# Sustainability and Yield in Marine Reserve Policy

#### LOUIS W. BOTSFORD<sup>1</sup> AND DAVID M. KAPLAN

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

#### **ALAN HASTINGS**

Department of Environmental Science and Policy, University of California, Davis, California 95616, USA

Abstract. In the process of implementing marine reserves, policy makers typically are occupied with (1) choosing the spatial configuration of areas to protect and (2) addressing the concerns of fishermen regarding the effects of proposed reserves on fishery yield. The spatial configuration is typically set by choosing the habitat, species, and ecosystems to protect, assuming that the associated species will be sustained in that configuration. The concerns of fishermen are typically addressed by describing various spillover mechanisms and suggesting that yields will increase. There is a growing scientific understanding of the effects of reserves on the sustainability of populations and fishery yield, and the practical implications of those results should be incorporated into policy decisions. While there are exceptions, analytical and simulation results from models with sedentary adults indicate that yield will increase only if a population has been fished hard enough to cause a substantial decline in recruitment. This is consistent with the rough equivalence between yields possible with marine reserves and conventional management. This equivalence is a useful benchmark in the absence of information on larval advection and spatial variability in productivity. With reserves, lower fishery yields will be obtained from species dispersing shorter distances. Both yield and preservation goals depend on species in reserves being sustainable. Sustainability of species in reserves will depend on their dispersal distances and the spatial configuration of reserves. Species will be sustained in marine reserves if the alongshore dimension of the reserve is greater than its mean dispersal distance (assuming little alongshore displacement of the dispersal pattern), but species dispersing all distances will be sustained in networks of reserves, if a specific fraction of the coast is covered. Yield will be greater as the size of individual reserves in that network becomes smaller. Shorter-distance dispersers are always more likely to persist. Sustainability and yield in marine reserves depend on three categories of uncertainty: (1) uncertainty in population response to management is less when employing marine reserves than in conventional management, (2) uncertainty in the slope of the stock-recruitment relationship at low abundance affects both reserves and conventional fishery management, and (3) uncertainty in the pattern of larval dispersal affects management by reserves much more than conventional fishery management. Most of the available results are modeling results, and there is a need for better empirical information on both sustainability and yield. We need to know more than just whether marine reserves sustain populations and increase yield; rather, we need to know which kinds of reserves (i.e., size and spacing) sustained populations and which kinds of species (i.e., dispersal distance) were sustained and showed increased yields.

### Introduction

Marine reserves are being proposed and implemented worldwide with two fundamental goals: preservation

of natural ecosystems and fishery management (Murray et al. 1999; Lubchenco et al. 2003). Reserves for fishery management seek to increase the yield to fisheries, while reserves for preservation are put in place to preserve areas with a natural, functioning ecosystem. The design of these reserves, or systems of

<sup>&</sup>lt;sup>1</sup> Corresponding author: lwbotsford@ucdavis.edu

such reserves, involves policy choices regarding how much area to protect and where it should be. The biological basis for these decisions typically has involved identification of the types of ecosystems, habitats, or species of concern to be protected, then a systematic procedure for choosing specific areas to meet preservation or fishery goals (e.g., Leslie et al. 2003; Roberts et al. 2003a, 2003b). The promise in the end is sustainable fisheries or ecosystems. Greater fishery yield is frequently promised on the basis of a description of the spillover mechanism that could bring about that greater yield.

Two key issues that need to be addressed in this planning process are: (1) how the design of reserves will affect sustainability of populations in a system of marine reserves and (2) how yield will change in affected fisheries. To date, both of these have been addressed in only a qualitative fashion by reserve planners, and projected outcomes have tended to be optimistic. This presents a problem in that if there is to be any truly lasting value from marine reserves, the reserves being designed and implemented now need to be able to live up to expectations.

Here, we describe current progress in assessing the sustainability afforded by various marine reserve designs and their effect on fishery yield. Sustainability involves the question of whether species in marine reserves will continue to persist under specific reserve designs, an issue that is relevant to both preservation and fishery goals. The effect of reserves on fishery yield is often treated as an issue of interest only for reserves designed with the goal of improving fishery yield. However, the effect of reserves on fishery yield is a central issue in the policy decisions for all marine reserves, including those intended purely for conservation. In virtually all marine reserves, fishing is the primary action being limited by the implementation of reserves; hence, any loss in fishery yield is a dominant cost in any cost-benefit analysis. In the first part of this presentation, we summarize evolving modeling results regarding sustainability and yield (see Gerber et al. 2003 for a comprehensive review of the models of marine reserves). In the second part, we present new simulation results that demonstrate how sustainability and yield interact in an example of marine reserves in a typical size-structured, fished population distributed over space.

Our discussion here is limited by three fundamental assumptions that must be kept in mind: (1) sedentary adults, (2) Laplacian larval dispersal, and (3) no movement of fishers. Assuming species with sed-

entary adults means that we focus on movement in the larval stage. These are the species that will be afforded the most protection in reserves, and uncertainty in larval dispersal patterns makes understanding their possible effects important. We are beginning to understand how coastal currents shape dispersal patterns (e.g., Jones et al. 1999; Swearer et al. 1999; Cowen et al. 2000; Warner et al. 2000; Botsford 2001; Shanks et al. 2003) but do not yet have enough information for practical reserve design. Here, we use the simplest dispersal pattern that contains the spatial scale of dispersal, Laplacian dispersal (exponential decay in settlement in both directions). The movement of fishers and consequent shift in effort with the advent of marine reserves is a key element in both sustainability and yield. For each of these assumptions, we point where results would differ if they were included, and we provide relevant references. For a description of modeling results regarding the effects of fish movement on the efficacy of marine reserves see Botsford et al. (2003) and Gerber et al. (2003). In addition to the limitations imposed by these assumptions, we also do not address all of the possible differences between marine reserves and conventional management, such as differences in habitat damage, bycatch, and political ease of implementation. For a more comprehensive review of issues beyond sustainability and yield, see Hilborn et al. (in press).

# Sustainability

Sustainability of fisheries is an issue that has received increasing attention since the late 1980s, resulting in explicit focus on the persistence of fished populations. Persistence has been described in terms of equilibrium conditions for age-structured populations (Sissenwine and Shepherd 1987). These conditions specify that a population with density-dependent recruitment will have a nonzero equilibrium as long as the number of eggs produced in the lifetime of an individual exceeds the inverse of the slope of the relationship describing the number of recruits produced by a specified number of eggs spawned (i.e., the stockrecruitment relationship with stock depicted in terms of total egg production) (Figure 1). Note that lifetime egg production (LEP) is a quantity known as  $R_0$  in ecology and eggs per recruit or spawning biomass per recruit in fisheries (Goodyear 1993). To compare that condition across species in general terms, fishery biologists express it as the fraction of the natural, unfished LEP, which we will denote FLEP (this quan-

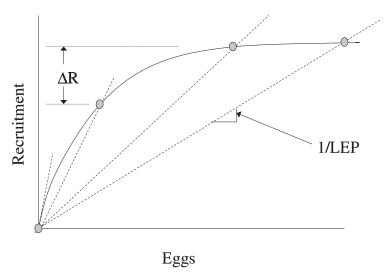


Figure 1. A schematic plot of the number of recruits produced for each value of total population egg production (solid line). Population equilibria for each level of fishing lie at the intersection of the dashed lines, which have slope 1/LEP (lifetime egg production). When 1/LEP equals the slope of the egg-recruit line at the origin, the population collapses to zero recruitment. Also shown is an example of the reduction in recruitment by the fishery that typically must be present for the implementation of reserves to increase yield.

tity is referred to as spawning potential ratio in fisheries). Considerable effort has gone into determining the value of that quantity required for persistence of marine fish (e.g., Clark 1990; Mace and Sissenwine 1993), with more recent efforts on meta-analysis to determine generic consistencies based on taxonomy (Myers et al. 1999) and upward adjustment of previously low values (Clark 2002; Ralston 2002).

The reason that this persistence condition is not useful in the assessment of population persistence in marine reserves is that a population distributed across a system of marine reserves is not the single, wellmixed population assumed above, but rather a metapopulation of such populations distributed over space, connected by dispersing larvae (Botsford et al. 1994). The recruits produced at each location end up distributed along the coast through the process of larval dispersal, and much of the recruitment at each location is produced elsewhere. Because of this additional complexity, a general expression for stability of these marine meta-populations has been difficult to obtain (Armsworth 2002). Researchers have, however, developed useful ways of describing population dynamics in terms of source-sink dynamics (Crowder et al. 2000; Lipcius et al. 2001).

Some results regarding persistence of simple meta-populations have been developed in the context

of marine reserves. Initial results assumed a population with sedentary adults, post-settlement densitydependent recruitment of the Beverton-Holt type (Beverton and Holt 1957) and larvae with a Laplacian dispersal pattern (i.e., exponentially decaying with distance in both directions) in a system of uniformly spaced reserves of width w and spacing s, along a coastline with uniform habitat, with fishing removing all fish between reserves (Botsford et al. 2001). The result was that for a single reserve of a certain width, species with mean dispersal distances less than or roughly the same as that width would persist. However, a system of uniformly spaced reserves of any width that covered a specific fraction of the coastline would allow persistence of all species, regardless of dispersal distance. The latter result indicated that a network of reserves could function in a way that was greater than the sum of the workings of the individual reserves (i.e., it was a "network result"). The specific fraction of coastline that needed to be covered was the value of FLEP required for persistence of the single, well-mixed population, as discussed in the previous paragraph. In this simple case, one can gain some intuitive understanding of why FLEP sets the minimum area in reserves by observing that the role of fishing in reducing LEP in the single, well-mixed population can be thought of as being replaced in the

case of the meta-population by reduction in the area in which larvae can settle and grow to maturity, due to fragmentation of the coastline by intense fishing between reserves. Alongshore advection made the reserve areas required for sustainability much larger (Botsford et al. 2001).

Subsequent analyses have refined and extended these results. Lockwood et al. (2001) has shown that the initial results hold for a variety of shapes of dispersal patterns centered on the origin, with the mean dispersal distance being the important characteristic. This is an important result, as dispersal patterns are generally poorly known. Also, these results have been extended to the case in which there is a specific level of fishing between reserves, and there are discontinuities in the quality of benthic habitat that create species boundaries (Lockwood et al. 2004). These results show how fishing at levels less than complete removal lead to population persistence with lower fractions of the coastline in reserves, while losses of larvae across species boundaries lead to requirements for a greater fraction of coastline in reserves.

## Fishery Yield

In its simplest form, the question in the minds of policy makers of how implementation of a marine reserve will affect fishery yield is essentially whether the loss of fishable area will be compensated for by changes in the population brought about by implementation of the reserve. Assuming that reserves are not going to affect individual growth and mortality rates outside the reserve, they will not affect yield per recruit, and we need consider only the effect on recruitment. For yield to increase with the implementation of reserves, the increase in recruitment due to the increased egg production from the reserves  $(\Delta R)$  must be large enough to compensate for the fraction of the area placed in reserves  $(\Delta A)$ , in other words,

$$(1 - \Delta A)(1 + \Delta R) > 1.$$

This requires not just an increase in egg production, but that the larvae produced are able to reach the fished areas to increase recruitment by the required amount. Thus, if recruitment has not been substantially reduced by the current fishery, there is little scope for recruitment to be increased by the additional egg production supplied by a system of marine reserves (Figure 1). In turn, the amount by which recruitment will have been reduced by fishing a certain amount will depend to

some degree on the slope of the egg—recruitment relationship at the origin (Figure 1).

This observation regarding the potential for reserves to increase yield raises the policy question of whether yield can be increased as much by changing management in a conventional way (i.e., by decreasing fishing effort). That question was addressed by analysis of a simple model with no adult movement, larval settlement equally distributed across the population, post-dispersal density-dependent recruitment only (Hastings and Botsford 1999). The answer, that the maximum yield problem for conventional management was mathematically the same as maximizing yield using reserves, indicates that there is a rough equivalence between reducing effort in conventional management and implementing marine reserves. This conclusion is also indicated by the invariant noted by Mangel (1998). This rough equivalence is consistent with results from a number of simulation studies of more complex models. The typical result is that marine reserves produce greater yield only for fishing mortality rates greater than a certain minimum value (e.g., Holland and Brazee 1996), or conversely, marine reserves are a means of guaranteeing sustainability even if the fishing mortality increases to very high values (e.g., Quinn et al. 1993).

The rough equivalence between conventional management and management by reserves provides policy makers with an easily computed benchmark estimate of the yield possible with marine reserves. Whether reserves or conventional management are actually superior depends on further detail, usually in an obvious way. For example, if compensatory density-dependence occurs prior to dispersal (e.g., density-dependent fecundity or indirect effects on fecundity such as density-dependent growth), reserves will have less advantage because reserves will increase density. On the other hand, if pre-dispersal density dependence is depensatory, such as in broadcast spawning, reserves will have greater advantage. Another example, fishermen shifting effort from inside reserves to outside, rather than simply leaving as assumed implicitly or explicitly in virtually all models of marine reserves (Gerber et al. 2003), is treated in several recent publications (Smith and Wilen 2003; Halpern et al., in press). In that case also, reserves have less advantage.

Situations involving substantial movement and heterogeneity in productivity can lead to exceptions to this rough equivalence. One example is populations with ontogenetic movement, in which specific life history stages can be protected (e.g., reserves can

be placed to protect spawning and rearing areas; Apostolaki et al. 2002). Other examples involve differences in larval productivity and substantial alongshore advection. When there are areas with excess larval production, and other areas with populations at less than the benthic carrying capacity, then reserves can provide greater yield than can any scheme with the same fishing effort at all locations. Morgan and Botsford (2001) showed that increasing protection of a single source population coupled to three sink populations could increase yield by an amount greater than that possible through conventional fishery management of all four populations. However, that advantage was not possible unless the source was known. Gaines et al. (2003) showed another example in which populations in the middle of a bounded area along a coastline with reversing currents could produce greater yield with reserves than with conventional fishing throughout. In the cases of these exceptions to the rough equivalence between conventional management and management by reserves, yield could increase even when the fishery has not diminished recruitment.

# Consideration of Both Sustainability and Yield

We know of only one general analysis that included aspects of both sustainability and yield. A comparison of the spatial configuration likely to be best for conservation with that best for yield indicated that for conservation one could use a small number of large reserves of a size that would allow persistence of the longest-distance disperser one desired to protect (Hastings and Botsford 2003). This was contrasted with the best configuration for yield, which was that configuration that sustained the population but also supplied the greatest export of larvae from reserves, a system of many reserves as small as practicable. For sustainability, this system needed to cover a certain fraction of the coastline, the minimum FLEP required for sustainability of the fished species, as noted above (Botsford et al. 2001). This analysis assumed the cost of a reserve for conservation was proportional to the shoreline placed in reserve and did not include the cost of fishery yield lost due to displaced effort. While that analysis provides valuable insight into the benefits supplied by different spatial considerations, it is now clear that cost of foregone yield is a significant issue in real policy decisions.

To demonstrate the spatial distributions of recruitment, catch, and biomass, and how they provide for sustainability and yield, we present here the results of simulations of a system of marine reserves along a coastline at different levels of fishing. The model consists of 100 size-structured populations with individuals growing according to von Bertalanffy growth with a truncated Gaussian distribution of values of  $L_{\infty}$  as in Smith et al. (1998) and Morgan et al. (2000; see Table 1 for parameter values). Density-dependent recruitment is represented as the Beverton-Holt type, with the slope  $(a_{\rm BH}$  in Table 1) set so that collapse occurs when LEP is 35% of the natural, unfished value. Reserves are equally spaced at four locations, and each covers either 2, 5, or 10 populations, so that 8%, 20%, or 40%, respectively, of the coastline is covered. We focus here on the consequences of larval dispersal distance, so adults are considered to be sedentary. Larval dispersal distance varies from 0 to 25 spatial units (each of the 100 populations is considered to occupy 1 spatial unit, s.u.). The model "wraps" dispersal at the boundaries to the other boundaries, so that there are no effects of species boundaries due to a change in suitability of benthic habitat or specific circulation features (Gaylord and Gaines 2000; Lockwood et al. 2004).

The changes in recruitment, yield, biomass, and LEP with fishing mortality rate for a single population without reserves are shown in Figure 2. Biomass and recruitment decline monotonically, while catch increases, then decreases. All are zero at the point where FLEP is 0.35, which occurs at approximately F = 0.11/year.

*Table 1.* Parameter values for population model. s.u. = spatial unit.

Parameter	Symbol	Value
Growth		
Maximum size	L.	118 mm
Standard deviation of	$\sigma_{_L}$	10 mm
maximum size	L	
Reproduction		
Size of first reproduction	1 $l_{_m}$	60 mm
Fecundity versus weight	m	
Coefficient	а	$5.47 \times 10^{-6}$
Exponent	b	3.45
Mortality		
Natural mortality	M	0.08/year
Fishing mortality	F	(0.05 - 0.2)/year
Size limit	$L_{_F}$	60 mm
Reserve size		0–10 s.u.
Number of reserves		4
Dispersal		
Dispersal distance		1–20 s.u.
Recruitment		
Beverton-Holt slope	$a_{\rm BH}$	0.00662
Beverton-Holt capacity	$C_{_{ m BH}}^{^{ m BH}}$	12,000,000

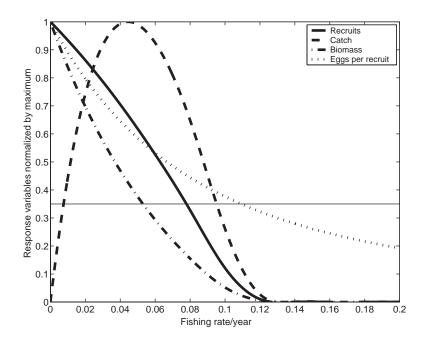


Figure 2. Performance of a single population of the model, used here without reserves, versus fishing mortality rate. Parameter values are set so that as fishing increases, recruitment, biomass, and catch go to zero near where FLEP drops below 0.35. This occurs at a fishing mortality rate of 0.11/year. All variables are given as a fraction of their maximum values, which are recruitment =  $2.35 \times 10^9$  individuals, biomass =  $7.25 \times 10^{12}$ , and catch =  $1.33 \times 10^{11}$ .

The response of catch to increasing fishing mortality rate changes as reserve area is increased (as suggested by the yield results above), but that response depends critically on dispersal distance (as suggested by persistence results; Figure 3). For this model, peak catch generally declines as more reserves are added, but the nature of that dependence changes with dispersal distance. The plot of catch with no reserves is, of course, the same as Figure 2, independent of dispersal distance. Having just 8% of the coastline in reserves (reserves of width 2 s.u.) is enough to provide persistence, and some catch, for low-distance dispersers. However, any response for species dispersing 10 s.u. requires at least 20% in reserves (reserves of width 5 s.u.), which provides persistence and higher catch out to a fishing rate of 0.2/year. Persistence of individuals dispersing long distances requires 40% in reserves. Note, however, that as the fraction in reserves increases, catch at lower dispersal distances always remains low.

These characteristics follow from the spatial distribution of catch as dispersal distance varies

(Figure 4). Catch is the highest of any location or dispersal distance at low dispersal distance just outside the reserves. However, for these short-distance dispersers it quickly drops to very low values as distance from the reserve increases. For dispersal distances greater than 10 s.u., on the other hand, catch between reserves varies little with space and dispersal distance. At a fishing mortality rate of 0.1/year, populations of long-distance dispersers would be sustained at high catch with 20% in reserves, as indicated by Figure 3, but for a fishing mortality rate of 0.2/year, catch would be much lower at high dispersal rates.

The spatial distribution of catch is largely determined by the spatial distribution of recruitment (Figure 5). Recruitment is highest for species dispersing short distances but extends only a short distance outside reserves. Recruitment inside reserves is less for long-distance dispersers, but it is evenly distributed over space between reserves. Note from the right hand side of Figure 5 that recruitment levels inside reserves decline faster at a fishing rate of 0.2/year than at 0.1/

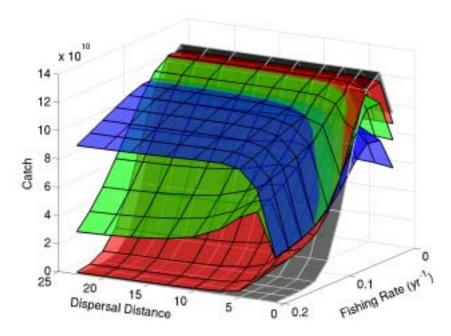


Figure 3. Yield for the meta-population of 100 size-structured populations linked by Laplacian dispersal with various mean dispersal distances as fishing mortality rate increases. The four surfaces indicate yield for no reserves (gray) and four equally spaced reserves of size 2 spatial units (s.u.) (8% in reserves; red), 5 s.u. (20% in reserves; green), and 10 s.u. (40% in reserves; blue).

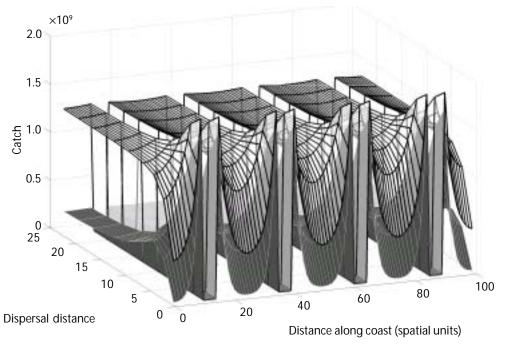


Figure 4. The spatial distribution of catch for the model in Figure 3, at different mean dispersal distance, and two fishing mortality rates, F = 0.1 (top mesh surface) and F = 0.2 (lower solid surface).

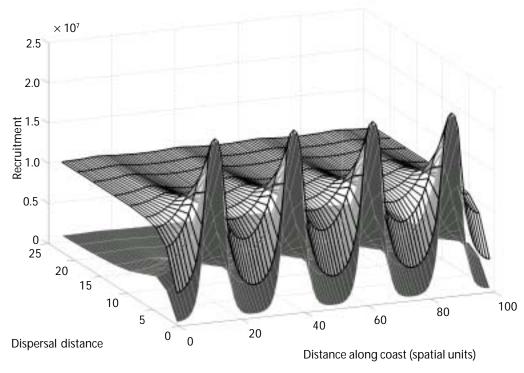


Figure 5. The spatial distribution of recruitment for the model in Figure 3, at different mean dispersal distance, and two fishing mortality rates, F = 0.1 (top mesh surface) and F = 0.2 (lower solid surface).

year. This follows from reduced connectivity, as fishing reduces populations to lower values.

The spatial distribution of biomass at each dispersal distance depends on the distributions of recruitment and fishing (Figure 6). Note that for this spatial configuration of reserves, the distribution of biomass over space is uniform for dispersal rates greater than  $10 \, \mathrm{s.u.}$  For lower dispersal rates, biomass declines rapidly, with distance from reserves reflecting the effect of spatial variability in recruitment. Differences between spatial distributions of biomass with fishing appear to follow the differences in recruitment.

#### Discussion

The primary message to decision makers from these results is that the spatial configuration of reserves and the spatial scale of dispersal of different species make a difference in the advisability and efficacy of marine reserves. Choosing reserve size and location solely because they contain the species, habitats, and ecosystems we want to protect will not guarantee their protection. Rather, we must set the spatial configuration to sustain the species we want to protect. The

design of the spatial configuration of the reserves will depend on the spatial scale of dispersal and the minimum value of FLEP required for that species.

A second message to policy makers involved in implementing marine reserves regards the potential loss in fishery yield, a dominant issue in formulating marine reserve policy. There need to be better attempts to assess the change in yield; pointing out that there will be greater egg production in reserves and that there may be spillover is not an adequate answer for decision making. The effects of reserves on yield of fished species will depend on how much FLEP has been reduced by fishing. This is consistent with the rough equivalence between the yield possible through reserves and conventional management. In the absence of detailed information on larval transport and benthic productivity, this equivalence is a valuable benchmark indicator of the effects of reserves on yield. It provides a link between the reserve option and conventional management options. If reducing effort in the fishery is an option, its effect on yield is, to a first approximation, the same as implementing reserves.

A third point for decision makers is the answer to the question of whether reserves are less suscep-

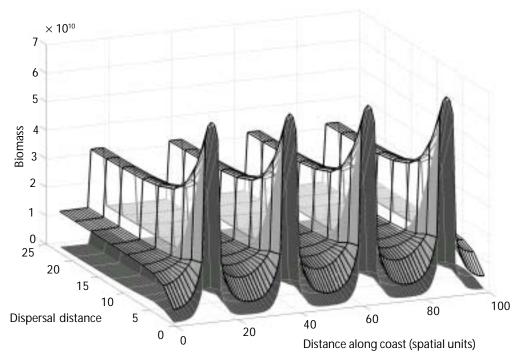


Figure 6. The spatial distribution of biomass for the model in Figure 3, at different mean dispersal distance, and two fishing mortality rates, F = 0.1 (top mesh surface) and F = 0.2 (lower solid surface).

tible to uncertainty than conventional fishery management. Reserves have been shown to be less affected by certain kinds of uncertainty (Lauck et al. 1998), and they can allow populations to persist and produce high yields even as uncertain fishing mortality rate increases to values that would cause collapse if there were no reserves (Figure 3; Quinn et al. 1993; Botsford et al. 2003). However, the above dependencies of sustainability and yield on the virtually unknown dispersal patterns and the uncertain value of FLEP suggest there is considerable uncertainty in projecting the effects of reserves. The best current, practical answer to the question is that managing a fishery by reserves instead of through conventional management decreases dependence on some kinds of uncertainty but increases dependence on others and does not change our dependence on a third kind of uncertainty. Susceptibility to uncertainty in dispersal distances is a new source of uncertainty incurred in spatial management. Uncertainty in the value of FLEP required for persistence is a dominant source of uncertainty in conventional fishery management, and it has the same effect in management by reserves. The other dominant source of uncertainty in conventional fishery management, uncertainty in the effects of fishing regulations on the population, is alleviated in management by reserves.

A fourth message to policy makers is to be aware of the difference between conditions for sustainability (population persistence) and conditions for yield. This is due to the fact that persistence, by definition, requires only a small part of the population to be extant at a single location, while catch depends on the abundance of the population over all space outside reserves. The consequence of this difference is that results regarding the effects of reserves on persistence cannot be used to infer the effects of reserves on catch and vice versa. An example of the differences is the fact that persistence and yield depend on dispersal distance in different ways; persistence is greater at shorter dispersal distances, but greater catch is possible at longer dispersal distances (Figure 3).

The above discussion of various dependencies on uncertainty raises the question of whether we know enough about dispersal and the required FLEP to begin to make use of each of them in the design of reserves. As noted in the Introduction, there is an awareness of the importance of knowing the minimum value

10 BOTSFORD ET AL.

of FLEP required for persistence, which stems from its role in conventional fishery management. While much remains to be learned regarding the way in which this parameter might vary with species, habitat (e.g., whether it is higher in an upwelling zone), and climate, research is ongoing (Myers et al. 1999, 2002; Ralston 2002).

While knowledge of the physical and biological factors that determine dispersal patterns is accumulating rapidly, our specific, usable knowledge of how species vary is probably limited to knowing the spatial scale of dispersal. Even with that simplification, it may be most prudent to limit our classification to shortdistance and long-distance dispersers. In that regard, for the model used here, there seems to be a difference in behavior between species dispersing greater than 10 s.u. and those dispersing less than 10 s.u. The effects of reserve design on short-distance dispersers could be evaluated by considering single reserves, while the effects on long-distance dispersers could be evaluated using the network of reserves and the fraction of the coastline covered. Much attention has been drawn recently to the fact that dispersal distances are much shorter for many species than we usually have thought them to be (Warner et al. 2002). The implication of that observation for reserves is commonly taken to be that reserves will work more often than not and that our uncertainty in dispersal distance is not a concern. The results here are a reminder that while reserves will "work," they will sustain those species with short dispersal distances, which provides less yield to fisheries than species dispersing longer distances.

Warner

(2002)

cited in

et al.

not

refer-

ences.

Add full

refer-

ence.

Since the results here were obtained primarily from modeling, a natural question is how they compare with empirical observations. These models assume an increase in biomass and mean age inside marine reserves, an effect that is consistent with empirical observations (e.g., Halpern and Warner 2002; Halpern 2003). Recent further probing into the available empirical data has shown that, as a category, exploited species increased in abundance in reserves, while unexploited species did not (Micheli et al., in press), consistent with the expectations outlined here. There are fewer systematic observations of effects outside reserves, such as increases in yield (e.g., Roberts et al. 2001), and even those rarely include the obvious dependent variables identified here. Reserves are often cited as having increased yield, but no information is presented on the level of fishing prior to reserve implementation. Since the most dramatic increases are typically cited, this often leads to confusion among the public, and among policy makers, by

giving them the impression that all reserves will increase fishery yield.

Further confusion regarding these somewhat complex issues occurs because of a lack of differentiation between scientific advice and advocacy of conservation. Most biologists have a conservation bias, and many advocate conservation of marine resources. However, marine scientists have a responsibility to identify advice given to policy makers as to whether it is science or advocacy. While there is probably wide agreement with this point, maintaining a level playing field when comparing reserves to conventional management is not always easy. For example, comparisons that assume a complex source-sink structure can show that reserves outperform conventional management, but to take advantage of that capability we would need to know the specific structure (i.e., the dispersal patterns, which are currently, typically unknown) (Morgan and Botsford 2002). We need to differentiate between (2002) -the ultimate potential of marine reserves and their not cited in current potential given existing knowledge.

Morgan and **Botsford** references. Add full reference.

In summary, marine reserves present a valuable new tool in the conservation of marine ecosystems and the management of fisheries. We have a good start on developing an understanding of their effects and the techniques for analyzing their efficacy and relating it to conventional management. We need to begin to integrate the understanding and techniques into marine policy making if we are going to make achievable projections regarding the promise of marine reserves.

## Acknowledgments

This work was supported by the Partnership of Education in Marine Resource and Ecosystem Management (PEMREM), California Sea Grant R/F 179, and the working group "Design of Tools for the Practical Design of Marine Reserves" at the National Center for Ecological Analysis and Synthesis that is supported by U.S. National Science Foundation (Grant DEB-94–21535), University of California, California Resources Agency, and California Environmental Protection Agency. We thank Churchill Grimes and Kenneth Frank for their reviews.

#### References

Apostolaki, P., E. J. Milner-Gulland, M. K. McAllister, and G. P. Kirkwood. 2002. Modelling the effects

- of establishing a marine reserve for mobile fish species. Canadian Journal of Fisheries and Aquatic Sciences 59:405–415.
- Armsworth, P. 2002. Recruitment limitation, population regulation, and larval connectivity in reef fish metapopulations. Ecology 83:1092–1104.
- Beverton, R. J. H., and S. J. Holt. 1957. On the dynamics of exploited fish populations. Fisheries Investigations (Series II) 19:1–533.
- Botsford, L. W. 2001. Physical influences on recruitment to California Current invertebrate populations on multiple scales. ICES Journal of Marine Science 58:1081–1091.
- Botsford, L. W., A. Hastings, and S. D. Gaines. 2001. Dependence of sustainability on the configuration of marine reserves and larval dispersal distances. Ecology Letters 4:144–150.
- Botsford, L. W., F. Micheli, and A. Hastings. 2003. Principles for the design of marine reserves. Ecological Applications 13:S25–S31.
- Botsford, L. W., C. L. Moloney, A. Hastings, J. L. Largier, T. M. Powell, K. Higgins, and J. F. Quinn. 1994. The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations. Deep-Sea Research Part II Topical Studies in Oceanography 41:107–145.
- Clark, W. G. 1990. Groundfish exploitation rates based on life history parameters. Canadian Journal of Fisheries and Aquatic Sciences 48:734–750.
- Clark, W. G. 2002.  $F_{35\%}$  revisited ten years later. North American Journal of Fisheries Management 22:251–257.
- Cowen, R. K., K. M. M. Lwiza, S. Sponaugle, C. B. Paris, and D. B. Olson. 2000. Connectivity of marine populations: open or closed? Science 287:857–859.
- Crowder, L. B., S. J. Lyman, W. F. Figueira, and J. Priddy. 2000. Source-sink population dynamics and the problem of siting marine reserves. Bulletin of Marine Science 66: 799–820.
- Gaines, S. D., B. Gaylord, and J. L. Largier. 2003. Avoiding current oversights in marine reserve design. Ecological Applications 13:S32–S46.
- Gaylord, B., and S. D. Gaines. 2000. Temperature or transport? Range limits in marine species mediated solely by flow. American Naturalist 155:769–789.
- Gerber, L. R., L. W. Botsford, A. Hastings, H. P. Possingham, S. D. Gaines, S. R. Palumbi, and S. J. Andelman. 2003. Population models for marine reserve design: a retrospective and prospective synthesis. Ecological Applications 13:S47–S64.
- Goodyear, P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. Canadian Special Publication of Fisheries and Aquatic Sciences 120:67–81.
- Halpern, B. 2003. The impact of marine reserves: do they work and does reserve size matter? Ecological Applications 13:S117–137.

- Halpern, B. S., S. D. Gaines, and R. R. Warner. In press. Export of production and the displacement of effort from marine reserves: effects on fisheries and monitoring programs. Ecological Applications.
- Halpern, B. S., and R. R. Warner. 2002. Marine reserves have rapid and lasting effects. Ecology Letters 5:361–366.
- Hastings, A., and L. W. Botsford. 1999. Equivalence in yield from marine reserves and traditional fisheries management. Science 284:1537–1538.
- Hastings, A., and L. W. Botsford. 2003. Are marine reserves for fisheries and biodiversity compatible? Ecological Applications 13:S65–S70.
- Hilborn, R., K. Stokes, J.-J. Maguire, T. Smith, L. W. Botsford, M. Mangel, J. Orensanz, A. Parma, J. Rice, J. Bell, K. L. Cochrane, S. Garcia, S. J. Hall, G. P. Kirkwood, K. Sainsbury, G. Stefansson, and C. Walters. In press. When can marine reserve areas improve fisheries management? Oceans and Coastal Management.
- Holland, D. S., and R. J. Brazee. 1996. Marine reserves for fishery management. Marine Resource Economics 11:157–171.
- Jones, G. G. P., M. J. Milicich, M. J. Emslie, and C. Lunow. 1999. Self-recruitment in a coral reef fish population. Nature (London) 402:802–804.
- Lauck, T., C. W. Clark, M. Mangel, and G. R. Munro. 1998. Implementing the precautionary principle in fisheries management through marine reserves. Ecological Applications 8:S72–S78.
- Leslie, H., M. Ruckelshaus, I. R. Ball, S. Andelman, and H. P. Posssingham. 2003. Using siting algorithms in the design of marine reserves. Ecological Applications 13:S185–S198.
- Lipcius, R. N., W. T. Stockhausen, and D. B. Eggleston.
  2001. Marine reserves for Caribbean spiny lobster: empirical evaluation and theoretical metapopulation recruitment dynamics. Marine and Freshwater Research 52:1589–1598.

  Lockwood et al. (2004) -- We don't
- Lockwood, D. L., A. Hastings, and L. W. Botsford. 2001. The effects of dispersal patterns on marine reserves: does the tail wag the dog? Theoretical Population Biology 61:297–309.
- Lockwood, D. L., A. Hastings and L. W. Botsford. 2004. The persistence of meroplanktonic populations on a bounded coastline with marine reserves. Submitted.
- Lubchenco, J., S. R. Palumbi, S. D. Gaines, and S. Andelman. 2003. Plugging a hole in the ocean: the emerging science of marine reserves. Ecological Applications 13:S3–S7.
- Mace, P. M., and M. P. Sissenwine. 1993. How much spawning per recruit is enough? Canadian Special Publication of Fisheries and Aquatic Sciences 120:101–118.
- Mangel, M. 1998. No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. Ecology Letters 1:87–90.

Update to "in press"?

Update to "in press"?

Lockwood et al. (2004) -- We don't allow submitted papers to be cited in the references section. Is this paper accepted? To what publica-

tion?

Micheli, F., B. S. Halpern, L. W. Botsford, and R. R. Warner. In press. Trajectories and correlates of community change in no-take marine reserves. Ecological Applications.

Morgan, L. E., and L. W. Botsford. 2001. Managing with reserves: modeling uncertainty in larval dispersal for a sea urchin fishery. Alaska Sea Grant College Program Report AK-SG-01-02:667–684.

- Morgan, L. E., L. W. Botsford, S. R. Wing, and B. D. Smith. 2000. Spatial variability in growth and mortality of the red sea urchin, Strongylocentrotus franciscanus in northern California. Canadian Journal of Fisheries and Aquatic Sciences 57:980–992.
- Murray, S. N., R. F. Ambrose, J. A. Bohnsack, L. W. Botsford, M. H. Carr, G. E. Davis, P. K. Dayton, D. Gotshall, D. R. Gunderson, M. A. Hixon, J. Lubchenco, M. Mangel, A. MacCall, D. A. McArdle, J. C. Ogden, J. Roughgarden, R. M. Starr, M. J. Tegner, and M. M. Yoklavich. 1999. No-take reserve networks: sustaining fishery populations and marine ecosystems. Fisheries 24(11):11–25.
- Myers, R. A., N. J. Barrowman, R. Hilborn, and D. G. Kehler. 2002. Inferring Bayesian priors with limited direct data: applications to risk analysis. North American Journal of Fisheries Management 22:351–364.
- Myers, R. A., K. G. Bowen, and N. J. Barrowman. 1999. Maximum reproductive rate of fish at low population sizes. Canadian Journal of Fisheries and Aquatic Sciences 56:2404–2419.
- Quinn, J. F., S. R. Wing, and L. W. Botsford. 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the redsea urchin, *Strongylocentrotus franciscanus*. American Zoologist 33:537–550.
- Ralston, S. 2002. West Coast groundfish policy. North American Journal of Fisheries Management 22:249–250.
- Roberts, C. M., S. Andelman, G. Branch, R. H. Bustamante, J. C. Castilla, J. Dugan, B. S. Halpern,

- K. D. Lafferty, H. Leslie, J. Lubchenco, D. McArdle, H. P. Possingham, M. Ruckelshaus, and R. R. Warner. 2003a. Ecological criteria for evaluating candidate sites for marine reserves. Ecological Applications 13:S199–S214.
- Roberts, C. M., J. A. Bohnsack, F. Gell, J. P Hawkins, and R. Goodridge. 2001. Effects of marine reserves on adjacent fisheries. Science 294:1920– 1923.
- Roberts, C. M., G. Branch, R. H. Bustamante, J. C. Castilla, J. Dugan, B. S. Halpern, K. D. Lafferty, H. Leslie, J. Lubchenco, D. McArdle, M. Ruckelshaus, and R. R. Warner. 2003b. Application of ecological criteria in selecting marine reserves and developing reserve networks. Ecological Applications 13:S215–S228.
- Shanks, A. L., B. Grantham, and M. H. Carr. 2003. Propagule dispersal distance and the size and spacing of marine reserves. Ecological Applications 13:S159–169.
- Sissenwine, M. P., and J. G. Shepherd. 1987. An alternative perspective on recruitment overfishing and biological reference points. Canadian Journal of Fisheries and Aquatic Sciences 44:913–918.
- Smith, B. D., L. W. Botsford, and S. R. Wing. 1998. Estimation of growth and mortality parameters from size frequency distributions lacking age patterns: the red sea urchin (*Strongylocentrotus* franciscanus) as an example. Canadian Journal of Fisheries and Aquatic Sciences 55:1236–1247.
- Smith, M. D., and J. E. Wilen. 2003. Economic impacts of marine reserves: the importance of spatial behavior. Journal of Environmental Economics and Management 46:183–206.
- Swearer, S. E., J. E. Caselle, D. W. Lea, and R. R. Warner. 1999. Larval retention and recruitment in an island population of a coral-reef fish. Nature 402:799–802.
- Warner, R. R., S. E. Swearer, and J. E. Caselle. 2000. Larval accumulation and retention: implications for the design of marine reserves and essential habitat. Bulletin of Marine Science 66:821–830.

Update to "in press"?