-history features that affect the extent and pattern of dispersal of most marine species—constraints on larval precompetency (i.e., a period of larval development before larvae are able to settle into adult habitat) and competency (i.e., a potentially limited period of larval development during which larvae are capable of settling)—thereby excluding developmental time lags that have strong effects on the role of ocean currents in recruitment (Gaylord and Gaines 2000). Thus in earlier models larvae could settle immediately after being released, minimizing dispersal from their natal site, or alternatively live as larvae forever. To overcome these limitations in our model, we modify the rate of larval production, m, and the larval settlement coefficient, c, to be functions of time. First, we release larvae as a seasonal pulse (rather than continuously through time). Such seasonal reproduction is characteristic of many marine species, and this

simplification allows us to incorporate a more realistic larval development period (three weeks) without having to track individual larvae. Once larvae are released, we allow settlement only during a finite window (three weeks) following the explicit precompetency period. These modifications, and their implications, are discussed in greater depth by Gaylord and Gaines (2000) with respect to a range of ecological and biogeographical issues.

Eqs. 1–3 are solved over a finite computational domain that is scaled according to the distances over which the model larvae disperse. These distances are strongly a function of the flow parameters, and we explore a range of values. In flow scenarios characterized by high levels of eddy diffusion, we use a coastline that spans a 960-km stretch of shore and an adjoining 200 km wide section of coastal ocean. For scenarios with reduced eddy diffusion, we employ a domain 10 times smaller. Of the total shoreline within these domains, we assume that only the central 50% contains habitat suitable for the existence of the species of interest. This mimics a situation where a species' range is constrained by available habitat or where a population is isolated from others. This habitat geometry also minimizes edge effects due to the finite dimensions of the solution space. The oceanic boundaries are "absorbing" (i.e., $L = 0$ at the oceanic edges), which means that larvae carried out of the computational domain by advection or eddy diffusion never return to it. Although this is a simplification, the boundaries are far enough from areas where important dynamics take place that this approximation does not materially affect solutions. Eqs. 1–3 are solved numerically using standard finite difference techniques. Gaylord and Gaines (2000) describe the precise methods employed

MODEL PARAMETER VALUES

As revealed in a dimensional analysis by Gaylord and Gaines (2000), the dynamics of the model above are dominated by a quantity that represents the relative strength of advective vs. diffusive alongshore transport. Gaylord and Gaines (2000) introduce a form of the dimensionless Peclet number, Pe, (calculated in their case as $v^2 T/K$, where T is the larval precompetency duration), as a simple index of this relative transport. Largier (2003) notes equivalently that the Peclet number can be viewed as the ratio of an advective length scale to a diffusive length scale, $L_{\text{adv}}/L_{\text{diff}}$ (but note that the definition he uses is the square root of the above definition of Pe). Unfortunately, despite the importance of Pe to both the dynamics of benthic marine populations and the efficacy of the reserves designed to protect them, field data for choosing appropriate model values for K in nearshore habitats are both sparse and variable.

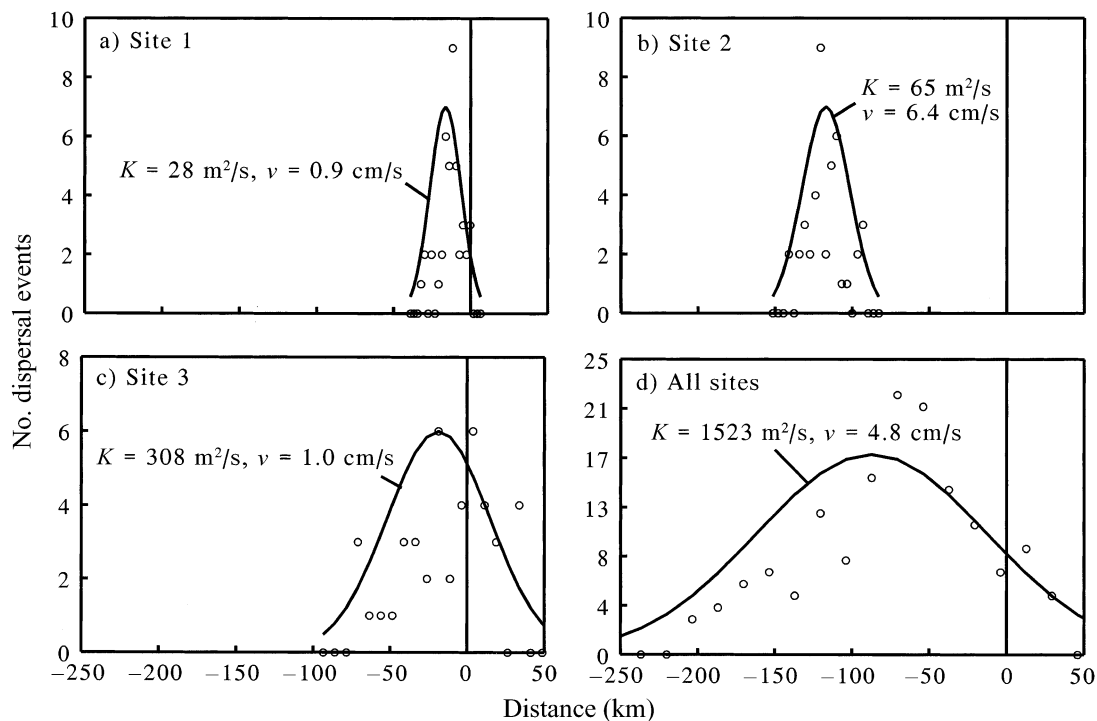To assist in placing bounds on nearshore values of K for model exploration, we present flow data from

FIG. 1. Distributions of estimated passive dispersal distance, derived from cumulative vector additions of near-surface Eulerian flow measurements conducted at three sites through a variety of seasons. Estimated dispersal distances are calculated assuming that larvae are in the water column for 3 wk. Eddy diffusivity (K) and mean velocity (v) are estimated from the flow data (Csanady 1973). Note the wide range in the relative strengths of advection and diffusion, as well as the elevated level of apparent diffusion in panel d that results from combining data from multiple locations. (a) Site 1: 34°25′30″, 119°55′54″, winter months; (b) Site 2: 34°27′42″, 120°17′24″, fall months; (c) Site 3: 34°43′36″, 120°37′36″, spring months; (d) Combined data from sites 1–3, during spring months.

three sites along the coast of central California. Fig. 1a–c depicts representative distributions of estimated alongshore transport derived from a progressive vector analysis (e.g., Washburn et al. 1999) of near-surface stationary current meter data recorded within a kilometer of shore. Velocities were integrated through multiple, successive segments of identical duration (the duration of the larval precompetency period), yielding multiple estimates (one for each segment) of effective transport distance. The overall distributions of these distances provide a first-order estimate of both mean transport distance from a given site and the level of diffusive spread about that mean. Such curves can be viewed as graphical representations of the relative strengths of advection and diffusion operating along a localized stretch of coast. When the peak of the distribution is offset substantially from zero, and the width of the distribution is narrow (as in Fig. 1b), L_{adv}/L_{diff} is large. When the peak is near zero or when the distribution is wide (as in Fig. 1c), diffusion tends to swamp the effects of advection. Clearly, as can be seen from the variability among Fig. 1a–c, the relative strengths of advection and diffusion in nature can vary widely as a function of location and season, even when the

population-biological scales (e.g., larval duration) remain constant.

The flow data of Fig. 1a–c come from sites separated by <150 km. If larvae are in the plankton long enough, and if substantial fluid exchange occurs among sites, this raises the possibility that larvae may be carried from one distinct oceanographic sector into another while dispersing. Analogous variability can occur in the mean pattern of flow over time (e.g., due to seasonal or interannual variability in circulation). Therefore, larvae released at different times within a reproductive season or in different years may experience different patterns of dispersal. Two standard methods exist for coping with such spatial or temporal variability: (1) account explicitly for regional or temporal differences in the mean flow field or (2) approximate the effects of spatial/temporal variation in the mean flow as elevated diffusion. The effects of the latter approach can be seen in Fig. 1d, where we have manufactured an artificial analogue to a region of strong spatial and temporal variability by combining data from sites a to c. The result is a marked increase in the apparent strength of diffusion (see also Largier 2003). Note, however, that, although it is appropriate to incorporate

TABLE 1. Model parameters.

Parameter	Description	Value
A	total available area per meter of shoreline, m	1
a	adult basal area, m²	1×10^{-4}
λ	larval death rate, s^{-1}	5.6×10^{-7}
μ	adult death rate, s^{-1}	variable
m	larvae produced per adult per year	1×10^5
K	eddy diffusivity, m²/s	10–1000
c	larval settlement rate, s^{-1}	5×10^{-5}
d	larval precompetency and competency duration, s	1.8×10^6

variability at scales smaller than population scales into a constant K when the variability is random and characterized by a single length scale (Okubo 1980), the implicit spatial or temporal aliasing when these restrictions are not met can obscure important patterns.

Additional information on model parameter values is given in Table 1. The primary literature sources for these values are provided and discussed by Gaylord and Gaines (2000). Values for the biological variables are based loosely on barnacle life histories (one of the few invertebrates for which sufficient data exist to allow estimation of both benthic and larval demographic parameters). Physical parameters are based on mean flow rates and levels of horizontal mixing expected in many oceanographic environments at the temporal and spatial scales we consider. Note that we examine here only an isolated population in an alongshore current, for example we exclude offshore export through upwelling (i.e., $u = 0$), to focus on implications of the simplest possible advective current field where there is no intrinsic capacity for larval retention, and where there is no larval input from other sources (perhaps the most challenging scenario from the view of resource managers). Gaylord and Gaines (2000) examine the dynamics of populations subjected to a greater diversity of flow fields in the broader context of a study of the causes of species borders.

PERSISTENCE OF MODEL POPULATIONS

In their original 1990 work, Possingham and Roughgarden noted a strong susceptibility of benthic populations with dispersing larvae to strong alongshore currents. They showed that rapid flows might sweep larvae downstream away from suitable habitat, preventing sufficient settlement to offset adult mortality, and causing a population to slowly ''slide'' downstream to extinction. Our modified model predicts a similar potential susceptibility to alongshore flow, even at speeds that can be typical of long-term mean flow rates in nature (1–2 cm/s; Fig. 2). Such results led Gaylord and Gaines (2000) to suggest that benthic marine populations with dispersing larvae may sometimes require specific mechanisms of larval retention and/or upstream sources of larvae for persistence (see also Cowen 1985 for early discussions of such source–sink concepts).

An additional important feature of the predicted vulnerability of populations to flow is the threshold nature of the vulnerability. Fig. 3 demonstrates that the transition from population persistence to extinction as flow speeds increase may be quite abrupt. At low rates of
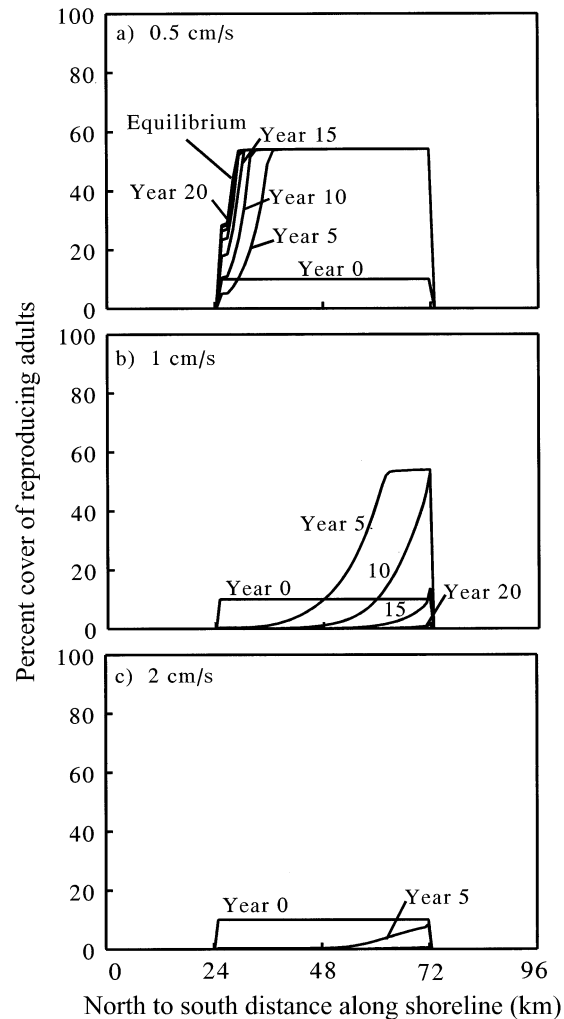

FIG. 2. Predicted adult shoreline distributions resulting from a uniform, constant, alongshore flow field: (a) $v = 0.5$ cm/s; (b) $v = 1$ cm/s; (c) $v = 2$ cm/s. The yearly adult mortality rate is assumed to be 50%, and the eddy diffusivity is 10 m²/s. See Table 1 for other model parameter values.
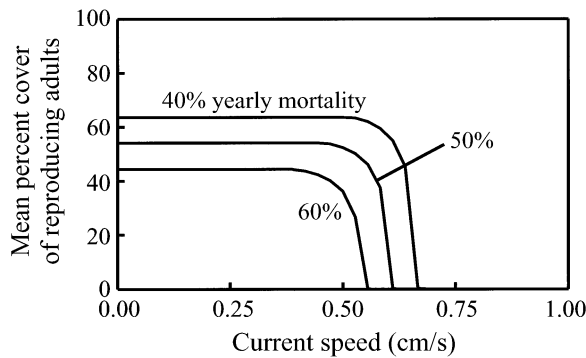
FIG. 3. Threshold effect of increasing flow rate on population persistence in a uniform, constant, alongshore flow field. The eddy diffusivity is 10 m²/s.

advection, the population size of adults on the shoreline is largely independent of mean current speed, as upstream diffusive fluxes counterbalance downstream advective fluxes. As velocities increase, however, there is an abrupt transition from the velocity-independent phase to conditions where advection overcomes diffusion and "washout" losses of larvae drive the species extinct. There is only a narrow range of mean velocities (the knees of the curves in Fig. 3) where advection alters population size without driving the species extinct.

Changes in adult mortality also interact with flow rate with two further implications. First, at low velocities, where population size is roughly constant, total population size increases as adult mortality rate declines. Second, the knee of the abundance/velocity curve slides to slower current speeds as mortality rate rises. This effect of mortality on the critical velocity for persistence suggests that human impacts on marine populations could have an important step-like effect. Activities that increase the mean mortality of adults (such as fishing, habitat destruction, or pollutants) might reduce the overall population size of impacted species, while simultaneously lowering the critical mean velocity. If the threshold velocity is reduced enough, mean velocities that would normally have little impact on the population size of a marine species could suddenly and unexpectedly provide an important driving force towards extinction (Fig. 3).

Figs. 2 and 3 examine the ability of marine populations to persist in the face of an invariant mean current field characterized by some specified level of eddy diffusion. Real ocean currents, however, may often exhibit greater variability. Eddy diffusion can be substantially higher with values of K of order 100 or 1000 m²/s (Fig. 1). The resulting enhanced diffusive spread of larvae can counteract downstream advective flux and potentially mitigate the "washout" effect (Fig. 4). Threshold velocities for population persistence (where advective fluxes start to overwhelm diffusive fluxes) are shifted to faster speeds. Close examination of the

model runs reveals that the critical velocity for each value of K corresponds to the same Peclet number. As a result, large increases in K lead to substantially smaller increases in the critical velocity for population persistence (Fig. 4). Since the Peclet number scales as the square of velocity, but linearly with K, the critical velocity increases as the square root of increases in K.

In addition to the quasi-random variability of elevated diffusion, there is also large-scale environmental variability that must be explicitly resolved as time or space dependence of the advection or diffusion terms in Eq. 1. For example, Gaylord and Gaines (2000) explicitly resolve large-scale spatial variability and year to year reversals in flow as deterministic variability in the mean velocity under conditions of large Pe. Their results suggest that infrequent directional changes in mean flow can interrupt predicted extinction trajectories by allowing intermittent bouts of exceptional recruitment to previously "upstream" populations.

The above impacts of circulation on population dynamics and persistence raise the question whether the effectiveness of marine reserves as conservation and resource management tools similarly depends on the pattern and variability of circulation. To explore this issue, we examine the effects of reserve size and configuration under a range of flow conditions, including widely varying Peclet numbers and explicit temporal variability in the mean flow.

MODELS INCORPORATING MARINE RESERVES

The restrictions imposed on human activities in marine reserves are designed to lower mortality rates of marine organisms within reserve boundaries. This effect can be mimicked by making mortality rates spatially explicit, with certain sections of coastline (reserves) having lower adult mortality rates than others. In our model, this is accomplished by defining μ as a function of position, with yearly mortality rates within reserves set to 20% and mortality in unprotected re-
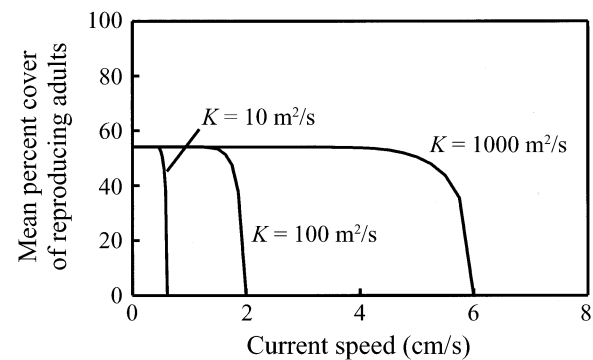

FIG. 4. Influence on persistence of the level of eddy diffusion in a uniform, constant, alongshore flow field. The yearly adult mortality rate is assumed to be 50%. Note that a 100-fold increase in the eddy diffusivity shifts the predicted critical velocity by only a factor of 10 (constant Pe).
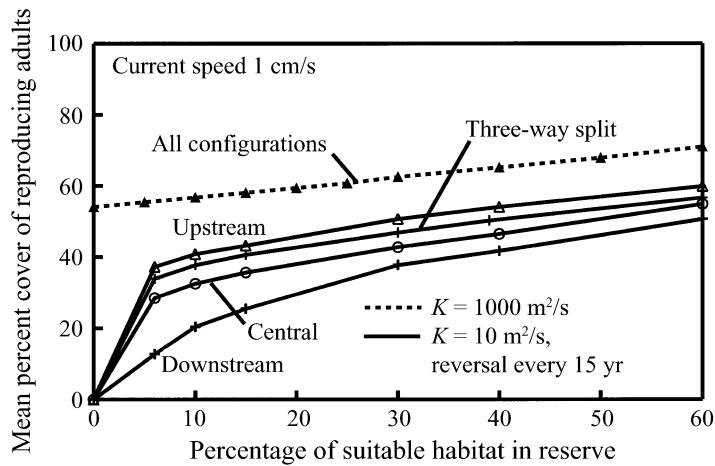
FIG. 5. Effect of reserve configuration and size on population abundance in a uniform alongshore flow of 1 cm/s. The dashed line corresponds to large diffusivity, $K = 1000$ m²/s, whereas solid lines correspond a scenario of small K, with flow reversals occasionally. Reserve configuration (i.e., upstream, central, downstream, or three-way split) matters in all cases where eddy diffusion does not dominate advection. Adult mortality rate is 50% outside a reserve, and 20% inside.

gions set to 50%. We then use our modified model with spatially explicit mortality to examine the influence of reserve size, spacing, number, and location. Given the diversity of goals set for marine reserves, we assess their impacts on three criteria: population persistence, total population size, and enhancement of economically important marine resources outside the reserves.

Effects of reserve size on population persistence

Our model suggests that reduced adult mortality inside reserves might enhance population persistence in at least two ways. First, since adult mortality rates alter the threshold for advection-driven extinction (Fig. 3), reserves could lower the risk of extinction simply by reducing mean mortality and shifting the knee of the abundance/velocity curve to the right. The ultimate direct benefits of this process are likely limited to specific cases where the flow conditions are close to critical Pe values, since even a marked rise in mean survivorship produces only a modest increase in the critical velocity. A second, perhaps more important, advantage of a reserve is that even if reduced mortality within reserves is insufficient to shift a population to the left of a velocity threshold, this reduced mortality could extend the time to extinction enough to capture long-term flow variability. Because the key to persistence is a capacity to restock upstream populations (Gaylord and Gaines 2000), sufficiently large variation in the mean flow can allow downstream advective losses such as those seen in Fig. 2b and c to be counteracted by occasional reductions in flow speed or reversals in the average current direction.

Effects of reserve size on population abundance

As noted already, the effects of elevated flow variability in models such as ours are typically examined in one of two ways—by increasing the strength of diffusion (i.e., by increasing L_{diff}) or by detailing explicitly deviations from the mean flow. Both forms of vari-

ability would be expected to offset advective losses, but would do so in somewhat different ways, with different consequences. For instance, if K is increased to a value of 1000 m²/s, populations persist even without reserves, up to more rapid flow rates (Fig. 4). The effect of a marine reserve in this situation is to cause the abundance of adults to rise linearly with the fraction of habitat in the reserve (Fig. 5, dashed line). In contrast, if the diffusive component of flow is held relatively small and variations in the mean flow are modeled explicitly (we use a simple example where $K = 10$ m²/s and mean currents of 1 cm/s reverse for 1 yr, every 15 yr), we would predict that an isolated population would be unable to persist in the absence of a reserve (Fig. 5, solid curves). In this case the addition of a reserve, even a small one encompassing only 5% of the total available habitat, causes an important transition to persistence. Further increases in reserve size produce monotonic increases in abundance.

Effects of reserve configuration on population persistence and abundance

Four reserve scenarios are explored in Fig. 5—a reserve at the upstream end of the habitat, a reserve at the downstream end, a reserve in mid-domain, and a set of three reserves of equivalent total size with one reserve each at upstream, downstream and mid-domain regions (see Crowder et al. 2000 for similar comparisons of reserve configuration but with simple stepping stone links between reserves.) The multiple curves in Fig. 5 indicate that the nature of flow variability can interact with reserve geometry to influence the outcome of a reserve, just as it did with reserve size. Where deviations from the mean velocity field are represented as enhanced horizontal diffusion, then symmetrical spreading dominates and reserve location becomes less important (Fig. 5, dashed line). For this to be true, L_{diff} must be comparable with the size of the reserve, L_{res}, and L_{adv} must be small. In contrast, if L_{diff} is relatively

small and L_{adv} is large, we find that reserve location plays a strong role. Thus, a single upstream reserve, a single reserve in the middle of suitable habitat, a single downstream reserve, and a system of three reserves of equivalent total size—one upstream, one centered, and one downstream—can all have different consequences (Fig. 5, solid lines). In this case, the upstream reserve results in the highest population abundance, with the three-way split reserve offering comparable population benefits.

Population abundance in the face of heavy exploitation

Up to this point, we have examined scenarios where mortality rates outside the reserve are not extreme (50% vs. 20% within the reserve). One driving force behind the establishment of reserves, however, is significant declines in population sizes in areas subjected to human disturbance, an indication of high rates of mortality in unprotected locations. In such cases, greater differences in reserve and nonreserve mortality rates may alter the way currents interact with reserve configuration. This possibility arises because larval production by adults outside reserves can make key contributions to recruitment within the reserve. For example, upstream reserves may receive recruits from downstream unprotected areas during flow reversals, and downstream reserves may receive recruits from upstream unprotected populations in years immediately following flow reversals. These processes each tend to periodically reestablish a species' range after contractions produced by advective losses in more typical years.

However, if unprotected areas outside reserves have substantially higher mortality, then few larvae will be produced outside reserve boundaries. This means that reserve populations will depend for the most part on local recruitment and larval input from other reserves. Under some circumstances, such a feature could alter dramatically the effectiveness of a given reserve configuration. For example, a single reserve would become almost entirely dependent on larvae that did not move beyond the reserve boundary (e.g., see Botsford et al. 2001), a problematic requirement for broadly dispersing species, particularly if L_{adv}/L_{diff} is large (see Largier 2003).

To address this issue of high mortality rates in unprotected areas, we focus on an extreme case. We assume exceptionally severe human impacts outside reserves such that nonreserve yearly survivorship is only 1%. As in previous model runs, yearly survivorship within reserves remains at 80%. Fig. 6 addresses this example of heavy exploitation: trajectories of population abundance for a species that has 30% of its habitat protected in one of the same four reserve geometries examined in Fig. 5. Once again, we observe a strong sensitivity to the nature of the flow variability
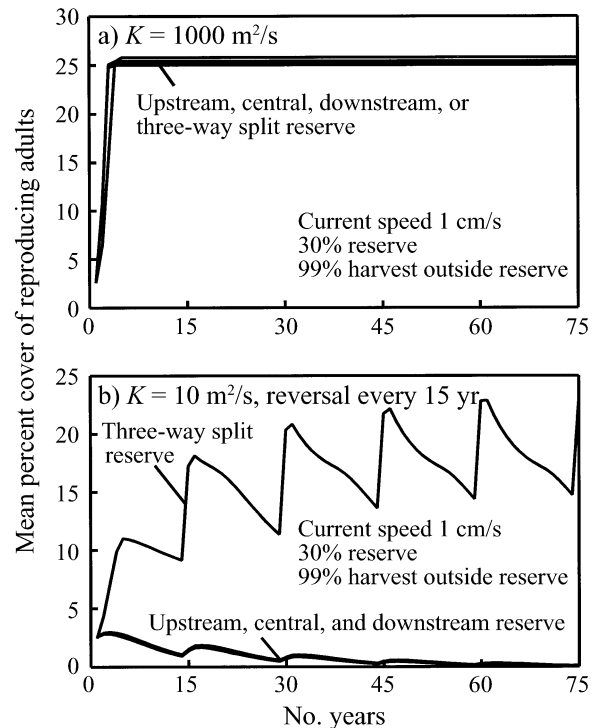

FIG. 6. Effect of reserves that encompass 30% of available habitat, for a variety of reserve configurations and two types of flow variability. (a) Time series of abundance for a high-diffusion scenario. (b) Time series of abundance for a low-diffusion scenario, but with occasional flow reversals. In the case of the upper panel, there is a predicted equilibrium level and no subsequent change in abundance through time. There is also no effect of reserve configuration. In the case of the lower panel, not only does a single reserve not allow for persistence, while a multiple reserve system of the same total size does, but the potential for substantial temporal changes in abundance emerges. Adult mortality rates are 20% within the reserves.

in the system. With fluctuations that are essentially diffusive, abundances reach an invariant equilibrium level (Fig. 6a), because there is adequate recruitment back to the reserve. By contrast, under the occasional flow reversal scenario (where L_{adv}/L_{diff} and L_{adv}/L_{res} are both large), reserve configuration is strikingly important. Even with a large fraction (30%) of the coastline set aside in reserves, all of the populations supported by a single reserve go extinct for exactly the reason mentioned above—the vast majority of larvae produced in the reserve are transported beyond the borders of the reserve to sites where they have little chance of becoming reproductive adults. Thus, we find that if L_{adv}/L_{diff} and L_{adv}/L_{res} are large, a single reserve is ineffective regardless of its location.

With the three-way split (i.e., multiple-reserve) system, on the other hand, even for the subset of challenging physical conditions where L_{adv}/L_{diff} and L_{adv}/L_{res} are large, a thriving population is supported (Fig. 6b). In this case, the advection of larvae plays a different
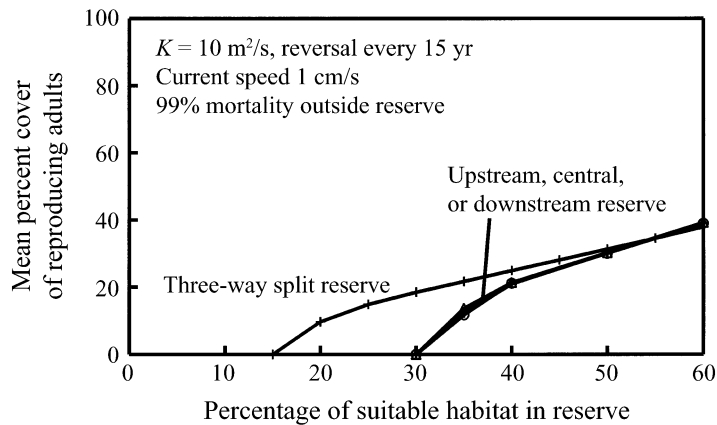
FIG. 7. Flow scenario of Fig. 6b explored for a wider range of reserve sizes. Increased adult mortality in unprotected regions greatly enhances the benefits of a multiple-reserve system over single reserves of equivalent total size (compare curves to analogous solid lines in Fig. 5 where adult mortality rates outside reserves are 50%, rather than 99%). Adult mortality rates are again 20% inside reserves.

role. Dispersal beyond the reserve boundary provides a mechanism for moving larvae among reserves. In the case of a rapid constant flow, such connectivity between reserves would be unable to keep a population from going extinct since the upstream reserve would never have a larval source. In the presence of directional variability in flow, however, all reserves at least occasionally receive larvae from some other reserve. Although the effectiveness of this mechanism for persistence depends on the spacing of reserves relative to the length scales of advection and diffusion, the data of Fig. 6b suggest that when flow occasionally varies in direction, multiple reserves may often possess substantial advantages over single reserves of equivalent total size.

These advantages will be most evident when large differences in survivorship exist between reserve and nonreserve regions, and when $L_{adv} - L_{diff}$ is greater than the length of an individual reserve component. In contrast, as we saw in Fig. 6a, if L_{diff} is large (and $L_{adv} - L_{diff}$ small or negative), the enhanced spread of larvae around the mean transport distance allows larvae to more readily reach protected habitat from a wider range of original locations, reducing the importance of reserve configuration.

The above advantages of multiple reserves under directional (but reversing) flow conditions were explored in Fig. 6b only for a single reserve fraction, 30% of the coastline set aside. We can, however, expand our view to examine how these benefits vary across a wider range of reserve sizes (Fig. 7). Given the same flow conditions as in Fig. 6b, all populations go extinct if <15% of the habitat is protected. For reserve fractions of 15–30%, a system of three reserves supports a persistent population, while single reserves are universally ineffective. It isn't until the reserve fraction becomes quite large ($L_{res} > L_{adv} - L_{diff}$) that all four reserve configurations allow persistence. The advantages of the system of multiple small reserves might also be expected to hold across a much broader array of flow

conditions than we explore here, since larval exchange can occur among different combinations of reserves under different velocity conditions (see also Stockhausen et al. 2000). In contrast, because single reserves must always subsist on propagules from adults within that reserve, they will be more vulnerable to essentially all conditions of faster flow speeds where L_{adv}/L_{diff} and L_{adv}/L_{res} are large.

Effect of reserves on managed marine resources

The apparent superiority under many conditions of the multiple reserve configuration raises a question. In the limit, as the number of reserves increases while their size decreases (to maintain a constant reserve fraction), one approaches a situation with essentially a uniform, but intermediate level of survivorship everywhere. In some sense this resembles the outcome from an effort-based management strategy where limits on take or fishing effort set mean survivorship. Is it possible, then, that the most efficient implementation of reserve strategies simply approaches an effort-based policy?

Much of the existing modeling of marine reserves has addressed the effectiveness of marine reserves as a fishery management tool relative to more traditional approaches (see Gerber et al. 2003 for review). Botsford et al. (2001) argue that the results from a wide range of modeling studies suggest four key principles. Two equate the use of marine reserves to standard practices in effort-based management—the effect of reserves on the yield achieved per recruit to the population is similar to regulating size limits (their principle 1; Beverton and Holt 1957, Guenette et al. 1998), and the effects of reserves on total yield is similar to regulating the mortality rate (their principle 2; Quinn et al. 1993, Holland and Brazee 1996, Hastings and Botsford 1999, Guennette and Pitcher 1999). Indeed, Hastings and Botsford (1999) have shown with a simple analytical model that resource management based on controlling effort is equivalent to resource management

based on controlling real estate when larvae disperse into a common larval pool. Given the finding that traditional approaches can be equally effective as management by reserves, or alternatively that reserves can increase yields only when fishing mortality exceeds the point of optimum yield, the value of reserves has increasingly been discussed in terms of benefits other than increasing yields (e.g., as a hedge against uncertainty, as an alternative when effort cannot be controlled, as a means of reducing incidental effects such as habitat destruction (Lauck et al. 1998), as a means of countering selection by fishing for early age of maturity and small size (Trexler and Travis 2000) or as a means of conservation of biodiversity (see Botsford et al. 1997). Few of these modeling efforts, however, have considered the impact of larval dispersal explicitly (see Quinn et al. 1993). Fewer still have examined the role of directional currents (but see Crowder et al. 2000, Stockhausen et al. 2000). Given the potential impact of advection on population persistence and population size shown above, we ask briefly whether advective flows can play equally important roles in the impact of marine reserves as resource management tools.

To address the role of reserves vs. other forms of fishery management in the face of current-driven larval dispersal, we compare two simple management scenarios. First, we regulate the fishery through protection of some fraction of the habitat in marine reserves. Second, we regulate the fishery by setting the fraction of the standing stock of adults that can be collected each year (which sets the mortality rate of adults above the background mortality rate). As above, this modeling exercise is not an exhaustive consideration of a wide range of physical conditions and species attributes. Rather, we explore a few example scenarios to test whether the advective/diffusive characteristics of dispersal can alter the relative effectiveness of the two management strategies.

We consider three different rates of mean advection (0.5, 1, and 2 cm/s), and model variability in flow about these mean speeds using the same two general constructs as before: a simple isotropic diffusion scenario with large K, and an explicitly reversing flow field with smaller K. We assume that in the absence of fishing, yearly survivorship of adults is 80%. For the reserve management scheme, we employ a system of three reserves (upstream, center, and downstream). We put no constraints on fishing outside the reserves and assume that the vast majority of unprotected adults are collected each year (leading to a 99% yearly mortality rate outside reserves, with 20% inside). Figs. 8a and b and 9a and b plot the mean fishery yield and mean population size, respectively, resulting from setting aside differing fractions of the coast in reserves. By comparison, Figs. 8c and d and 9c and d plot the mean fishery yield and mean population size, respectively, for different harvested fractions of the population. Note

that the level of protection from fishing increases from left to right in all figures. For reserves, protection increases as the fraction of habitat in reserves increases. For quota control, protection increases as the fraction of the population harvested declines.

Considering the effect on yield first, both management approaches generate yield vs. level of protection curves that peak at intermediate levels of protection (Fig. 8). This functional form is characteristic of findings from nearly all models of fisheries management. The influence of current speed on yield is negligible when K is large (more precisely, when L_{adv}/L_{diff} is small; Fig. 8a, c), and pronounced when K is small (more precisely, when L_{adv}/L_{diff} is large; Fig. 8b, d). In those cases where currents do matter, faster velocities decrease yields at all levels of protection under either management scheme, and increase the fraction of the population that must be protected to achieve optimal yields.

The differences in consequences of management strategy can be summarized as follows:

1) Maximum yields from reserves range from being modestly lower ($K = 1000$ m²/s) to substantially higher ($K = 10$ m²/s) than those from quotas.

2) The yield vs. protection curves are broader and typically flatter near the peaks for reserve management than for quota management. As a result:

a) Errors in estimating the optimal reserve fraction would have smaller impacts on yield than errors in setting the optimal quota. For example, with $K = 10$ m²/s and $v = 0.5$ cm/s, reserve fractions between 5% and 60% all exceed the maximum yield from quota based management.

b) Yields from quota management fall off abruptly to the left of their peaks (i.e., where the fraction of the population fished exceeds optimal levels). Thus, populations go extinct when the fraction fished slightly exceeds optimal values. This abrupt transition and sensitivity to uncertainty is widely found in models of quota and effort based management (see Ludwig et al. 1993, Botsford et al. 1997, Roughgarden 1998).

c) Yields fall much more gradually if the reserve fraction is less than optimal. For both levels of eddy diffusion that we explore and all three current speeds, populations persist even when reserve protection is only 60% of the optimal value.

With respect to population size, both management strategies lead to declining total population sizes as the level of protection drops (Fig. 9). As with yield, the strength of the effect can increase strongly with current velocity, but only when K is small. At all velocities and levels of diffusion, however, population sizes decline more rapidly with quota management as the protection level decreases, than with reserve management. Therefore, consistent with the results for yields, suboptimal choices with quota management are far more likely to lead to extinction.
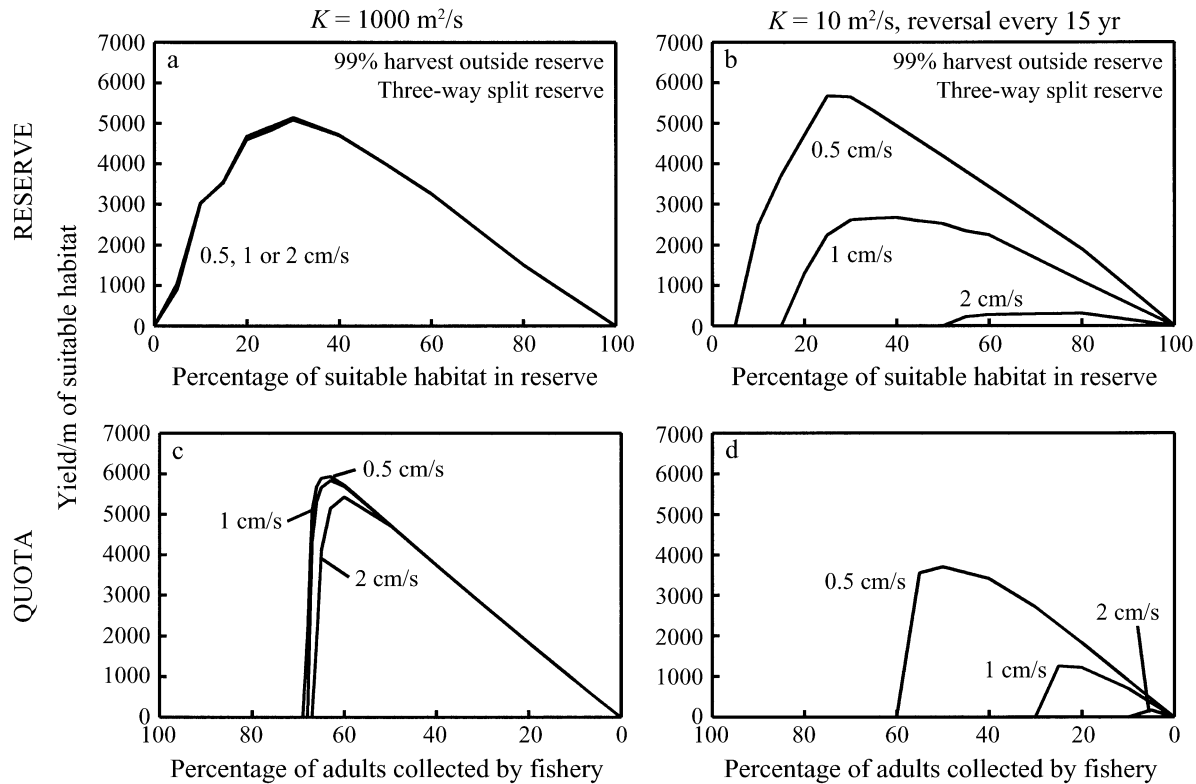
FIG. 8. Yield as a function of the level of fishery protection, for two different management strategies, under conditions of two different types of flow variability. (a) Reserve management strategy, with 20% yearly adult reserve mortality, in a strongly diffusive flow. (b) Reserve management strategy, with 20% yearly adult reserve mortality, in a reversing flow with reduced eddy diffusion. (c) Effort-based management strategy, in a strongly diffusive flow. (d) Effort-based management strategy, in a reversing flow with reduced eddy diffusion. Results for three different alongshore current speeds are shown.

Finally, Fig. 10 combines the effects of the two protection schemes on yield and abundance by examining yield as a function of population size. This measures the resource benefit (in terms of fisheries yield) as a function of the mean abundance of adults. The results again show that the character of flow variability can have important consequences. If variability is treated as diffusion, one would predict that quota methods provide slightly greater yields for a given population size than reserve strategies. This feature presumably arises because of the tendency for uniformly lower abundance levels in the quota system, which prevents any strong density dependent reductions in larval settlement that might otherwise arise within densely packed reserves. However, even moderate increases in the mean flow rate (actually, increases in L_{adv}/L_{diff}), begin to offset the potential advantages of the quota scheme (compare Fig. 10a and c). Indeed, with sufficiently large increases in the strength of advection relative to diffusion, the picture is reversed, and clear benefits of the reserve management approach emerge. In such situations, the often higher yields observed in Fig. 8 for the reserve management strategy are not simply a consequence of the maintenance of higher population sizes (Fig. 9). When

the effect of population size is removed, the advantage of the reserve-based strategy is still substantial. Thus, for cases where advection is not dominated by diffusion, the reserve based approach provides, in essence, both conservation and fisheries benefits at the same time. Population sizes are increased relative to the optimal quota approach (enhancing the conservation benefit), while yields from the fishery are simultaneously increased.

REPRESENTING FLOW VARIABILITY AS EDDY DIFFUSION

In any discussion of the effects of currents on population dynamics and marine reserves, it is necessary to adequately account for the nature of flow variability about the mean flow velocity. Largier (2003) emphasizes that the flow parameters used in advection–diffusion analyses should be those that operate at the temporal and spatial scales defining the question of interest. For issues of reserve design and protection of marine resources, these scales are those of the population, and may span tens to even hundreds of kilometers and several years. Quasi-random variability at time and space scales smaller than these population scales may,
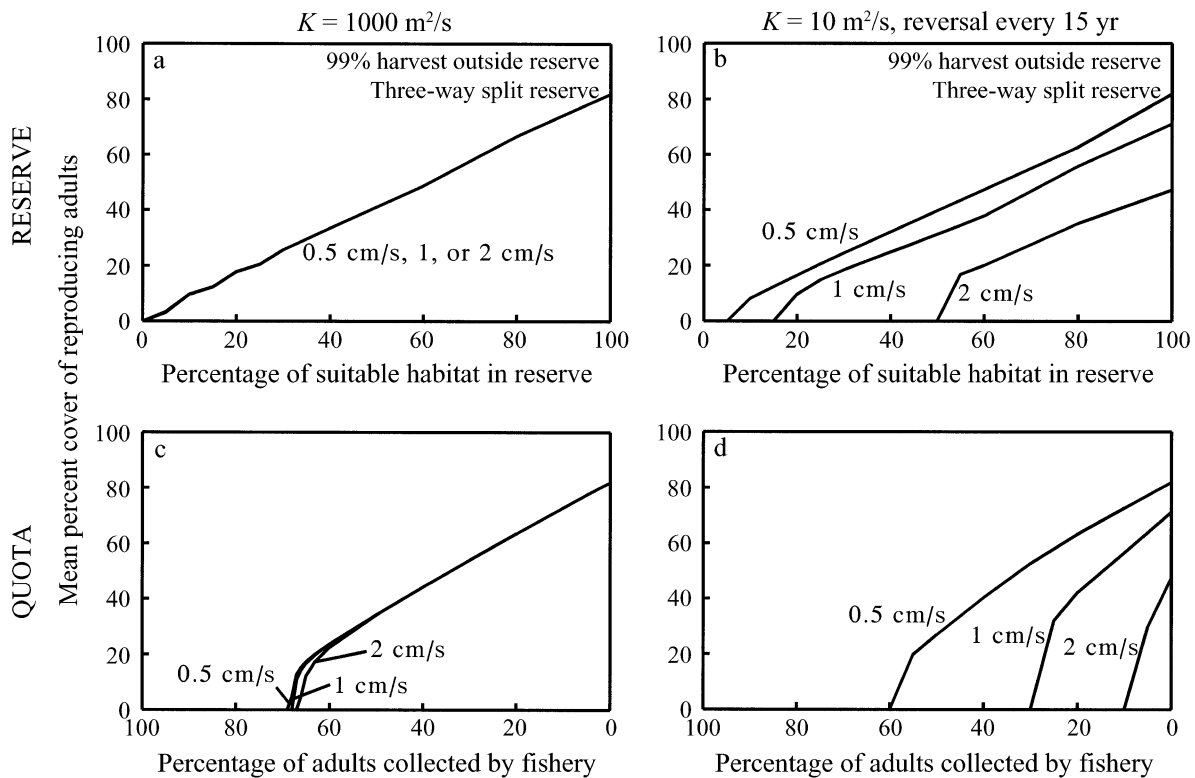
Fig. 9. Adult population size as a function of the level of fishery protection, for two different management strategies, under conditions of two different types of flow variability. (a) Reserve management strategy, with 20% yearly adult reserve mortality, in a strongly diffusive flow. (b) Reserve management strategy, with 20% yearly adult reserve mortality, in a reversing flow with reduced eddy diffusion. (c) Effort-based management strategy, in a strongly diffusive flow. (d) Effort-based management strategy, in a reversing flow with reduced eddy diffusion. Results for three different alongshore current speeds are shown.

in many circumstances, be adequately represented as a bidirectional spreading of dispersing larvae. However, there may also be nonrandom fluctuations and large-scale variability that cannot be aggregated in this way. For example, there is increasing empirical evidence that such large-scale spatial and temporal variation in advection can dominate diffusive flows and affect population dynamics and distributions (Cowen 1985, Roughgarden et al. 1988, Wares et al. 2001). Furthermore, environmental variability may not be fully independent of population factors—specifically, one can think of an example where southward flows correlate with high larval concentrations and a simple diffusion approach would yield incorrect predictions. Thus, although our knowledge of larval dispersal is poor, requiring that we often resort to simplified parameterizations of flow variability, it is clear that one has to be careful about the scale over which one aggregates. Largier (2003) discusses this issue in more depth.

We can offer at least two scenarios in particular where ecological pattern might be obscured by modeling large-scale variability as eddy diffusion. Compare, for example, the two time series of mean percent cover in Fig. 6a and b. In Fig. 6b, temporal variability

in the flow is modeled as a periodic reversal (see also Gaylord and Gaines 2000). Under these circumstances, we found that the persistent population never reached equilibrium but instead progressed at steady state, declining and recovering through time. Given these temporal changes in abundance, the roles of density-dependent factors might be expected to also change through time (we might imagine, for instance, a situation where increased per capita predation at low abundance exacerbates threats to a prey species, or where recruitment limitation arises during episodes of high abundance). Furthermore, if there is additional stochastic behavior built into the system, unpredictable abundance shifts could exacerbate extinction risks during years of already-low population size. If the large-scale temporal variability in flow is incorporated simply as increased eddy diffusion, one obtains results similar to Fig. 6a, which misses the above complications, many of which could strongly influence a species' ability to persist.

The second scenario where an eddy diffusion tack might obscure pattern is where persistent spatial features in the flow are modeled simply as variability. Consider the converging flow field of Fig. 11a. The
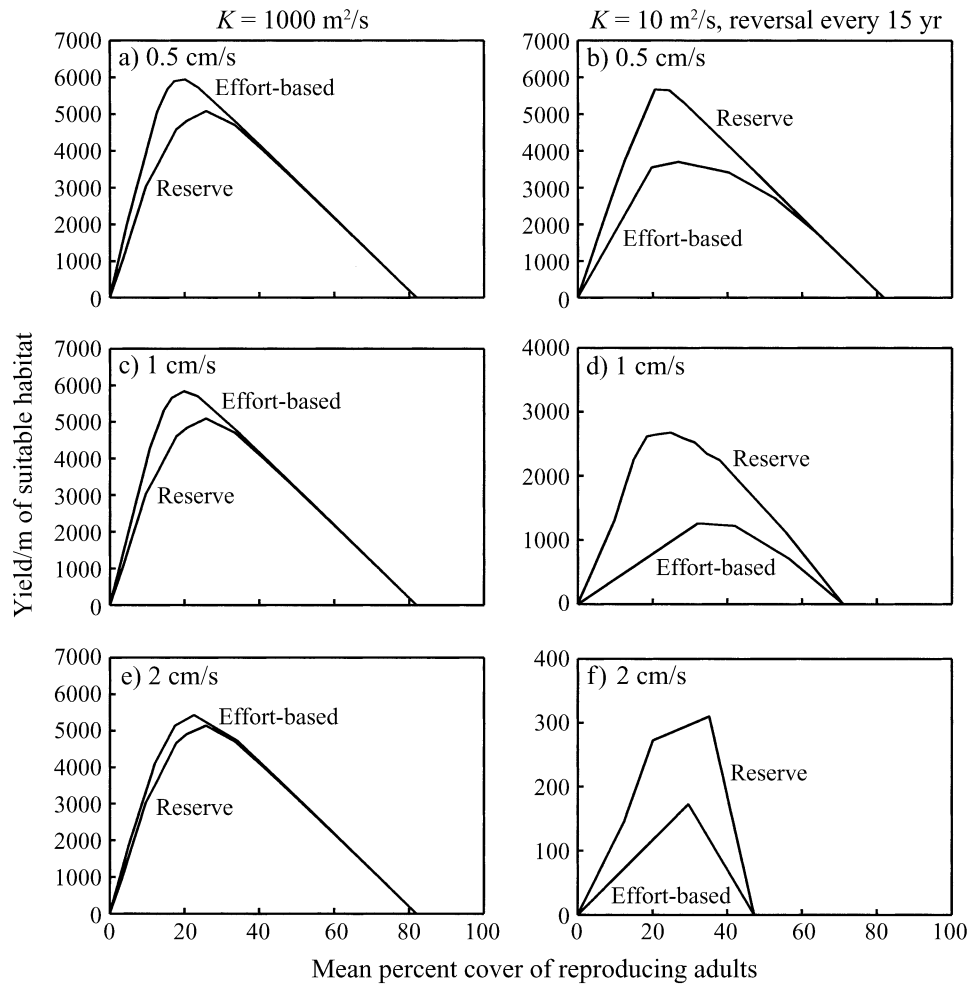
FIG. 10. Yield per adult population size, for reserve or effort-based management, under two different types of flow variability and three current speeds. Yearly adult reserve mortality rates are 20%.

mean flows recorded at two stations north and south of the convergence are assumed to be of equal but opposite magnitude. Random flow motions around these means introduce some variability, and two separate distributions of dispersal distance ensue, one for each station. If data from these two measurement stations are combined, however (Fig. 11b), the apparent mean advection drops to zero, and the apparent random variability greatly increases (as we saw, for example, when K rose to 1500 m²/s after we manufactured the composite Fig. 1d). In fact, if there is much noise in the station-specific distribution estimates, the bimodal character of the composite distribution could easily become obscured, providing no clue as to the true discontinuity in the flow field. Clearly, predicting dispersal consequences based on such composite information could lead to far different conclusions than an analysis that explicitly incorporates the nonrandom current features of a flow field with specific spatial character (e.g., Gaylord and Gaines 2000).

CONCLUSIONS

Nearly all papers published on marine reserves raise three questions: how big should they be, where should they be, and how many should we have? Size, location, and number are the three focal issues. The question of interreserve spacing is implicit in this. Despite posing these three questions, however, theoretical studies of marine reserves have ultimately provided substantial insight into only the first—the ideal marine reserve size. From the perspective of both species persistence and resource management, models of reserves have predicted responses that scale with reserve size. Typically the response is nonlinear (e.g., fisheries yields peak at intermediate reserve size). These findings are beginning to provide a framework for decision makers that can help establish goals for the fraction of marine habitat set aside in reserves.

By contrast, we have gained only limited theoretical insight into the issues of reserve location and reserve
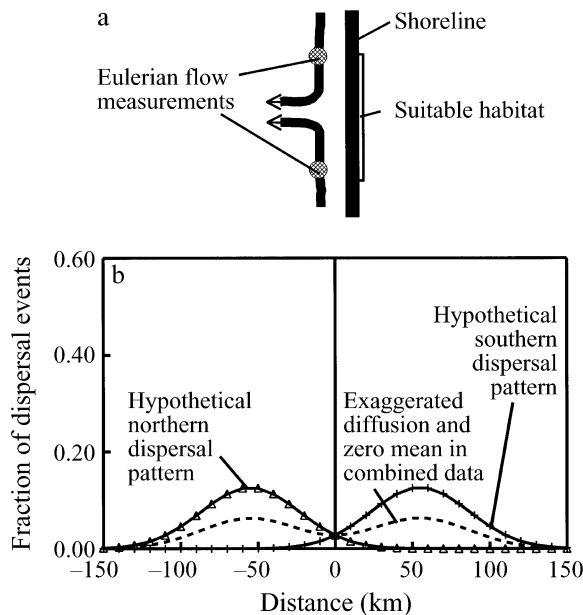
FIG. 11. Potential spatial aliasing that may arise when flow data from multiple locations are inappropriately combined to estimate a large-scale diffusion parameter. (a) Example of a converging flow field possessing explicit spatial character, and sites where flow sensors could easily be deployed within it. (b) Hypothetical distributions of dispersal distance estimated from data recorded at each of the two sites (triangles and solid curves), and the curve that would result from combining their data (dashed curve).

number from the dozens of published theoretical studies of marine reserves (but see Quinn et al. 1993, Stockhausen et al. 2000, Tuck and Possingham 2000, and Botsford et al. 2001). We believe that part of the reason for this slow progress is the lack of explicit consideration of larval dispersal in ocean currents. As was also emphasized by Stockhausen et al. 2000, even the simplest current regimes can create a spatially structured environment where sites become differentially connected through movement of larvae by flow. Some locations may receive more larvae than others and certain sites may be more important to population persistence than others. Since currents can create a spatially structured world even in the absence of variation in habitat quality, different locations may have different value with respect to both conservation and resource management. Therefore siting reserves in different locations may have very different consequences. To put it another way, reserves are unavoidably a spatially explicit management tool. The benefits of reserves over simple effort based management in a strongly advective world (e.g., with respect to fisheries yields in Figs. 8 and 10) follow because siting reserves in different locations allows for the possibility of taking advantage of the patterns of flow-generated connectivity among sites. Whether similar benefits may be obtainable by a

spatially explicit effort based management strategy awaits further study.

We have repeatedly made the caveat that this is not an exhaustive look at the role of currents in the optimal design of marine reserves. Although rates of advection had a substantial potential impact on nearly every issue we examined, these impacts can be somewhat mitigated by strong diffusive effects. Further, these simulations have explored only a small part of the problem. We have focused on a single species operating within a relatively limited subset of oceanographic conditions. Demographic parameters (e.g., larval durations, adult movement, forms of density dependence) vary widely among species. Perhaps most intriguing here is the role of variation in larval behavior. Species with different larval behaviors may experience different ''mean'' velocities in three-dimensional current fields by exploiting vertical flow structure (see, e.g., Hill 1991). When such behaviors are combined with differences in larval duration, the influence of marine reserves on multispecies systems could be quite complex. Efforts directed at understanding this complexity are still in their early stages but will likely provide important additional insights into the effective management of marine resources.

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