# PRINCIPLES FOR THE DESIGN OF MARINE RESERVES

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*Abstract.* The theory underlying the design of marine reserves, whether the goal is to preserve biodiversity or to manage fisheries, is still in its infancy. For both of these goals, there is a need for general principles on which to base marine reserve design, and because of the paucity of empirical experience, these principles must be based on models. However, most of the theoretical studies to date have been specific to a single situation, with few attempts to deduce general principles. Here we attempt to distill existing results into general principles useful to designers of marine reserves. To answer the question of how fishery management using reserves compares to conventional management, we provide two principles: (1) the effect of reserves on yield per recruit is similar to increasing the age of first capture, and (2) the effect of reserves on yield is similar to reducing effort. Another two principles answer the question of how to design reserve configurations so that species with movement in various stages will be sustainable: (3) higher juvenile and adult movement lowers sustainability of reserves for biodiversity, but an intermediate level of adult movement is required for reserves for fishery management, and (4) longer larval dispersal distance requires larger reserves for sustainability. These principles provide general guidelines for design, and attention to them will allow more rapid progress in future modeling studies. Whether populations or communities will persist under any specific reserve design is uncertain, and we suggest ways of dealing with that uncertainty.

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

## INTRODUCTION

Marine reserves are under consideration as a tool for improving fishery management and protecting biodiversity, yet there is a paucity of information on which resource managers can base reserve design. When the use of reserves is considered, the basic questions concern the size of reserves, the fraction of coastline to be covered, and where reserves should be sited (e.g., Agardy 2000). The answers to questions such as these depend on the specific goal of the reserves, primarily whether they are intended to improve fishery management or protect biodiversity. They also depend on the life history and dispersal characteristics of the species present and the existing fishing pressure. Ideally, these questions of design should be answered on an empirical basis; we should be able to compare results from reserves with different sizes, spacing, and species, for example, to formulate future designs.

Unfortunately, the data required to answer these questions are not available. Information from existing reserves has been gathered to assess whether the reserves have a positive affect, not to compare the efficacy of different reserve designs or differential effects among species. Some studies of existing reserves have shown that abundance is higher in or near reserves (e.g., Roberts 1995, Russ and Alcala 1996*a*, *b*, Halpern 2003); however, most studies compare abundance between the reserve and control sites after the implementation of reserves. Conditions before and after implementation of a reserve can rarely be compared because data are rarely available from the reserve area before implementation. Also, there have been only a few studies of the effects of reserves on areas outside reserves. For example Russ and Alcala (1996*b*) found there was spillover of commercial fish species from a reserve in the Philippines, but McClanahan and Kauna-Arara (1996) did not detect this effect in reserves in Kenya.

There have been some efforts to develop qualitative criteria and rules on which to base reserve siting (e.g., Hockey and Branch 1997, Leslie et al. 2003, Roberts et al. 2003*a*, *b*). These include criteria such as maximizing biogeographic representations within reserves, maximizing habitat heterogeneity, including vulnerable habitats, including critical life stages, including areas with rare and endemic species, and avoiding areas subject to frequent human or natural disturbance. They are a mixture of goals and qualitative rules based on biological and societal needs and intuition. They are necessary for reserve siting, but do not answer all of the questions regarding design issues. While these qualitative reserve-siting schemes are needed to select the combination of locations that contain the desired species, communities, or habitat types, they do not specify the combination of

reserve locations, sizes, and spacing necessary to sustain the species or communities desired.

Because of the lack of an empirical basis for the design of marine reserves, a number of researchers have turned to modeling as a way of combining the complex array of factors to project the efficacy of different reserve designs (Dayton et al. 2000). Because of their nascent stage of development, and life-history differences (primarily the ubiquity of larval dispersal in marine systems), results from terrestrial reserves do not provide useful principles for the design of marine reserves (e.g., Simberloff 2000). Here, we develop principles in a form that will be useful to resource managers, based on models for marine reserves. These principles complement siting rules by addressing the more quantitative questions regarding size and spacing of reserves. They can be viewed as providing a means of specifying reserve designs that will achieve the goals implicit in the siting rules.

This synthesis is colored by the fact that most studies of reserve design have been oriented toward fisheries. They have involved analysis of the design of reserves to achieve the goal of maximizing yield while maintaining persistence of a single species. Since this is a report of current status, we base the principles described here on the available mix of studies. While not aimed at that purpose, fishery studies provide some insights into achieving the other major stated goal of marine reserves, preserving biodiversity. Reserves for fishery management and biodiversity have a common goal, persistence of the target population(s), but obviously differ in their attention to yield outside of the reserves (see Hastings and Botsford 2003 for a discussion of the latter issue). The principles developed here are based on analyses of deterministic models with no accounting for uncertainty. The need for additional modeling and development of additional principles along these lines is described in *Discussion.*

PRINCIPLES OF RESERVE DESIGN

The principles developed thus far address two major questions in the design of marine reserves: (1) how will the outcome of marine reserves compare to conventional fishery management through size limits and effort control, and (2) how does the nature of movement of the species we are trying to protect affect the design of marine reserves?

*Fishery management by reserves vs.
conventional means*

A question being asked by fishery managers is whether reserves are better or worse than the way they are currently managing using size limits and effort control or catch control. Since fishing effort is notoriously difficult to control, reserves may be a better option (Ludwig et al. 1993, Botsford et al. 1997, Guenette et al. 1998). Assessment of the performance of reserves

relative to existing practices is useful in establishing a rough idea of performance. Resource managers currently have a wide range of expectations regarding the yields possible through management by reserves. The following two principles narrow that range by direct comparison to ideal conventional management through control of size and numbers caught.

*Principle 1: The effects on yield per recruit of adding reserves is essentially the same as increasing the size limit.*—This first principle states that in terms of yield per recruit, where growth overfishing is the primary issue, adding area in reserves to a fishery is similar to increasing the age of first capture or the lower size limit. This fact was contained in the analysis by Beverton and Holt (1957). In their plot of yield per recruit vs. fishing-mortality rate (Beverton and Holt 1957: Fig. 18.23; see also Guenette et al. 1998), placing increasing fractions of the total area into marine reserves leads to an almost identical effect to that of increasing the age of first capture. This can be seen by comparing different slices through the yield surface (Beverton and Holt 1957: Fig. 17.14) at increasingly greater age of first capture. One of the benefits of both increasing the area in reserves and increasing age or size limits is that yield per recruit becomes less sensitive to increasing effort. Because removals are less, this suggests that the impact on eggs per recruit will also be less for a given value of fishing mortality rate, making the overall fishery less sensitive to increasing effort.

*Principle 2: The effect on yield of adding reserves is essentially the same as decreasing fishing mortality.*—This second principle states that, as far as sustainability or recruitment overfishing goes, the addition of marine reserves can be viewed as a reduction in fishing mortality rate. This principle follows from several studies of models with full descriptions of reproduction in terms of a stock–recruitment relationship, and some description of the larval phase (Quinn et al. 1993, Holland and Brazee 1996, Guennette and Pitcher 1999, Hastings and Botsford 1999, Sladek Nowliss and Roberts 1999). The models of Holland and Brazee and Sladek Nowliss and Roberts both include stock–recruitment relationships, and describe the larval phase as a larval pool. In both of them, adding reserves increases yield only when the population has already been fished beyond the point of maximum yield.

This effect is illustrated in results from a model of the red sea urchin in northern California, in which reserves have a positive effect on yield only when harvest rate is high (Fig. 1; Quinn et al. 1993). In contrast to the models in Holland and Brazee and Sladek Nowliss and Roberts, this model included larval dispersal explicitly (Fig. 1). It considered a metapopulation of 24 subpopulations, where larvae from each subpopulation dispersed the equivalent of twice the distance between adjacent subpopulations, in both directions. It also included an Allee effect in recruitment. Without reserves,
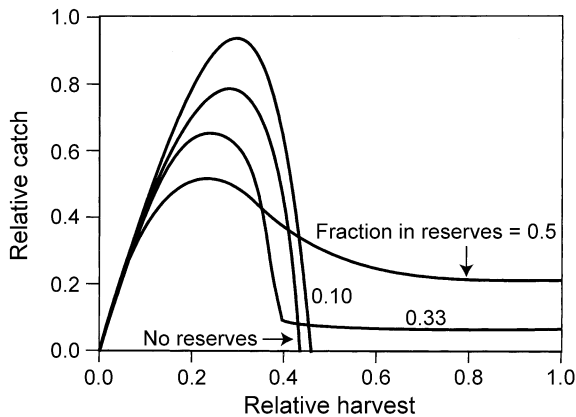
FIG. 1. Results from a model with 24 subpopulations linked by larval dispersal (Quinn et al. 1993) illustrate Principle 2 regarding the similarity of the effect on yield of increasing reserves to that of reducing harvest rate. At low harvest rates (fraction removed from fished area per year), relative catch (number removed plotted on an arbitrary scale) is reduced by increasing the fraction of subpopulations in reserves to a third or half (every third or every other population, respectively), but this is the fraction necessary to sustain the population at high harvest rates (redrawn from Quinn et al. [1993]).

as harvest rate increases catch first increases, then declines, with the population going extinct near a harvest rate of 0.6 yr$^{-1}$. Adding a reserve every sixth subpopulation reduces the maximum catch possible because the fishable area is reduced, and the population still goes extinct at high harvest rates ($>0.6$ yr$^{-1}$) in spite of the reserves. However, adding a reserve every third subpopulation increases catch at high harvest rate, and adding a reserve every other subpopulation provides an even higher sustained yield at high harvest rate.

Another source of this principle is the recent analysis of the question of whether management by reserves or conventional control of fishing mortality provided greater yield (Hastings and Botsford 1999). The result was that, for populations with the specific characteristics of post-dispersal density-dependence only, dispersal via a larval pool, and sedentary adults, the problem of choosing the optimal fraction in reserves was mathematically identical to that of choosing the optimal fishing mortality rate. While this equivalence strictly applies only to specific conditions, the result is useful as a benchmark (point of comparison) for populations with slightly different conditions. In many cases, the effect of the difference on this equality can be easily determined. For example, for populations with predispersal density dependence, since reserves increase predispersal density, conventional management will produce greater yields. This study also showed that the optimal area set aside in reserves was the same as the fractional escapement under conventional management for semelparous species, and that it was less for iteroparous species. Because the optimal escapement for a semelparous species can

be easily determined graphically from the stock–recruitment relationship, this provides an initial estimate of the maximum area in reserves.

The essence of this principle is also reflected in Mangel's (1998) analysis of reserves using a simple logistic model with an implicit larval pool. He demonstrated that yield depended only on the product of fishing mortality and area not in reserves, not on the specific values of each (see also Mangel 2000*b*).

### *Effects of movement on yield and persistence*

Because the implementation of marine reserves imposes spatial variability in mortality rate, species characteristics that change spatial distributions, i.e., movement during the larval, juvenile, or adult phases, have important implications for reserve design. Because different species can have different patterns of movement, whether it be random dispersal or directed migration, reserves can affect species differently. Managers need to know how reserves will affect species with different movement characteristics so that they can anticipate how reserves will affect target species, and predict differences in effects between species. The models that have examined the effects of dispersal on reserve effectiveness lead to the following principles.

*Principle 3: Reserves for preserving biodiversity are most effective for species with low rates of juvenile and adult movement, while reserves for fishery management are most effective for species with intermediate rates of adult movement.*—This principle is rather obvious for reserves for biodiversity, but it describes an important trade-off in reserves for fishery management. The fact that that the direct benefits to fishery yield from capturing juveniles and adults will be greatest for species with intermediate rates of juvenile and adult movement (i.e., home ranges smaller than reserve sizes) follows from analyses of the dependence of yield per recruit and eggs per recruit on the fraction placed in reserves (Polacheck 1990, DeMartini 1993). These analyses examined the consequences of reserves for species with different rates of adult and juvenile movement. Because the analyses are on a per-recruit basis, they do not include larval dispersal. For species with high rates of juvenile and adult movement, individuals spend too much time outside of reserves for the reserves to provide sufficient protection. For species with very low movement rates, i.e., sessile or sedentary species, individuals rarely move out of reserves, hence are rarely captured, and provide only the benefit of larval transport.

*Principle 4: Larger fractions of coastline in reserves are required for species with longer dispersal.*—This principle states that species with long-distance larval dispersal will generally require a greater fraction of the coast in reserves for the population to persist. A corollary of this principle is that a reserve of any specific size will provide for greater reproductive success in species with lower dispersal distances. This principle fol-

lows from the analysis by Botsford et al. (2001) of the effect of reserve configuration and larval dispersal distance on sustainability of a population. Their model included larval dispersal but no adult or juvenile movement. They computed the fraction of natural settlement that would result from various combinations of spacing and width of periodically spaced reserves assuming a Laplace dispersal kernel (i.e., decaying exponential in both directions) and an infinite coastline. For long-distance dispersers, the fraction of natural settlement was equal to the fraction of coastline in reserve, while for shorter distance dispersers, implementing reserves on the order of a mean dispersal distance could provide the same fraction of natural settlement with a lower fraction of the coastline in reserves.

This led to the question of what fraction of natural settlement is necessary for a sustainable population. This quantity is the same as the fraction of natural egg production in the life of a recruit, necessary for a sustainable population, a quantity used by fishery biologists to diagnose overfishing. Fishery biologists use values near 35%, though higher values may be necessary for some species (Clark 1991, Mace and Sissenwine 1993). Adoption of that value provided a range of sustainable reserve configurations from a high fraction (35%) of coastline in small reserves, relative to the dispersal distance, to a lower fraction in large reserves, approximately the mean dispersal distance in width (see Botsford et al. 2001 and Hastings and Botsford 2003 for further details and various trade-offs between these).

## DISCUSSION

These four principles address two of the foremost questions in the design of marine reserves: (1) how will their use in fishery management compare to using conventional methods, and (2) for both biodiversity and fishery management, how does the sustainability of populations in reserves of various spatial configurations depend on movement patterns of individuals? The answer to the former question, put simply, is that management using reserves produces roughly the same catch as the use of conventional management tools, with increasing reserves corresponding to reducing effort and increasing the size limit (Principles 1 and 2). While that statement requires some caveats regarding the effects of uncertainty, it leads to the question by managers, then why use reserves? One answer to this question is that they should be used because effort is so very difficult to control because of a constant resistance to catch limitations. Reserves provide a buffer against increasing effort (i.e., as in Fig. 1). However, we are learning that there is often the same resistance to the implementation of reserves that there is to catch limitation (e.g., Rieser 2000). Thus reserves are similar to conventional management in this respect also. This is important because that resistance (to reducing effort and implementing reserves), and its interaction with uncertainty through the

ratchet effect is a fundamental force driving overfishing (Ludwig et al. 1993, Botsford et al. 1997).

While the effects of reserves on age structure, and hence lifetime yield (i.e., yield per recruit) and reproduction (i.e., eggs per recruit), are about the same as raising the size limit (Principle 1), for some species at least, the effects on total yield of increasing the size limit and implementing reserves are also similar, in both the long and the short term (Sladeck Nowliss 2000).

The effects of differing rates of movement among species lend complexity to reserve design for both fishery management and preserving biodiversity. For fishery management, one would not employ reserves for species with highly mobile adults, and if they were used for sedentary species the benefit would be solely from larval export (Principle 3). A good example is the recent demonstration by Martell et al. (2000) that larger reserves would be needed for ling cod populations with small-scale movements. Principle 4, which addresses the effects of movement during the larval stage only, says that sustaining a species by reserves alone would nominally require ~35% or more of the coastline, but if that were not possible then either (1) effort would have to be controlled so that the shortfall in larval production was made up in the fished areas or (2) larger reserves could be employed with a lower fraction of coastline in reserves.

For the design of reserves to maintain biodiversity, the implications of the two principles regarding movement are, in one sense, less stringent; since the design is required to meet only the conditions for persistence, it does not have to maximize yield (see Hastings and Botsford 2003). However, they are more complex in the sense that they concern more than one species. Reserves that attempt to maintain a natural variety of species will not maintain species with high rates of juvenile and adult movement (Principle 3), and they will tend to maintain species with shorter larval dispersal distances, at the expense of long-distance dispersers (Principle 4). A secondary consequence is that they could provide a genetic selective pressure for lower juvenile and adult movement and shorter distance larval dispersal. Placing a larger fraction of the coastline in reserves reduces this problem, however, it is unlikely that fractions of coastline even as large as 35% will be placed in reserves in the near future.

Because reserves have been cited as a means of overcoming the uncertainty in fishery management by conventional means (Clark 1996, Botsford et al. 1997), it is surprising to some that the design principles for marine reserves, like conventional fishery management, depend on considerable uncertainty. As illustrated in Fig. 1, reserves reduce the risk of collapse due to uncertainty in the harvest rate. However, as discussed under Principle 4, sustainability of populations in reserves depends on dispersal distance and the fraction of lifetime reproduction necessary for persistence, both

of which are poorly known. When reserves are used to manage fisheries, their performance will also depend on how intensively the population is currently being fished, including how fishing effort shifts in response to implementation of reserves (e.g., Wilen et al. 2002). Most of these same uncertainties also affect the management of fisheries using conventional methods. Conventional fisheries management, however, has a well-developed theory for dealing with uncertainty by adjusting fishing intensity to produce various degrees of risk (e.g., Deriso 1985, Quinn and Deriso 1999).

The sensitivity of sustainability in marine reserves to uncertainty in dispersal distances is critical, since dispersal characteristics are known for only a handful of short-distance dispersers (Grantham et al. 2003, Shanks et al. 2003). There have been some attempts to incorporate larval linkages in models of reserve design (Roberts 1997, Crowder et al. 2000, Stockhausen et al. 2000), but the larval dispersal phase is in need of a stronger empirical foundation. Retention zones, areas that tend to accumulate larvae prior to settlement, are an aspect of larval dispersal of great importance to reserve design (e.g., Wing et al. 1998*a*, *b*, Warner et al. 2000). Exuma Cays Land and Sea Park in the Bahamas is a good example of recent empirical attention to movement issues as they affect the success of reserves (Chiappone and Sullivan Sealy 2000).

With regard to the uncertainty in the fraction of lifetime reproduction necessary for persistence, though the value typically agreed upon is 35%, empirical attempts to determine that value range from 20% to 70% (Mace and Sissenwine 1993). We note that the analysis qualitatively described here (Botsford et al. 2001) is not the same as arbitrarily setting aside a certain fraction of a species range as in Dahlgren and Sobel (2000), rather it involves calculating the fraction of lifetime reproduction needed for persistence (sustainability). The fraction of coastline needed and the size of reserves follow from the dispersal distance and the lifetime reproduction required for sustainability, rather than being chosen a priori.

Management of fisheries by conventional means and by reserves are susceptible to most of the same uncertainties, but with different relative susceptibilities. Both depend on uncertainty in the value of the fraction of lifetime reproduction necessary for persistence, but reserves are more sensitive to uncertainty in dispersal, while conventional management is more sensitive to uncertainty in harvest rate. This suggests that the combination of reserves and conventional management is a ''portfolio'' approach. Conventional fishery management has not been concerned in the past with knowing dispersal; spatial linkages have been largely ignored. As stocks become more intensively harvested, knowing the sources of recruits is becoming more important, especially in the presence of spatially varying harvest rates and productivity (e.g., Fogarty 1998).

Possible methods of coping with the uncertainties involved in the design and projected efficacy of marine reserves include decision analysis, meta-analysis, and adaptive management. Decision analysis makes management choices based on the expected outcomes, where that expectation is based on a statistical description of the uncertainties (Peterman and Anderson 1999). An example involving marine reserves is Botsford et al.'s (1999) use of decision analysis to accommodate the uncertainty involved in the fraction of lifetime reproduction needed for persistence. That study determined the fraction of coastline in reserves that maximized the expected value of catch over the distribution of values of the slope of the recruitment survival function at the origin, for the northern California red sea urchin fishery. A similar approach to uncertainty in dispersal patterns is taken in Morgan and Botsford (2001). For the same fishery, they determined the reserve configuration that maximized catch over the distribution of possible dispersal mechanisms.

The meta-analysis that would be useful in this context would be the ongoing efforts to establish relationships between poorly known quantities, such as dispersal characteristics and the fraction of lifetime reproduction required for persistence, and other life history characteristics (e.g., Myers et al. 1999). Knowledge that taxonomic (or other) categories of species had similar dispersal rates or similar required fractions of natural lifetime spawning, would reduce the uncertainty in the design process.

Adaptive management involves monitoring the consequences of management actions and responding to results (see Parma et al. 1998). The application of adaptive management suggested here is monitoring of responses to the use of various reserve configurations for various species. It is regrettable that very little of the information that has been collected from existing marine reserves is useful in the design of future reserve configurations. We need to know more than just whether individuals can become larger in reserves, and export individuals out of reserves. What is needed is information on species that do or do not persist in reserves of different sizes and spacing in different flow fields and community structures.

The principles distilled here from modeling studies of marine reserves (see Guenette et al. 1998 and Gerber et al. 2003 for reviews) appear to provide the beginning of a potentially valuable theory for the design of marine reserves. Further progress will be most rapid if future modeling results and empirical observations can be placed in the context of the relationships that have been thus far identified and described here. Since the design of reserves depends on a complex combination of interacting factors, the challenge will be to design future modeling studies and empirical assessments so that they assess new dependencies other than those described here, without confounding effects. Additional

modeling is needed in at least three important areas: (1) the relative susceptibility to uncertainty of conventional fishery management vs. management by reserves, (2) how to site reserves with regard to local productivity and dispersal paths, (3) the effects of the other significant source of movement, the response of fishers to implementation of marine reserves. There have been several analyses of how reserves can reduce susceptibility to uncertainty (Lauck et al. 1988, Mangel 2000a, Allison et al. 2003), but no studies comparing uncertainties in conventional management to those in management with reserves. There has also been at least one study directed at the second subject (Tuck and Possingham 2000). Tuck and Possingham used a two-patch model with simplified larval redistribution to show that sources should be protected. It seems there would be more to learn regarding more realistic models incorporating coastal circulation (e.g., Morgan and Botsford 2001). Wilen et al. (2002) have begun investigation of the third issue by showing how spatial distributions of various characteristics change with the addition of fisher movement.

In summary, there appears to be a promising initial understanding of how to design systems of marine reserves and estimate their benefits to coastal ecosystems. There is also good reason to expect that even better understanding is possible through similar additional modeling studies. It would also seem beneficial to begin to integrate the general findings summarized here into the ongoing discussion of the need for marine reserves. With the high degree of uncertainty inherent in the management of marine ecosystems, we need to minimize any additional uncertainty caused by unrealistic expectations regarding the future benefits of this promising management tool.

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