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POPULATION MODELS FOR MARINE RESERVE DESIGN: A RETROSPECTIVE AND PROSPECTIVE SYNTHESIS

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Abstract. We synthesize results from existing models of marine reserves to identify key theoretical issues that appear to be well understood, as well as issues in need of further exploration. Models of marine reserves are relatively new in the scientific literature; 32 of the 34 theoretical papers we reviewed were published after 1990. These models have focused primarily on questions concerning fishery management at the expense of other objectives such as conservation, scientific understanding, recreation, education, and tourism. Roughly one-third of the models analyze effects on cohorts while the remaining models have some form of complete population dynamics. Few models explicitly include larval dispersal. In a fisheries context, the primary conclusion drawn by many of the complete population models is that reserves increase yield when populations would otherwise be overfished. A second conclusion, resulting primarily from single-cohort models, is that reserves will provide fewer benefits for species with greater adult rates of movement. Although some models are beginning to yield information on the spatial configurations of reserves required for populations with specific dispersal distances to persist, it remains an aspect of reserve design in need of further analysis. Other outstanding issues include the effects of (1) particular forms of density dependence, (2) multispecies interactions, (3) fisher behavior, and (4) effects of concentrated fishing on habitat. Model results indicate that marine reserves could play a beneficial role in the protection of marine systems against overfishing. Additional modeling and analysis will greatly improve prospects for a better understanding of the potential of marine reserves for conserving biodiversity.

Key words: biodiversity; conservation; density dependence; larval pool; marine protected area; migration; population model; spatial harvest; stochasticity; yield per recruit.

INTRODUCTION

Marine reserves have become a widely advocated approach to marine conservation, and the number of newly established no-take reserves has increased dramatically in recent years (Allison et al. 1998, Palumbi 2000). Although the current fraction of the world's coastal waters fully protected in marine reserves is extremely small and unevenly distributed, the move to expand marine reserve networks is international. In the midst of this effort toward the establishment of marine protected areas (MPAs), some fundamental questions remain largely unresolved. Under what conditions are marine reserves beneficial? How do movement rates influence the potential benefit of marine reserves? How big should a single marine reserve be? What fraction of a particular region should be conserved? What sort of protection should marine reserves afford to organisms, habitats, and ecosystem processes? Where should marine reserves be sited? Can we design effective networks of marine reserves, given our imperfect knowledge of marine populations and ecosystems? Here we assess the state of mathematical theory to answer these questions.

Although there is a well-developed theory of terrestrial reserves (Gilpin and Diamond 1980, Higgs and Usher 1980, Pressey et al. 1993, Possingham et al. 2000), a corresponding theory for marine systems is nascent. In addition, the theory that has been developed for marine reserves differs markedly from terrestrial reserve theory (Carr et al. 2003). Terrestrial reserve models often are based on assumptions from island biogeography theory or focus on the representative selection of different habitat types. Consequently, they

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tend to focus on preserving species or habitat richness and effects of fragmentation on metapopulations of reserves. In contrast, existing marine reserve models are generally targeted at single species, with an emphasis on population dynamics under conditions of human exploitation, while neglecting the details of multispecies, biogeographic patterns.

Although there has been an increase in the number of marine reserves designated to conserve marine species, there has not been a concomitant increase in our understanding of marine reserve theory. In many cases, resource managers and stakeholders expect to see major benefits in the short term after establishment of a marine protected area (e.g., a 5-yr time frame was proposed to determine efficacy of no-take zones in the Channel Islands Marine Sanctuary, Aramié et al. 2003). Thus, an important question from a modeling standpoint is the development of theoretical approaches that allow us to predict biologically reasonable time frames under which MPAs will be tractable in monitoring efforts. Further, continually updating models with empirical data from monitoring efforts will ensure that models reflect the best available scientific information (National Research Council [NRC] 2001).

In addition to the scientific challenges we face in designing marine reserves, there are management challenges that arise from social, economic, and institutional entities (NRC 2001). Responsible agencies are charged with the task of balancing the needs of stakeholders with goals to ensure persistence of marine populations. Confounding this problem are the fragmented local, state, federal, and international entities responsible for governing the worlds oceans. While these issues are beyond the scope of our review, moving toward interagency cooperation in implementing MPAs is therefore critically important to resolve the complex and often conflicting jurisdictional responsibilities governing the worlds oceans (NRC 2001).

We review existing marine reserve models with three goals in mind. First, in an effort to look for robust conclusions that are independent of model details, we classify existing models, clustering them primarily by whether the model is for single or multiple species, key life-cycle elements, larval redistribution mode, density-dependent recruitment mode, and whether adult migration, stochasticity, and rotating spatial harvest are included in the model. Second, we summarize the findings of existing models and the implications for marine reserve design. Finally, we identify key theoretical issues relevant to marine reserves that remain largely unexplored and could profitably be addressed in the future.

The aim of this synthesis is to satisfy some of the urgent needs of policy makers and managers for guidance on how to design scientifically defensible marine reserve networks. We provide this guidance by synthesizing results to date and proposing future directions. While a variety of papers have indirect implications for marine reserves, we limit our review to published population models that explicitly address critical questions in marine reserve design. Before delving into our analyses of existing models, we briefly describe the characteristics of the marine reserve problem: (1) the objective of the modeling, (2) the control variables, and (3) the societal goals for reserves.

Objective of Models—Strategic vs. Tactical Situations

Models can be either strategic or tactical (Levins 1966), and both types of models are needed for marine reserves. Strategic models tend to be simpler, with less detail, and they are developed to answer broad, overarching questions. For marine reserves, they would provide insights into key considerations for the design and implementation of reserves, such as what fraction of a given area (e.g., coastline, habitat type, species range) should be placed in the reserve system, how many reserves do we need, what is the optimal distribution of reserves, how will stochasticity influence the effectiveness of reserves, and which types of data are most critical to obtain. In contrast, tactical models are often more complex, containing details appropriate to specific situations, and they are often designed to make local decisions regarding a specific situation. In the case of reserves, they would be models created for the design of particular reserves or decisions about management of a particular system or species. Without strategic models to provide general principles, it is more difficult to structure the analyses and interpret the output from tactical models, and to extrapolate robust generalizations from specific models. Similarly, strategic models alone, in the absence of tactical models, may be too abstract to provide practical guidance for specific decisions. Strategic models dominate most of the existing literature on models of marine reserves, as one might expect in these early stages of development. Future development of tactical models is therefore needed to complement existing models and progress toward a general theory of marine reserves.

Control Variables

To be useful, models must include control variables that we actually have the potential to influence through management or policy actions. Possible control variables include the number of reserves, size of reserve, and fishing effort outside the reserve. The choice of a particular control variable depends on the objective of the model and will fundamentally influence results and recommendations. As such, it is important to explicitly state all control variables. For example, because no-take reserves are generally proposed in the context of existing fishery management schemes, activities outside of reserves will also influence the efficacy of the reserve.

The usual control variable is the fraction of the area protected. However, whether fishing effort or size limits are also being managed will have a profound influence on model results.

OBJECTIVE OF RESERVES

Any approach to understanding the utility of reserves has to be developed in the context of the objective of the reserve (Agardy 1994). Possible objectives that could be assessed through modeling are: to maximize population abundance, to minimize rate of population decline, or to minimize the probability that the population falls below some quasi-extinction threshold. Models may be used to estimate the measurable change in abundance after reserve establishment, time to reach steady state after establishment, and cumulative increase after reserve establishment (NRC 2001). For reserves designed to enhance fisheries the primary goal to assess would be the increase in equilibrium yield. However, managers may not have a single clear objective. Most marine reserve models have been developed in the context of increasing various measures of fishery yield, some models have focused on population persistence, but few have sought to decrease extinction probability or maintain diversity. Even if, ultimately, the objective is to have multipurpose reserves, initial theoretical approaches will have to be designed to focus on a single objective, or a weighted set of objectives, and the objective will need to be stated precisely. We therefore briefly summarize some of the primary objectives of marine reserves.

Biodiversity and conservation

One important, potential goal of reserves is the preservation of biodiversity. To make this goal operational, investigators typically focus on specific single characteristics, such as persistence of a single species, maintenance of genetic diversity, maintenance of species diversity, or maintenance of ecosystem services. The fact that we know of only one multispecies marine reserve model (Walters et al. 1997, Walters 2000; see *Management of renewable resources*) indicates that marine reserve theory has emphasized single species issues at the expense of multispecies considerations. Multiple-species considerations have been limited to comparisons of responses by species with different life history traits. Even so, issues of species viability have just begun to be explored (Botsford et al. 2001, Gerber et al. 2002, Gaines et al. 2003). In cases where the goal is to recover a threatened or endangered population, a focus on the viability, or persistence, of that population would be appropriate. A more detailed view would not focus solely on the persistence of a species at acceptable species abundance, but would explore the genetic diversity of the species, and how that might be affected by marine reserves (Palumbi 2003).

Taking a single-species approach neglects a number of important issues, such as the nature of species interactions, including competition and predation. By focusing only on a single species, one will miss some of the features that change the impact of marine reserves—a system that might appear to preserve a target species of interest, but not its prey, would ultimately fail. Additionally, such a system might fail to adequately protect wide-ranging apex predators. Unlike most marine reserves, in terrestrial systems, reserve size is often indexed to the area required for a viable population of top predators. To incorporate multispecies dynamics into marine reserve models, one might consider the distribution of top predators as indicators of biodiversity hotspots (Reeves 2000), a description of several populations of a small number of species (Neigel 2003) or a community or habitat approach. Additionally, an approach based on communities or habitats naturally leads to one based on habitat representation, asking whether a system of reserves preserves not just biodiversity, but also some of the consequences of the biodiversity for ecosystem services.

Management of renewable resources

Management of renewable resources leads to a very different set of objectives for reserves than approaches focused on maintenance of biodiversity. In the management of a renewable resource, the main objective is usually to maximize sustainable yield, but other objectives, such as minimizing the risk of collapse, minimizing the susceptibility to poorly known parameters, and minimizing variability in catch are also important (Hilborn and Walters 1992, Hilborn et al. 1995, Shea et al. 1998). Some analyses have assessed measures of the transient effects of implementing a reserve, such as the drop in catch immediately after implementation, the time to reach steady state, and the present value of the catch (e.g., Holland and Brazee 1996, Botsford et al. 1999, Sladek Nowlis and Roberts 1999, Gerber et al. 2002). In the past decade, fishery analysts have become increasingly concerned about preventing overfishing (Sissenwine and Shepherd 1987), and many fishery management plans now involve a sustainability threshold below which drastic actions are taken, in addition to the target of maximum yield (Caddy and Mahon 1995). These thresholds are chosen to indicate the reproductive potential of the population, and reserves are essentially a new tool for maintaining that potential (Botsford et al. 2001, 2003, Hastings and Botsford 2003).

Scientific research, education, recreation, tourism

Marine reserves can provide opportunities for educational, recreational, and economic activities (Allison et al. 1998, Ballantine 1991). No-take zones in the marine environment are important venues for scientific research providing a ‘‘control’’ from which to explore the impact of human exploitation. However, few marine reserves have been established in prime fish habitat (as these areas are defended by fishers), just as U.S. National Parks generally occur on land that is unsuitable for farming or grazing. Economics-based behavioral models that incorporate uncertainties associated with fishermen behavior merit further investigation (Sanchiro and Wilen 2001). Theoretical examinations of the economic value of marine reserves have been hindered by the difficulties associated with measuring nonmarket benefits. Further, measuring the benefits and costs of marine reserves is obscured by perceived and de facto property rights to marine reserves (NRC 2001).

It is important to consider these societal goals as we explore existing marine reserve models. Models can be used to answer questions regarding the design of marine reserves, but the answers will depend on the goals or criteria used. We will need to consider a range of criteria to develop a robust theory of marine reserves. Next we will classify existing marine reserve models to identify what we have learned from them as a basis for identifying needs for further development of models of marine reserves.

A Taxonomy of Existing Models

Models that have been developed explicitly for marine reserves are relatively new in the scientific literature. Only two of the 34 modeling papers we reviewed were published before 1990 (Beverton and Holt 1957, Sluczanowski 1984). To see how the field is evolving, we start with a classification of models based on the features they include. Much like biological taxonomy, the models can be divided between a number of natural dichotomies: (1) single- vs. multispecies models, (2) whole life cycle vs. cohort models, (3) dispersing vs. local recruitment, (4) pre- vs. postdispersal density dependence, (5) unstructured vs. age/size-structured populations, (6) dispersing vs. resident adults, (7) deterministic vs. stochastic dynamics, and (8) permanent vs. rotating reserves. While other distinguishing features might be relevant to classifying marine reserve models, the above eight features encompass the critical assumptions of existing marine reserve models. Table 1 provides a synthesis of how existing models can be classified within this taxonomy, as well as important results and recommendations for future research. Before discussing the details of the clustering of particular models within these broad categories, we briefly examine each dichotomy.

Single vs. multispecies.—Despite broad discussion of the need to consider multispecies issues in marine conservation and fisheries management (Gerber et al. 1999, NRC 1999, 2001) we know of only one model that focuses explicitly on multispecies aspects of marine reserves (Walters et al. 1997, Walters 2000). Based on the ECOPATH modeling framework, this spatially explicit model estimates changes in biomass after reserve establishment based on trophic interactions. A few additional models address multispecies issues indirectly by comparing how reserves will impact species with different life-history characteristics (e.g., DeMartini 1993, Attwood and Bennett 1995, Sladek Nowlis and Roberts 1999, Botsford et al. 2001, Gaines et al. 2003). None of these models, however, include species interactions. Rather they compare results from single-species models with parameter values chosen to represent different life-history classes.

Single cohort vs. multigeneration models.—Some models follow an approach, commonly used in fisheries, which omits all aspects of reproduction that occur after egg production, primarily because they are poorly known (Beverton and Holt 1957, Botsford and Hobbs 1986). These models follow a cohort, computing the effects on cohort abundance vs. age for (1) fishing at different intensities over different ages, and (2) placing different fractions of the cohort in reserves. From abundance vs. age and the dependence of weight and fecundity on age, they calculate the biomass yield in the lifetime of a cohort, normalized to yield per recruit (YPR), and egg production normalized to eggs per recruit (EPR), respectively (Beverton and Holt 1957, Polachek 1990, DeMartini 1993, Botsford and Hobbs 1986). Because fecundity varies with age in approximately the same way as biomass of mature fish, spawning stock biomass per recruit (SSB/R) is commonly used instead of eggs per recruit (EPR). For simplicity, we use EPR here and make no distinction between the two. The YPR/EPR approach is strategic in the sense that it illuminates the effects of fishing and reserves on yield and the potential for reproduction without allowing them to be occluded by the poorly known relationship between egg production and recruitment.

Other models explicitly include the complete life cycle in a multigeneration framework (Quinn et al. 1993, Attwood and Bennett 1995, Holland and Brazee 1996, Sladek Nowlis and Yolalovich 1998, Sladek Nowlis and Roberts 1999, Crowder et al. 2000, Gerber et al. 2002, Gaines et al. 2003). Some of these models explicitly incorporate larval dispersal for species with planktonic larvae while others make simplifying assumptions about the distribution of larvae.

Explicit dispersal vs. a larval pool.—One of the most daunting theoretical challenges facing studies of the impact of marine reserves is understanding the influence of dispersal among reserves. The prominence of marine life histories with planktonic larvae means that dispersal of juveniles will be a key component of the connectivity between marine populations. Few models have attempted to explicitly consider the dispersal of larvae along a coastline (Quinn et al. 1993, Attwood and Bennett 1995, Stockhausen et al. 2000, Armsworth et al. 2001, Botsford et al. 2001, Gaines et al. 2003). Rather, most models have simplified the problem by considering the plankton as a well-mixed larval pool. Planktonic larvae produced along a continuous coastline (Holland and Brazee 1996, Sladek Nowlis and Roberts 1999) or from discrete sites (Lindholm et al. 1998) enter a common larval pool and are redistributed equally among adult populations. We refer to this simplification as the larval pool, equal redistribution assumption (LPER). The last half of this assumption (equal redistribution) is also implicitly made in single cohort models. The models of Tuck and Possingham (1994, 2000) differ by allowing nonsymmetric movement between two adult sites. This approach assumes, however, that the details of larval dispersal do not affect the conclusions.

Pre- vs. postdispersal density dependence.—Density dependence occurs solely in recruitment in the models reviewed. When dispersal is included in models, one must specify whether the density dependence in recruitment occurs before or after dispersal (e.g., Botsford et al. 1994). A few models include predispersal density dependence within the adult phase, wherein the density of adults influences the per-capita production of larvae prior to their dispersal (e.g., Quinn et al. 1993). However, the vast majority of reserve models include only postdispersal density dependence, which yields an effect of density on recruitment to a particular site (e.g., Holland and Brazee 1996, Sladek Nowlis and Roberts 1999, Gaines et al. 2003). Postdispersal density dependence can be either an effect of the density of larvae, the density of adults, or both on per-capita recruitment rates. The forms of density dependence in recruitment can be quite diverse, but two common families of functions dominated the models reviewed—an asymptotic relationship between density and recruitment (e.g., a Beverton-Holt type; Beverton and Holt 1957) vs. a "humped" relationship, wherein total recruitment declines at high densities (e.g., a logistic or a Ricker type; Ricker 1954).

Unstructured vs. age/size-structured populations.—The majority of models include no population structure. A few models include explicit age structure (Holland and Brazee 1996, Lindholm et al. 1998) or size structure (Quinn et al. 1993, Sladek Nowlis and Roberts 1999). The single-cohort models include age or size structure as the emphasis for the age at which to begin harvesting a cohort to maximize yield per recruit.

Dispersing vs. resident adults.—Although adult movement into and out of reserves is likely to be important for many pelagic species (as opposed to benthic or intertidal species) it has only been included in a few models (e.g., Pitcher et al. 2000). For the most part, adult movement has been the focus of the single-cohort models (Polachek 1990, DeMartini 1993).

Deterministic vs. stochastic/uncertain world.—Even though many marine populations exhibit highly stochastic recruitment, and population dynamics are poorly understood, most of the models included neither process error nor observation error. This is in contrast to fishery models that routinely strive to take uncertainty into account (e.g., Hilborn and Walters 1992, Ludwig et al. 1993). A randomly varying recruitment term is included in a few models, examining the effects of reserves on damping variability and environmental uncertainty (Sladek Nowlis and Roberts 1999, Mangel 2000*b*). Another model includes randomly varying fishing mortality rate as a means of assessing uncertainty in estimating and controlling fishing mortality rate (Lauck et al. 1998). Few fisheries management models incorporate uncertainty associated with fishermen behavior (Sanchiro and Wilen 2001).

Permanent vs. rotating reserves.—A modified version of a permanent marine reserve is a rotating spatial harvest (RSH). The coastline is divided into a number of management zones and each management zone is fished only once every specified number of years, where the rotation period typically is varied from two to five years. For example, RSH was practiced until recently in the fishery for the red sea urchin in the state of Washington (Pfister and Bradbury 1996) and is being considered as a fishery management tool on Georges Bank (Murawski et al. 2000).

IMPLICATIONS OF MODEL FINDINGS FOR RESERVE DESIGN

Single-cohort models: yield per recruit and eggs per recruit

Beverton and Holt first broached the impact of unfished areas on the yield to a fishery in their classic tome on fisheries management (Beverton and Holt 1957; see also Guenette et al. 1998). Beverton and Holt formulated models of cohorts with natural mortality, fishing mortality (with a single age of first capture), and movement between areas proportional to abundance in the source area. The transfer coefficient, depicting the fraction of individuals moving from one area to another per unit time, depends on the propensity for movement and the shapes of the areas (i.e., it is proportional to the relative perimeter of each area). Their results indicate that the effect of increasing reserve area is similar to increasing the lower age limit of the fishery. As the amount of unfished area increased, the shape of the dependence of YPR on fishing mortality rate (F) changed from one that would result from the assumed age of first capture to one that would result from a higher age of first capture (compare Fig. 1A to Fig. 1B). This essentially follows from the fact that increased protected area leads to increased survival and an older age distribution. To obtain a more realistic view of what might occur if marine reserves were instituted, they assumed that the original fishing effort would be concentrated outside of the reserves (i.e., fishing mortality rate would be multiplied by the ratio of fished areas to unfished areas). With this assumption, at low reserve fractions, fishery yield increased with increasing fraction in reserves when that fraction was

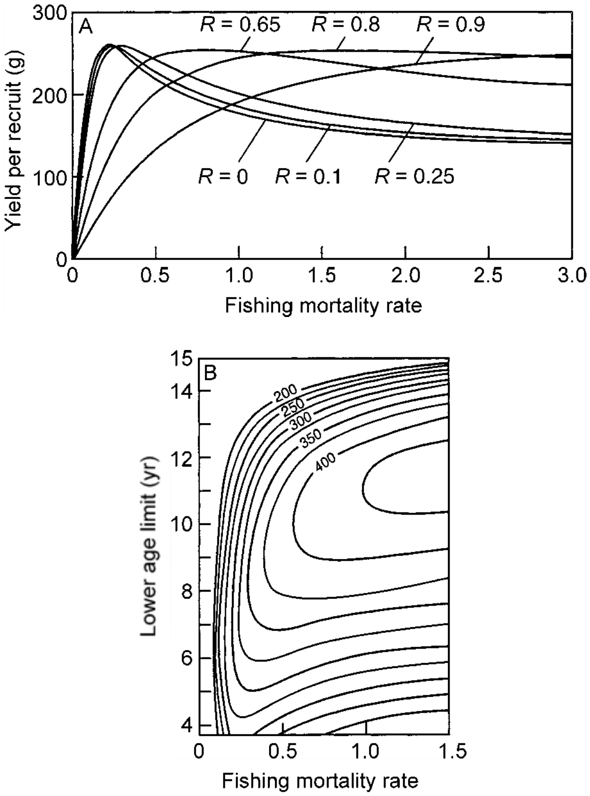

FIG. 1. A comparison of the effects on the yield per recruit at each fishing mortality rate of (A) placing increasing area in reserves (R = fraction of area in reserves) with the effects of (B) changing the lower age limit of the fishery. Life-history parameters are for plaice in the North Sea. This comparison shows that placing increased area in reserves is similar to moving the lower age limit to higher values. The figure is redrawn from Beverton and Holt (1957).

low, but decreased when the fraction in reserves was high, generating an optimal reserve fraction (Fig. 1).

Based on Beverton and Holt's model, Polachek (1990) used a two-component spatial model to consider the fate of a single cohort when only a portion of the population is vulnerable to fishing. The Beverton and Holt (1957) model was extended to include non-knife-edge net selectivity (i.e., an approximation for gear selectivity). As the relative sizes of the reserve vs. the fished area varied, effort was redistributed accordingly. Polachek (1990) found that reserves had a low potential for increasing YPR beyond what was possible by controlling effort, but that higher EPR was possible, especially at lower movement rates. As movement rates increased, larger areas were needed for reserves to achieve gains.

DeMartini (1993) used Polachek's (1990) model to assess the impact of reserves on three reef fishes with different life histories. DeMartini's (1993) conclusions mirror those of Polachek; he found little increase in YPR with the addition of reserves, but that their addition increased EPR. In addition he found that (1) for the species with high movement rates, potential gains in EPR were negated by movement out of the reserve and subsequent capture; (2) for the species with low movement rates, gains in YPR were low because individuals rarely moved out of the reserves to be captured; but that (3) gains in EPR were greatest for the species with low movement rates. DeMartini's results indicate graphically the lack of effect on both EPR and YPR for low fishing mortality rates (e.g., $F < 0.5$; Fig. 2). They also show that for larger values of F (e.g., $F = 1.5$), there is a greater change in EPR and greater values of EPR (expressed as a fraction of the pristine state) for species with lower rates of movement (Fig. 2). Further, they indicate that for species with low rates of movement, when half of the area is placed in reserves, YPR declines by about half, while YPR can actually increase for species with higher rates of movement (Fig. 2). Russ et al. (1992) also used Beverton and Holt's (1957) model described above to examine the effects of fluxes of postsettlement fishes across the boundaries of a reserve in the Philippines. Similar to

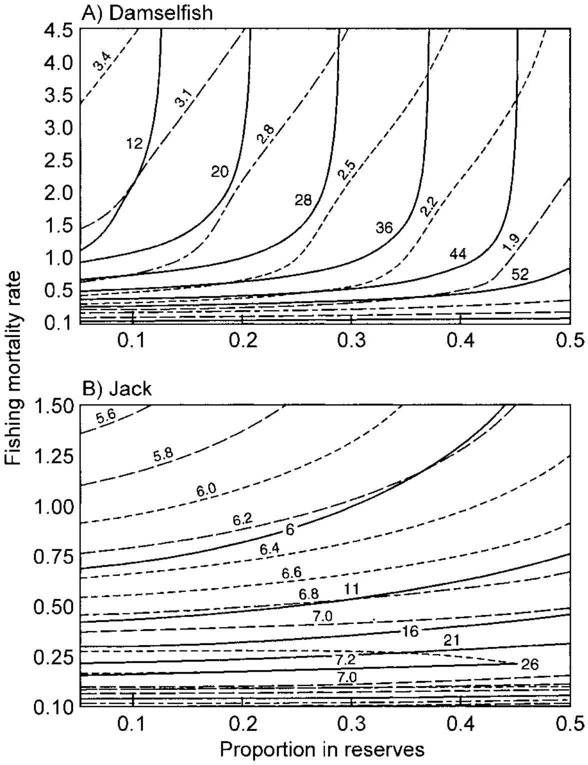

FIG. 2. Lines of constant yield per recruit (YPR; dashed lines) and constant eggs per recruit (EPR; solid lines) over a range of values of fishing mortality rate, F, and fraction of area in reserves, R, for two species of reef fish. The movement rate across boundaries for the jack is 25 times that for the damselfish. Reserves appear to have little effect at low fishing mortality rates; at higher fishing rates, they have a greater effect on EPR for species with lower movement rates. Redrawn from DeMartini (1993).

Polachek and DeMartini, they found that reserves enhanced YPR only at high levels of fishing mortality.

Taken as a whole, these single-cohort models have allowed analysts to determine the effects of reserves on a cohort's postrecruitment mortality. One advantage to this approach is that the consequences of reserves on cohort abundance, yield and egg production can be isolated without being affected by changes in recruitment. This approach assumes that features of reserve design will not impact recruitment per se, but will impact how that recruitment gets expressed. Instead of removals depending solely on fishing mortality rate, they depend on the reserve size and configuration, how fishing mortality is redistributed, and movement rates of fish. YPR/EPR models indicate that reserves may increase the minimum age in the fishery and increase the fishing mortality rate by concentrating effort. The key insight is that isolation of the cohort effects from those of larval transport and recruitment suggests that moderate rates of random juvenile and adult movement will be optimal (see description of DeMartini in the previous paragraph). Very low and very high rates are suboptimal. High adult movement allows little protection of EPR by reserves, and low adult movement allows no increase in catch per unit area protected. Results for complete populations may, of course, be different in light of the effects of larval dispersal, but it is useful to isolate the effects of reproduction.

In addition to these assessments of permanent reserves on both juvenile and adult stages, others using single-cohort models have focused on ontogenetic closures and rotating closures. For example, Die and Watson (1992) calculated yield, market value, and eggs per recruit to evaluate the use of spatial closures as a proxy for seasonal closures and a size limit. Because separate cohorts of shrimp populations develop through the year in nearshore waters, and younger, smaller shrimp are spatially segregated, a spatial closure accomplishes the goal of not allowing harvest of smaller individuals. Interestingly, Die and Watson (1992) found that increasing the size of reserves had little effect on YPR but a strong positive effect on EPR.

Similarly, Lindholm et al. (1998) used a spatially explicit, age-structured, dynamic model to evaluate the significance of marine reserves on survivorship of 0-yr fish over a 12-mo period. They found that the export of fish beyond the reserve was sensitive to reserve configuration. As protected areas were increased, the survivorship outside of reserves fluctuates with configuration of new portions of reserve. They concluded that the design of marine protected areas is sensitive to juvenile migration rates and the size of the population targeted for protection. Thus, they propose that habitats outside of reserves are particularly important to juvenile survival.

Sluczanowski (1984) also used a model similar to the Beverton-Holt model to describe how the biomass, YPR and the number of eggs produced depend on the period between intensive fishing visits in a rotating spatial harvest scheme (RSH). He suggested that longer closures may significantly increase egg production while causing only a marginal increase in yield. Botsford et al. (1994, 1998) also examined the advantages of RSH, using a size-structured model for a fishery on a species with an Allee effect in recruitment. The Allee effect in this case was represented as a decline in efficiency of broadcast spawning in the red sea urchin in northern California. Specifically, egg production declined to insignificant levels when spawning density fell below a certain threshold. They showed that RSH produced no significant difference in YPR characteristics; the frequency of harvest merely replaced and played the same role as fishing mortality rate. As rotation frequency increased YPR increased, as it would if fishing mortality rate were increased. However, there was a significant improvement in EPR. With constant fishing at high rates spawning biomass was always less than the threshold of the Allee effect, but with RSH, low enough rotation rates allowed the density of spawning adults to increase occasionally to a value greater than the threshold, thus preventing recruitment overfishing.

Pfister and Bradbury (1996) also assessed rotating spatial harvest in the Washington state red sea urchin fishery using a three-stage model. We address their results under cohort approaches because their model was driven by constant recruitment. Their model also included immigration into every stage, which will have an unusual effect on dynamics and may also be biologically unrealistic for the species, since adults are sedentary. Their results for different fishing rates and rotation rates are given in terms of the number of harvestable urchins, rather than the number caught, so it is difficult to compare them to the other studies here which give results in terms of biomass caught. When an Allee effect was added, the population declined continuously for all combinations of fishing rate and rotation rate.

One generality from modeling work that explicitly considers RSH in marine reserve design is that the period between harvests is likely to be a significant factor influencing the efficacy of the particular reserve. This will be a fruitful intersection of theory and practice as we begin to develop experimental approaches to examine the efficacy of MPAs.

Models with complete life-cycle dynamics

Population models that include explicit reproduction allow the most comprehensive assessment of the effect of marine reserves on single populations. However, because they include more detail, the mechanisms underlying results are more difficult to determine and tend to be more tactical as opposed to strategic. In spite of this specificity, they do seem to consistently obtain a

TABLE 1. Classification of published marine reserve models, indicating number of models categorized in each class of model attributes within our taxonomy, general approach and relevant findings, and recommendations for future modeling work on marine reserves.

Model attribute and number of models	Approach and findings	Issues in need of further exploration
Number of species Single species: 33 Multispecies: 1	Including trophic responses likely to reduce efficacy of MPAs	Single-species models may suggest optimistic results; future models should examine effects of multispecies interactions.
Life cycle Explicit reproduction: 22 Single cohort: 12	Single-cohort models allow assessment of effects of reserve, given lack of data on relationship between egg production and recruitment	Need data on recruitment patterns, spatial relationships, and physical oceanography for multigeneration models.
Larval dispersal Expicit dispersal: 7 Larval pool: 23 None: 4	Most models assume simplified mixed larval pool redistributed equally among adult populations	Few models have attempted to consider dispersal of larvae along a coastline explicitly.
Density dependence Predispersal: 8 Postdispersal: 26	Postdispersal density dependence affects recruitment at a particular site while postdispersal dependence can measure effect of density of larvae, adults, or both on recruitment	Predispersal density dependence should be explored in future marine-reserve modeling endeavors.
Population structure Unstructured: 21 Structured: 13	While most models include no population structure, some include age or size structure	Models that do not explicitly incorporate population structure ignore important biological features.
Adult movement Dispersing: 9 Resident: 25	Most models for benthic and intertidal species appropriately assume no dispersal of adults	Adult movement is likely to be important for many marine species and should be incorporated in future models.
Population dynamic Deterministic: 29 Stochastic: 5	Most models include neither process error nor observation error	Models for marine populations should examine effects of stochastic recruitment as well as parameter uncertainty.
Reserve position Permanent: 28 Rotating: 6	Few models have considered effects of rotating spatial harvest on reserve efficacy	Spatial rotation of reserve zones should be considered as a management option in future marine reserve models.

common result that reserves are of value only when fishing effort is high enough that the population would otherwise be recruitment overfished. For populations with complex life-cycle dynamics, the specific approaches taken to incorporate density dependence, recruitment, population structure, adult movement, population dynamics, and reserve position (Table 1) will have important implications for model results. Here we describe structured models first, then describe approaches with logistic or Ricker models with no age structure.

Quinn et al. (1993) used a 24-stage-structured model with explicit larval dispersal, density-dependent fecundity, and two Allee effects (limited fertilization success of the broadcast spawner at low densities and a refuge for juveniles beneath the spine canopy of adults), to represent the dynamics of red sea urchins distributed along the northern California coast. As harvest rate increased, in cases with no reserves or with reserves spaced too far apart, yield increased to a maximum, then declined to zero. With reserves close enough, relative to dispersal distance, yield increased to a lower maximum, but did not decline to zero, even when harvest rate was 1.0. The requirements for an effective reserve system varied with the scale of dispersal and the nature of the two depensatory mechanisms (fertilization success and juvenile refuges). Their results suggest that multiple reserves, spaced more closely than the mean larval dispersal distance, appear to be an effective conservation strategy to guard against increasing fishing effort.

Attwood and Bennett (1995) also used an age-structured model to assess the benefits of reserves for three recreationally fished species. For two of the species, white steenbras and galjoen, juvenile and adult migration were important, whereas for the third, more sedentary species, blacktail, only larval dispersal was important. Although reproduction was included for all three species, recruitment was set to decline when the population declined past one-tenth of the unfished spawning biomass (a value rarely reached). Results were presented in terms of the way that yield, YPR, and spawning-stock biomass depend on reserve size and spacing, where spawning-stock biomass (SSB) represented the total size of all sexually mature fish in the population. In all three species, YPR was insensitive to the addition of reserves beyond the optimal value of fishing mortality rate. The addition of reserves, how-

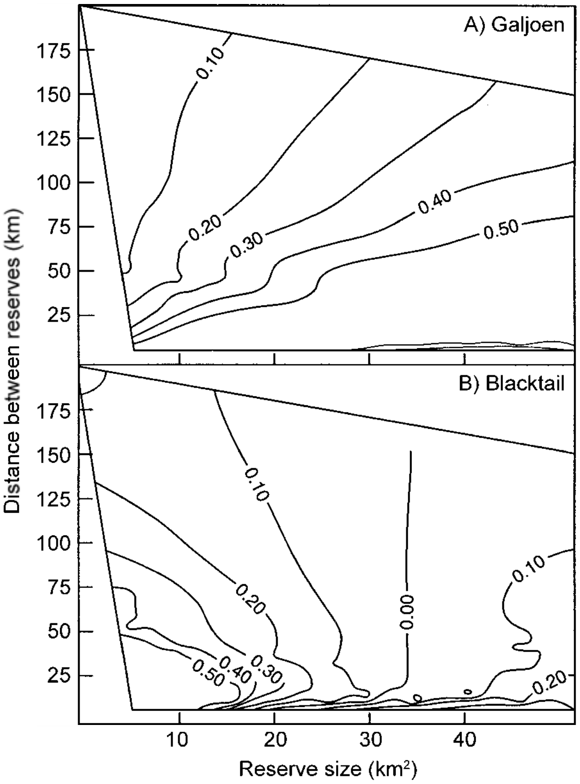

FIG. 3. Contours of yield for two species of southern African fishes: a species with significant adult movement galjoen (*Dichistius capensis*) and a species for which the dominant movement is in the larval stage (blacktail, *Diplodus sargus capensis*). Yield is expressed as the fractional increase relative to the yield with no reserves. For the former, yield appears to depend on the fraction of the coastline in reserves, while for the latter it does not. The figure is redrawn from Attwood and Bennett (1995).

ever, did increase EPR. For the species without larval dispersal, contours of both YPR and SSB followed lines of constant fraction in reserves when plotted against reserve size and spacing. Thus, yield for these species would also depend on the fraction in reserves (e.g., Fig. 3A). Yield for the species with larval dispersal, however, depended more on reserve size than on spacing, and increasing the size of reserves beyond 30 km led to no subsequent increase in yield (Fig. 3). In a step toward multispecies evaluation of reserves, Attwood and Bennett (1995) determined the region of the reserve size and space that would satisfy the requirements of all three species.

Holland and Brazee (1996) also used an age-structured model with postsettlement compensatory density-dependent recruitment, adult migration, and the LPER assumption for larval dispersal. They evaluated the catch obtained with different reserve designs under various levels of fishing effort, using parameter values from red snapper in the Gulf of Mexico. Their analysis evaluated the transient effect of reduced catch immediately after imposing reserves by using catch discounted over 60 yr (i.e., present value) as their objective criterion. Reserves provided no benefit if effort could be controlled. This is apparent in their results for different fishing mortality rates (Fig. 4). If fishing mortality rate was low ($F = 0.75$ yr^{-1}), increasing the area in reserves diminished yield because fishable areas are reduced. For higher fishing mortality rates (e.g., $F = 2.0$ yr^{-1}), the addition of reserves first increased yield by increasing reproduction, then decreased yield as the effect of removing fishable area became significant. For the cases in which effort exceeded optimal levels, the optimum fraction of area in reserves varied from 15% to 19%, and the gain in present value of catch ranged from 3% to 8%.

Sladek Nowlis and Roberts (1999) used a discrete size-structured model with asymptotic postdispersal density dependence and an LPER assumption to evaluate the effects of various levels of fishing effort and marine reserves. They concluded that marine reserves could increase long-term catch if populations were overfished and managers had no control over fishing effort. For two of the three species analyzed, the optimal reserve area was near 70–80% of the total area. They also showed that having reserves reduced natural variability in fish abundance. The short-term effects of putting such large areas into reserves were described in another publication, Sladek Nowlis and Roberts (1997). Sladek Nowlis and Yoklavich (1998) used the same model to predict that refugia could decrease variability in the annual catch of bocaccio.

Botsford et al. (1999) used a size-structured model of the northern California red sea urchin fishery with an LPER assumption to determine whether reserves were advisable for a fishery whose overfishing status was unknown. In this relatively new fishery, catch has declined dramatically, but it is not known whether recruitment has declined. The uncertainty regarding overfishing is essentially due to uncertainty in the slope of

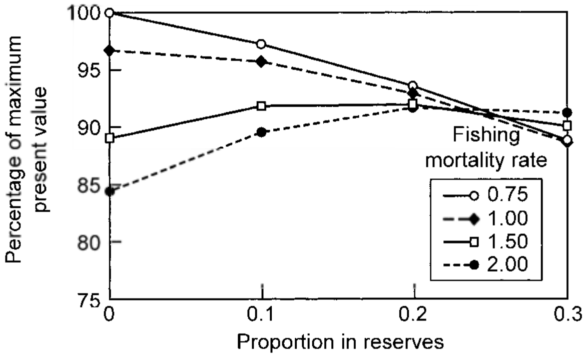

FIG. 4. The present value of harvest over the first 60 yr after the institution of marine reserves for various levels of fishing mortality rate. Reserves are beneficial when populations are heavily fished. The figure is redrawn from Holland and Brazee (1996).

the stock-recruitment function at low stock levels. Botsford et al. accounted for this uncertainty by using a decision analysis that compared mean yield for each fraction of coastline in reserves. The mean yield was a weighted mean of the yield that would result from each possible value of stock-recruitment slope, where the weightings were the a priori probabilities of value of the slope. For this fishery, with a nonzero probability of overfishing, the optimal fraction of coastline in reserves at the current fishing mortality rate was 0.15.

Hastings and Botsford (1999) used a simple age-structured model and an LPER assumption to show that, for populations with sedentary adults and post-dispersal density-dependent recruitment in which recruitment depends on larval density, the maximum yield is the same whether one manages by reserves or specifying fishing mortality rate. This study is strategic in that it omits much detail, and some situations will not satisfy the stated conditions. Its primary value is as a general baseline from which other situations can be judged. For example, for populations with predispersal density dependence, since reserves increase predispersal density, effort management will likely provide greater yield than management via reserves.

St. Mary et al. (2000) hypothesized that an effective marine reserve system should include a diversity of protected habitats, each appropriate to a different life stage. They use a population model that includes two benthic life stages (juvenile and adult) that use spatially distinct habitats; model results suggested that all life stages need not be incorporated into the design of a reserve. As such, more detailed study of stage structured models is needed for effective reserve design.

Tuck and Possingham (2000) analyzed a model with no size or age structure, but with some spatial structure and flexible larval exchange between populations. They used a two-patch spatially explicit population model to address the problem of how to optimally exploit a population connected by dispersing juveniles to an unprotected population. They applied dynamic programming techniques to determine the optimal policies for harvesting, and found that optimal policies for exploiting local populations do not depend on migrating larvae leaving local populations. They also provided numerical examples to explore the degree to which maximum yield is obtained from exploiting the sink population, rather than the source. A major conclusion was that conserving a larger fraction of larvae from source populations makes a better reserve system than protecting sinks with low larval export. Similarly, Crowder et al. (2000) developed a spatially explicit model to address hypotheses regarding MPA effects on fisheries. Their results suggest that optimal siting of MPAs is highly dependent upon source–sink population dynamics. In particular, they use a simple exponential population growth model with a number of patch habitats of different size and distance to show that the placement of reserves in sink habitats has the potential to harm rather than help fish populations. Similar to Tuck and Possingham (2000), these results suggest that identifying and protecting source habitat is critical to sustaining fish populations.

Guenette et al. 2000, Martell et al. 2000, and Stockhausen et al. 2000 develop tactical, spatially explicit models to examine the efficacy of MPAs for particular fisheries: northern cod in Newfoundland, lingcod in the Strait of Georgia, and spiny lobster in the Caribbean, respectively. Guenette et al. 2000 used an age and spatially-structured model that includes a Beverton-Holt recruitment function to examine the efficacy of reserves as compared to other management measures for northern cod in Newfoundland. In their model, random movements of adults around target cells were specific for each age and month of year, and determined the seasonal trajectory of spatial movement. They found that temporal closures in fishing activities with reserves of moderate size (20%) would have prevented the collapse of the fishery for northern cod. Martell et al. (2000) also use a spatial model to estimate effects of age-dependent seasonal migration and dispersal on harvest mortality rates. Model results suggest that lingcod is not adequately conserved given the small size of existing reserves in the Strait of Georgia. Finally, Stockausen et al. 2000 used a spatially explicit population model to examine the joint effects of marine reserve design and larval dispersal via hydrodynamic currents on spiny lobster. They found that when reserve size was expressed as the fraction of coastline protected, larval production decreased for some reserve configurations; thus suggesting that the interplay between larval dispersal, reserve location, and reserve size be considered in determining optimal reserve size.

Botsford et al. (2001) also assessed the dependence of population persistence on larval dispersal distance and reserve configuration. They assumed Laplacian dispersal (i.e., exponentially decaying with distance from the source) and periodically spaced reserves to show that the fraction of natural larval settlement was greater for shorter distance dispersers than longer dispersers. A value of this quantity adequate for persistence could be obtained by a single large reserve of width on the order of a dispersal distance, or all dispersal distances could be provided for by a system of small reserves covering 35% of the coast. Since larval dispersal distances are poorly known, the dependence of persistence on larval dispersal was an additional source of uncertainty. Their model suggests the potential for (1) genetic selection for shorter larval dispersal distances and (2) changes in community structure for individuals dispersing different distances. This is an important multispecies issue that suggests differential responses by species with different dispersal distances that could affect community composition. Although it ignores subsequent interactions, it warrants further study. Hastings and Botsford (2003) built on these result using a model similar to Hastings and Botsford (1999) to compare reserves designed for conservation to reserves designed for fisheries. Population persistence in reserves with the conservation goal could be most economically achieved by reserves as large as practicably possible, but the fishery goal is best achieved by many small reserves covering a larger fraction of the coast.

Gaines et al. (2003) develop a population dynamics model for marine organisms with relatively sedentary adults whose larvae are transported in a simple flow field in both diffusive spreading and directional characteristics. They found that advection can play a dominant role in determining the efficacy of reserves. In particular, their results suggest that, with strong currents, multiple reserves can be more effective than single reserves of the same total size, and may also outperform effort-based management in terms of fishery yield. The key new issues explored are dispersal by currents that allows asymmetry in the pattern of dispersal. Many conclusions depend on the strength of advection. For example, in some cases, increases in the size of individual reserves often are no longer effective means of promoting persistence of populations. With advective currents, multiple reserves become far better than single large reserves. The other key finding is that, with explicit dispersal, fisheries yields with a reserve strategy can greatly exceed those of effort management. This is because advective currents create much more of a spatial structure to the dynamics, which greatly favors spatial solutions (i.e., reserves).

Several of the models that included complete life histories used a logistic or Ricker population model (i.e., with no explicit age or size structure). Pezzey et al. (1998, 2000) used the classical logistic model fishery result with carrying capacity proportional to reserve area, and catch proportional to density rather than abundance. In their model, eggs and larvae are mobile but adults are not and there is open access to fishing outside the reserve. They found that equilibrium catch was increased by the addition of reserves only if the prior ratio of stock to carrying capacity is less than a half (i.e., it had been harvested to below MSY). Otherwise equilibrium catch was decreased by the addition of reserves. Results suggest that long-run stability is improved by reserves, and coral reef reserves could increase annual catches worldwide. Lauck et al. (1998) used a semelparous Ricker model to show that reserves can be beneficial in coping with uncertainty. The uncertainty they used was randomness in the harvest rate, and they computed the probability of maintaining the stock above 0.6 of the carrying capacity for 20 yr. This probability was higher with more area in reserves.

Mangel (1998) also used a discrete-time logistic model to evaluate how the fraction of habitat assigned to a reserve affects the sustainability of a specified take under a random environment. He determined the fraction of the population that needed to be in a reserve in order to maintain the population at a specified fraction of carrying capacity, with harvest rate set at a specific value. Mangel (2000*a*) used a similar population model to suggest that reserves can help guarantee sustainability of the fishery, even when fishing mortality outside the reserve cannot be very well controlled. Mangel (2000*b*) used a stage-structured population model that includes variable natural mortality that is correlated by a random process driven by environmental processes. Fishing pressure is also assumed to fluctuate, and adult movement is modeled. Mangel (2000*b*) suggests an interesting paradox based on model results: fishery yield is small when a small fraction of habitat is protected due to variability in catch, and small when habitat is protected because there is so little catch. However, he reports that while reserves did not increase fishery yield in his model, they did decrease variability in catch.

Man et al. (1995) used a presence/absence metapopulation model with two types of patches, fished and unfished, to assess the efficacy of marine reserves in conserving exploited populations and increasing yield. Similar to other models, they assume that fishing effort associated with reserve areas disappears rather than getting reallocated. They found that, in cases where local extinction due to fishing was high, reserves are most beneficial because they provide a source of recruits to overfished areas.

Taken together, these models generally indicate that if fishing effort is high enough to cause recruitment overfishing without reserves, reserves can help prevent overfishing and promote a sustainable level of catch. Specifically, reserves are most effective when the rate of fishing significantly reduces recruitment to the exploitable stock, causes a greatly reduced spawning stock, a decreasing proportion of older fish in the catch, and generally very low recruitment year after year. Alternatively, if fishing effort is not intense, reserves have little or a negative effect on yield as they begin to remove areas from fishing. However, in such cases reserves will still increase egg production. Most of these models make the LPER assumption, but spatially explicit models are beginning to examine the interplay between larval dispersal and reserve configuration. The results from Attwood and Bennett (1995) indicate that, at least in the cases where larval dispersal is relatively unimportant, configuration of reserves makes little difference in yield, rather it depends solely on the fraction of coastline in reserves. Tuck and Possingham (2000), Crowder et al. (2000), and Guenette et al. (2000) broach the important issue of spatial variability in productivity. We anticipate that the advantages of reserves for fishery yield will increase as we begin to explicitly incorporate spatial variation in dispersal into models of marine reserves.

Models with multiple species

We know of only one model that explicitly incorporates interactions between species (Walters et al. 1997, Walters 2000). The first paper describes the general model functions (ECOPATH, ECOSIM, ECOSPACE) rather than documenting results of a specific assessment of marine reserves in that way as the other papers reviewed here do. The second paper applies ECOSPACE to suggest that dispersal, trophic responses, and spatial fishing-effort responses are all likely to reduce the efficacy of small MPAs. In general, these models are likely to be widely used since they are relatively easy to download from the internet and start running simulations on a PC. In doing so, it is important to realize the limitations of the model (Walters et al. 1997). ECOPATH is structurally and empirically based on a trophic mass balance. Model parameters are determined from information on productivity and consumption per unit biomass, as well as fishery removals, for each species in the ecosystem. For many of the species, these will be unknown, and borrowed from other species and systems. This static structure (ECOPATH) is then converted to a dynamic system (ECOSIM) with the static system as the equilibrium state, and differential equations describing how production rate, consumption rate, and rate of biomass growth of each species depend on each other (Walters et al. 1997). In some cases, the model is unlikely to represent dynamics very far from equilibrium, and will not necessarily behave in the right way when leaving the equilibrium (see caveats in Walters et al. 1997). This dynamic model is then put into an Eulerian spatial model with rather coarse resolution that can contain reserves with no fishing (ECOSPACE; Walters et al. 1997, Walters 2000). Because of the many ways that predation and trophic dynamics can vary with relative abundances, and the other determinants of abundance left out of the model one can have little confidence that the model is actually making a prediction of the behavior of a specific system in response to reserves. Adding a spatial component increases uncertainty regarding whether the model represents a real system. However, the model has heuristic value and contains useful mechanisms that should be studied further and accounted for in assessment of the efficacy of marine reserves. In addition to the potential movement of different trophic levels in and out of reserves, the model depicts movement of fishing effort in response to abundance and fishing costs. Only the single cohort models have addressed the redistribution of effort, and in a simple ad hoc way (Sanchiro and Wilen 2001).

Directions for a Theory of Marine Reserves

Most of the existing models of marine reserves have been motivated by the desire to answer fundamental questions about the design and potential effectiveness of marine reserves. In this section, we assess the degree to which relevant questions have been answered, based on our synthesis of model results (Table 1). We then identify critical ecological processes that merit future investigation in the quantitative assessment of marine reserves.

Have existing models addressed the relevant objectives of marine reserves?

Models for marine reserves have focused primarily on questions concerning fishery management, ignoring other objectives such as biodiversity conservation, scientific understanding, recreation, education, and tourism. However, it is important to recognize that one of the necessary components of sustainable fishery management is to preserve the fished stock. Maintaining reproductive potential does this, a goal that fishery management has in common with population viability analysis. As a consequence, although population viability was not considered explicitly as a goal in many modeling efforts, insight gained from examinations of fishery yield may have utility in future studies of population viability. However, the explicit effects of random environment and the reduction in probability of extinction due to multiple populations will have to be included.

Within the realm of fishery management, several objectives were addressed in the models we reviewed. The primary objective was maximizing yield. Almost all of the models focused on that objective. A second objective was minimizing variability in yield (Sladek Nowlis and Roberts 1999). A third objective was minimizing the effects of uncertainty on fishery management (Lauck et al. 1998, Mangel et al. 2000*b*, Gaines et al. 2003).

It is possible that some of the other objectives, providing pristine areas for scientific understanding, recreation, education, and tourism may not require the detailed models that are needed for fishery and biodiversity goals. In these, the issues are more qualitative, rather than quantitative, and value may be best described simply as increasing linearly with habitat set aside. Nonetheless, theoretical examinations of the economic value of marine reserves have been hindered by the difficulties associated with incorporating fisher behavior and nonmarket benefits. Developing approaches to examine multiple goals will therefore be a fruitful intersection of natural and social science in future theoretical work on marine reserves.

Are marine reserves beneficial, and under what conditions?

From the models reviewed there appears to be a clear, partial answer to this question, at least for the goal of fishery management: marine reserves appear to be effective at maintaining yield when fishing effort is high enough to cause a decline in recruitment without reserves. This result was obtained in all of the models with complete reproduction where it was assessed (e.g., Quinn et al. 1993, Holland and Brazee 1996, Sladek Nowlis and Roberts 1999). This result is consistent with the equivalence between reserve management and standard effort management demonstrated by Hastings and Botsford (1999) and the invariant formulated in Mangel (1998). However, most models that we considered did not reallocate fishing effort after reserve establishment. Overfishing can be prevented either by the institution of reserves or by being able to control effort. For many fisheries, managers are uncertain about whether the population is being overfished. Botsford et al. (1999) demonstrated a means for dealing with this situation using decision analysis when some information is available.

The fact that reserves increase yield only when a fishery is recruitment overfished should not be taken to mean that they are of little use. First, reserves provide other benefits, such as a hedge against uncertainty, and the preservation of systems in a pristine state (Clark 1993). Second, fishing effort cannot be controlled in many fisheries, and many believe that the constant increase in uncertainty because of the inability of fishery management institutions to account for uncertainty (i.e., the "ratchet effect," proposed by Caddy and Gulland 1983, is the root cause of global overfishing; Ludwig et al. 1993). Third, the advantages of reserves for fisheries management may grow substantially as we move away from simple assumptions about uniform dispersal of larvae (Gaines et al. 2003). Fourth, reserves present a simultaneous solution for management and conservation of multiple species.

A second condition for the efficacy of reserves is that as movement rates increase, larger areas are needed for reserves to achieve benefits. If juveniles and adults move a great deal, larger reserves will be needed for their conservation. For example, Atlantic cod (*Gadus morhua*) around Newfoundland may move beyond 40 miles (64 km) within a couple years (Templeman 1974), thus relatively large areas will be needed to conserve Atlantic cod. If there is little movement (e.g., urchins, abalone), reserves will benefit EPR, but animals will not leave reserves to be caught. Because the latter result follows from the YPR/EPR analysis (DeMartini 1993), it must be qualified by consideration of the larval phase, the part of the life history left out of the cohort approach. Reserves will perform better than indicated by single cohort analysis of species with low rates of adult movement when their contribution through larval dispersal is considered.

Other benefits, having to do with uncertainty and environmental viability, have been addressed, but further investigation would be fruitful. One analysis indicated that reserves reduce variability in catch (Sladek Nowlis and Roberts 1999). The analyses by Lauck et al. (1998) and Mangel et al. (2000*b*) concluded that reserves made fisheries less sensitive to uncertainty. Where the goal is conservation (e.g., population viability), the answers are less clear. Recent analyses by Hutchings (2000) suggest that many stocks that have experienced long declines may require more than 15 yr to recover. Tactical, species-specific models would be useful here to identify optimal reserve design to promote population recovery.

How big will marine reserves need to be in order to be effective?

The optimal size of marine reserves will ultimately be determined based on particular conservation needs and goals, quality and amount of critical habitat, levels of resource use, efficacy of other management tools, and characteristics of species or biological communities needing protection (NRC 2001). Within the modeling context, the optimal size of reserves clearly depends on the definition of efficacy, which for most of the models reviewed was yield in a fishery. Effective or optimal sizes of reserves or reserve networks depended on details of each model, and only a few modeling studies have attempted to determine the general considerations underlying optimal size (e.g., Hastings and Botsford 1999, Botsford et al. 2001). However, from the general conclusion that reserves provided increased yields when fishing mortality rates were high, we can conjecture that the optimal size will be that which brings egg production up to the level that provides adequate recruitment. Thus, it will depend on the fishing mortality rate in areas outside reserves, being greater for greater fishing mortality rates. This appears to be consistent with results in Holland and Brazee (1996), Sladek Nowlis and Roberts (1999), and Botsford et al. (1999). Hastings and Botsford (1999) also found for a wide range of biological conditions that marine reserves could offer equivalent yield to conventional fishery management tools. For species that reproduce over long life spans, the fraction of area that needs to be protected in reserves is smaller than the fraction of the adult population that needs to be protected under conventional fishery management. Botsford et al. (2001) note that persistence of species with all possible dispersal distances requires placing 35% of the coastline in reserves, if there is complete removal outside of reserves. The value of 35% is the fraction of lifetime reproduction required for sustainability determined in analysis of overfishing, and it is a source of uncertainty in both conventional fishery management and reserves. This contrasts with proposals to protect 20% of a population in reserves, however the optimal amount of reserve area required to meet a given management goal may be higher or lower depending on the characteristics of the location and its resident species (NRC 2001). A proposed priority in implementing reserve sites should be to include vulnerable areas rather than to achieve a percentage goal for any given region (NRC 2001).

What types of connectivity must be maintained within a reserve network?

While the importance of this question is widely appreciated (e.g., Roberts 1997), it is only beginning to be answered. In multigeneration models, linkages among reserve and nonreserve areas can be made by adult and juvenile movement or by larval dispersal. Several of the complete population models described here included larval dispersal (Quinn et al. 1993, Attwood and Bennett 1995, Crowder et al. 2000, Tuck and Possingham 2000), and only one considered movement of adults outside of reserves (Attwood and Bennett 1995). Most models represented larval dispersal by making the LPER assumption that larvae produced in reserve and nonreserve areas enter a common larval pool from which recruits are derived. Exceptions include Tuck and Possingham 2000, where the fraction recruiting to site could be set independently, and Crowder et al. (2000) who included patch specific dispersal and density dependence for larval settlement. Recruitment from pool to reserve areas was assumed to be proportional to the fraction of the reserve area in the entire system (Holland and Brazee 1996, Botsford et al. 1999, Hastings and Botsford 1999, Sladek Nowlis and Roberts 1999). This assumption makes it possible to model reserves in a way that tacitly ignores their geography, allowing all reserve and nonreserve areas to be equally connected by larval dispersal. This is essentially the demographic equivalent of the island model of population structure common in population genetics (Wright 1978), in which all populations are connected by equal gene flow (Palumbi 2000).

The LPER assumption does not describe population geography or larval dispersal in a realistic way, and it is probably optimistic in terms of the effects of reserves on total larval settlement. It is made primarily because the distribution of larval dispersal distances is a largely unresolved issue empirically and theoretically. However, existing results give us some idea of what characteristics will be important to reserve design. For example, we can speculate that reserving populations that effectively deliver recruits (Quinn et al. 1993, Tuck and Possingham 2000) is important.

The LPER assumption leaves out any consideration of the effect of the configuration of marine reserves on successful larval settlement and general population persistence. LPER models effectively assume that there is only one reserve, or that a system of reserves will function equivalently no matter what the size distribution of reserves. For example, if reserves make up 30% of the total system area, LPER assumptions are that the transport of larvae in and out of the reserve boundaries is the same whether there are 100 tiny reserves each making up 0.3% of the area or if there are three large reserves of 10% each. Clearly, ability of reserves to self-seed or contribute propagules to other reserves will depend critically on the size and shape of the reserves relative to larval dispersal and on the spacing of reserves relative to current-mediated transport. This dependence will be greatly affected by local specific current conditions and is likely to vary substantially from year to year. Our general lack of understanding of the explicit role of space in marine population dynamics will hamper the development of applied marine reserve design models because reserve design is, by definition, a spatial issue. Nonetheless, some promising theoretical approaches have been developed to set the stage for future empirical work. For example, Botsford et al. 2001 and Gaines et al. 2003 present promising approaches to examine the degree to which persistence of populations within reserves depends on the interplay of dispersal distance and spatial configuration of reserves.

What are the key ecological processes that need to be assessed in future models?

There are a large number of ecological processes with implications for the design of marine reserves (NRC 2001). Clearly, the models described here represent simplifications of reality, and many additional processes could potentially be included in model description. Here, we outline the kinds of processes that could be included and indicate the kinds of mathematical or modeling approaches that have been used (and those that have gone ignored) and when simplifications are likely to be possible. Ultimately, the art of modeling is the ability to determine what can safely be ignored and isolating the factors that are most important.

The most important general aspect of the problem in the design of marine reserves that has not been widely developed in the analyses is the distribution of marine reserves over space. This aspect has been ignored primarily because it depends on movement in the sea, which is poorly understood. Unfortunately, there is little information about average dispersal of most marine larvae. In general, estimates of dispersal distances are indirect (Levin 1990) and are derived from inferences about larval biology (e.g., Strathmann 1993) or the genetics of adult populations (Palumbi 2003). Very few data are available that are derived from direct observations of realized larval dispersal distances (Grantham et al. 2003).

Setting up marine reserves is fundamentally a question that is spatially oriented. Any description of spatial dependence, other than a complete mapping of each individual within a spatially varying matrix of habitat quality, represents an approximation, so the goal of future modeling is not to achieve a realistic description of space, but to retain sufficient information. The simplest spatial models subdivide the area considered into different classes, but ignore any explicit description of the proximity of different parts of the habitat, in the tradition of most metapopulation models (Hastings and

Harrison 1994). The most detailed description of space would include descriptions of habitat and other variation on a small scale. For example, specific features of coastlines, such as points, or locations of ocean currents, will have a large local effect on recruitment and dispersal processes. Another issue not considered in most of these model is variation in habitat quality and habitat-specific demography. All reserve habitat is assumed to be of equal utility in these models. Such information can only be realistically included in the context of spatially explicit simulation approaches. Ideally, some intuition about the role of such small scale, but potentially important, features can be obtained from these simple spatially implicit approaches.

The stage at which movement occurs for a species also will have a large effect on the impact of marine reserves and the description of this movement is one of the most fundamental issues in models of marine reserves (Roughgarden et al. 1988, Possingham and Roughgarden 1990, Botsford et al. 1994). There are species where only adults move, only juveniles move, neither stage moves, or both stages move. Movement can also depend on the density of the mobile stage, or on the density where settling may occur. Ideally, as input to the models, one would use a complete description of the probability of moving between any two locations in the habitat, as this is a process that can have very large effects on the impact of marine reserves. However, especially with movement of pelagic larvae, it is essentially impossible to directly measure this ''dispersal kernel.'' Instead, one typically must use a variety of reasonable descriptions of movement and consider the robustness (to changes in movement) of any results on the role of reserves. In some cases, especially in the context of simulation approaches, one can attempt to infer movement of pelagic larvae from knowledge of physical oceanographic processes (Hill 1990, Richards et al. 1995, Botsford et al. 1998, Hofmann 1988, Ortner et al. 1999). Even though adults can be tagged, and their movement followed, the impact of reserves may be influenced by the degree to which adult movement is density dependent. This is another aspect of movement that will be extraordinarily difficult to quantify. Modeling must be focused on the robustness of results to changes in the ecological processes that lead to movement. More information about the spatial patterns of movement will allow us to consider the critical life history stages that should be placed in reserves (Quinlan and Crowder 1999).

Knowledge of the form of density dependence at different stages in the life cycle is critical for understanding the role of marine reserves. For example, density dependence in the stock-recruitment relationship can occur either predispersal (at spawning) or postdispersal (at settling), or both, and this will have very different implications for reserve design. As we have seen, movement can also potentially be density dependent. In all of these cases, the impact may depend on the functional form chosen to describe density dependence. Thus, in any future generic models, different functional forms should be examined.

Models of marine reserves thus far are, for the most part, deterministic. The few exceptions indicate that the effects of random oceanographic processes and demographic and environmental stochasticity, as well as uncertainty in model structure and parameter values are important. Realistic accounting of these sources of randomness not only makes it more difficult to determine the optimal distribution of reserve size, shapes, and spacing, but also is necessary to examine other benefits of reserves such as lower susceptibility to uncertainty and reduced effects of environmental variability. We suspect that the importance of marine reserves for fishery management will increase once stochasticity is introduced in to the models as the reserves may provide a hedge against the combination of overfishing and unfavorable environmental events.

Another aspect of reserve design in need of further understanding, at least in a fishery context, is the redistribution of fishing effort that would occur after the creation of reserves. This aspect has been treated in a simple obvious way in single cohort models (Beverton and Holt 1957, Polachek 1990, DeMartini 1993), but studies of the behavior of fishermen in response to patchy resources, price, and port location (e.g., Sanchirico and Wilen 1999) suggest the effects may be more complicated. A related issue is the effects of greater concentration of fishing effort in the area outside reserves on benthic ecology (Dayton et al. 1995). Most analyses of marine reserves ignore the fact that the harvesting sector will respond spatially to closures (Sanchiro and Wilen 2001). Most models assume constant fishing mortality and simply remove fishing effort in reserves rather than reallocating it. Resolution of these issues will be critical as we begin to use models to assess the efficacy of MPAs, and more modeling work is needed to understanding the mechanisms that determine the spatial behavior of harvesters.

In summary, models of marine reserves have established several key findings that appear to be general: (1) reserves increase yield when effort is so high that the population would otherwise be overfished, and (2) reserves may be less appropriate for species with high rates of juvenile and adult movement. It is now time to move on to research that addresses the extant questions to which managers are going to need answers: (1) How does larval dispersal affect reserve design? (2) Which configurations of marine reserves lead to sustainable populations? (3) How do different types of density dependence affect the efficacy of reserves? (4) How should spatial variability in productivity be accounted for? (5) How should patterns of larval transport affect design of reserves? (6) How will reserves serve to mitigate uncertainty in parameter estimates? There is increasing optimism regarding the value of marine reserves, and growing impetus for their rapid implementation, in spite of the fact that we know little about how they work (Ballantine 1991). That approach can be justified based on the reversal of burden of proof implied by the precautionary principle, but that does not obviate the need to attempt to understand their effects. It is only through increased understanding of the principles that underlie the design of marine reserves that we will be able to confidently project their effects, and avoid their falling out of favor simply because of failed promises.

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