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MARINE RESERVES ARE NECESSARY BUT NOT SUFFICIENT FOR MARINE CONSERVATION

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Abstract. The intensity of human pressure on marine systems has led to a push for stronger marine conservation efforts. Recently, marine reserves have become one highly advocated form of marine conservation, and the number of newly designated reserves has increased dramatically. Reserves will be essential for conservation efforts because they can provide unique protection for critical areas, they can provide a spatial escape for intensely exploited species, and they can potentially act as buffers against some management miscalculations and unforeseen or unusual conditions. Reserve design and effectiveness can be dramatically improved by better use of existing scientific understanding. Reserves are insufficient protection alone, however, because they are not isolated from all critical impacts. Communities residing within marine reserves are strongly influenced by the highly variable conditions of the water masses that continuously flow through them. To a much greater degree than in terrestrial systems, the scales of fundamental processes, such as population replenishment, are often much larger than reserves can encompass. Further, they offer no protection from some important threats, such as contamination by chemicals. Therefore, without adequate protection of species and ecosystems outside reserves, effectiveness of reserves will be severely compromised. We outline conditions under which reserves are likely to be effective, provide some guidelines for increasing their conservation potential, and suggest some research priorities to fill critical information gaps. We strongly support vastly increasing the number and size of marine reserves; at the same time, strong conservation efforts outside reserves must complement this effort. To date, most reserve design and site selection have involved little scientific justification. They must begin to do so to increase the likelihood of attaining conservation objectives.

Key words: biodiversity; harvest refugia; marine parks; marine protected areas; open populations; population replenishment; reserve design.

INTRODUCTION

The recent recognition of the profound influence of humans in marine systems (e.g., GESAMP 1991, Norse 1993, Chandler et al. 1995, Dayton et al. 1995, Done et al. 1995, Lubchenco et al. 1995, National Research Council 1995, Twilley et al. 1995, Weber and Gradwohl 1995, Allison et al. 1996) has been the impetus for strong marine conservation advocacy. One vehicle for marine conservation that has received much interest recently is marine reserves. The designation of such protected areas has expanded dramatically over the last few decades (Kelleher et al. 1995*a*). Marine reserves are now strongly advocated by many managers and biologists because reserves may offer types of protection not provided by other management strategies: specific protection of critical areas (Salm and Clark 1989, Norse 1993), intrinsic prevention of overfishing (Davis 1989, Dugan and Davis 1993), and even enhancement of fisheries (Plan Development Team 1990, Castilla and Fernández 1998).

Compared to their marine counterparts, terrestrial reserves have an extensive theoretical basis (Meffe and Carroll 1994). Indeed, a large portion of theory used in conservation, such as island biogeography (Diamond and May 1981), patch dynamics (Pickett and Thompson 1978), population genetics (Soulé and Simberloff 1986, Boyce 1992, Lande 1995), and even keystone species (Frankel and Soulé 1981), has been focussed on the problems of reserves. Even many of conservation biology's major controversies, such as the "SLOSS" debate ("single large or several small" reserves; Soulé and Simberloff 1985) and the effectiveness of corridors (Noss 1987, Simberloff and Cox 1987, Simberloff et al. 1992), have revolved around the design of reserves and how to most effectively protect populations within the limited areas available. Because the implementation of marine reserves is relatively new and the theoretical and empirical framework for their design is still in its infancy, it may be tempting to draw heavily from reserve experiences in the terrestrial realm. But marine

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systems differ fundamentally from terrestrial systems in the scale and variability of processes (Steele 1985). For example, in marine systems, ocean currents have a great influence on dispersal of both organisms and pollutants and, thus, create much stronger regional influence over local patterns (Palmer et al. 1996) than in terrestrial systems. Further, human impact on biotic communities differs between marine and terrestrial systems: in terrestrial systems, autotrophs and herbivores are commonly exploited (examples include logging of trees and hunting of animals), whereas in the ocean human exploitation is usually directed at top-level predators (i.e., by fishing). Such differences have profound consequences for the potential effectiveness of marine reserves and thus the guidelines developed for terrestrial reserves may be inadequate.

A large literature has developed on marine reserves, their use, effectiveness, and potential (see Roberts and Polunin 1991, Rowley 1992, Carr and Reed 1993, Roberts 1997). Empirical evidence in several cases has demonstrated that reserves can harbor more diversity, higher abundance, and larger organisms (Castilla and Bustamante 1989, Durán and Castilla 1989, Alcala and Russ 1990, Bennett and Attwood 1991, Polunin and Roberts 1993, Francour 1994, Roberts 1995, Jennings et al. 1996), and even wholly different community structures (Castilla and Durán 1985, Moreno et al. 1986). Whether these patterns can always be attributed causally to the presence of reserves is often less clear. In some studies, the impact of reserves is much less apparent (Cole et al. 1990, Roberts and Polunin 1992). Routine monitoring of reserves is far from common (Kelleher et al. 1995*a*) and in general, the elements conferring effectiveness have not yet been established.

The political, social, and economic issues involved in the design, site selection, and implementation of marine reserves are as essential and complex as they are for terrestrial reserves. However, the need for social and political acceptance of a reserve can compromise the biological issues, thereby undermining the conservation intent. The conservation goals of a reserve plan will not be met if the reserve is designed, implemented, or protected poorly. The optimum size, number, and distribution of reserves are still very uncertain. Furthermore, reserves are not simple, low cost methods of protection. They often require an intensive political lobbying effort (Ballantine 1991, Kelleher et al. 1995*a*), extensive preliminary research, and a long-term enforcement and management commitment. Ineffective reserves are a waste of such effort and can potentially lead to a false sense of security about the state of marine resources (Rowley 1992, Carr and Reed 1993).

This paper considers the reasons that reserves are necessary for marine conservation and articulates some definitions and goals of reserves. It also addresses limitations of reserves, summarizes the conditions under which they will be more effective, and finally outlines major design, evaluation, and research challenges to ensure that reserves fulfill their conservation potential. Our primary points are that (1) marine reserves are essential to marine conservation, (2) their efficacy can be greatly enhanced if their design and implementation are scientifically sound, but (3) their potential effectiveness is limited by large-scale processes that must be explicitly addressed by conservation measures outside as well as inside reserves.

Definitions and Uses

Many different names have been given to marine areas that are, to some degree, protected by spatially explicit restrictions (Ballantine 1991, McNeill 1994). Marine protected areas, parks, reserves, harvest refugia, and sanctuaries are some of the commonly used terms. These areas have a huge range of potential functions including conserving biodiversity, tourism (Ballantine 1991, Rowley 1992), protecting sensitive habitats (Norse 1993), providing refuge for intensively fished species (Dugan and Davis 1993), enhancing the production of target species, providing a management framework for sustainable multiple use (Kenchington and Agardy 1990, Agardy 1994), serving as a demonstration of the extent of human impacts in coastal environments (Durán et al. 1987, Keough et al. 1993), or a combination of these goals. The term "marine protected area" (MPA) has emerged as a commonly used term implying conservation of species and communities. The World Conservation Union (IUCN 1988) provides the following definition of an MPA: "Any area of intertidal or subtidal terrain, together with its overlying water and associated flora, fauna, historical and cultural features, which has been reserved by law or other effective means to protect part or all of the enclosed environment."

While different designations undoubtedly have many important distinguishing characteristics, for the purposes of evaluating their biological effectiveness, three principal considerations are critical:

1) What are the biological goals of protection? Examples of goals include: to provide undisturbed critical habitat, to provide local release from fishing for some species, to act as centers of dispersion of propagules into surrounding areas, and to maintain high biomass or high diversity.

2) What types of human activities are restricted? Restrictions can be placed on: commercial and/or sport fishing (few or all species restricted), personal or subsistence collection, construction, tourism, education, and/or research.

3) To what degree are these restrictions followed or enforced? This can range from very strong compliance to no protection at all. Although protection on paper may be strict, compliance may be weak (e.g., Camhi 1995).

Marine reserves have been designated in a wide variety of habitats and regions, with a variety of designs, conservation goals, and degrees of protection (Salm and Clark 1989, Ballantine 1991, McNeill 1994, Kelleher et al. 1995*a*, *b*, *c*, *d*). We focus on reserves (or areas within integrated MPAs) where most or all human activities are restricted and compliance with those restrictions is high. We use the term "reserve" in this paper to refer to these areas of high, spatially explicit protection. Further, to distinguish between two of the most common types of reserves, we use the terms "fishing refugia" and "biodiversity reserves."

Why Marine Reserves are Necessary

While many strategies have been proposed for the protection of marine populations, including the improvement of water quality (GESAMP 1991), prevention of overexploitation through fishery-wide limits (Davis 1989, Bohnsack 1992), and the prevention of the further spread of exotic species through strict regulations on commerce, reserves offer a fundamentally different type of protection: a spatially explicit form, often permanent, that permits a degree of restriction on human activities that is not universally appropriate. For example, it may not be feasible for economic, political, or social reasons to indefinitely restrict all fishing of some economically important species. However, preventing fishing in spatially limited areas may be socially acceptable and still provide some protection to the species by providing an absolute refuge. Therefore, reserves are especially important as protection of critical areas such as nursery grounds, spawning grounds, and foci of high species diversity.

Because reserves allow strong local control of human activities, they are especially appropriate where local human impact, such as fishing pressure, pollution threats (e.g., sewage outfall), and habitat disturbance, is heavy. Probably the most important biological use of marine reserves is as a refuge from fishing pressure for some or all species in an area. By releasing a population from fishing pressure, that population then becomes structured by natural mortality instead of fishing mortality (Bohnsack 1992). Reserves can, therefore, increase the density and average size of individuals (Polunin and Roberts 1993, Roberts 1995). Because larger, older individuals are typically much more important to reproduction in a population than young, small individuals, this change in the population structure can drastically increase the reproductive output of the population protected in reserves (Bohnsack 1992). Therefore, reserves could potentially enhance fisheries by acting as centers of dispersal of propagules and adults into the areas surrounding the reserve. These reserves are often termed "harvest refugia;" we prefer the term "fishing refugia," as it conveys the idea that target species are wild, and not cultivated, organisms (Norse 1993). Although such "refugia" effectively reduce the total area available to be fished, many researchers and managers suggest that if refugia are designed well, the overall yield within a region will be higher (Plan Development Team 1990, Ballantine 1991, Castilla and Fernández 1996).

Although some studies have shown striking increases in the standing biomass of protected species (e.g., Alcala 1988, Roberts 1995), two important points should be noted. First, it is still difficult to demonstrate that fishing refugia serve as emigration or propagule sources for surrounding areas (Bustamante and Castilla 1990, Tegner 1993, Roberts 1995, but see Attwood and Bennett 1994). Second, local populations and communities respond to sources of variation other than anthropogenic perturbations, including variable recruitment (reviewed by Caley et al. 1996) and long-term trends in resource availability (e.g., Holbrook and Schmitt 1996). Even protected populations may experience complex cycles that may be due to complex interactions among the species in the reserves (e.g., Castilla and Durán 1985). For instance, because recruitment of many temperate reef fishes is influenced by the abundance and species composition of macroalgae at a site (Levin 1993, Carr 1994*a*, *b*), macroalgal dynamics can cause year-to-year variation in the size and age structure of local fish populations independent of protection within reserves. Also, large increases in the density of commercial species may lead to the impoverishment of nontarget species (Carr and Reed 1993, Cognetti and Curini-Galletti 1993).

Fishing refugia could perform a second, equally important, role of serving as a buffer against management errors and recruitment failure. Because managers of traditional fisheries must base catch limits on predictions of highly variable parameters, there is always the potential for catch limits to be set too high during periods of high environmental stress on a population. In such cases, protected populations could potentially serve as recovery populations (Bohnsack 1992). However, unless fishing refugia are designed to be self-replenishing, they will be reliant on replenishment from exploited populations in the same manner that they are intended to contribute to the recovery of exploited populations (Carr and Reed 1993).

Marine reserves may serve many other purposes. A side benefit of fishing refugia is the protection of nontarget species. Fishing practices disrupt more than just target species in at least two ways. First, the capture process often kills many nontarget species through simple by-catch (Andrew and Pepperell 1992, Dayton et al. 1995) and habitat degradation (Peterson et al. 1987, Alcala and Russ 1990, Riemann and Hoffmann 1991). Second, fishing can drastically change the community structure by removing species with influential roles (Castilla and Durán 1985, Estes et al. 1989, Dayton et al. 1995). Reserves can also provide sites for research to advance understanding of marine systems and pro-

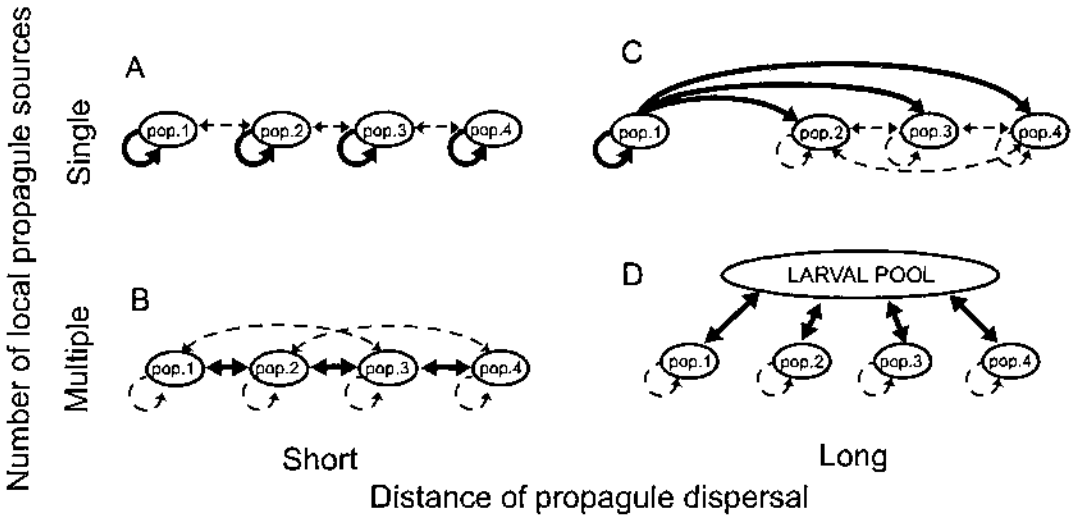

FIG. 1. Models of population replenishment. Patterns are distinguished by the distance of propagule dispersal and the number of local propagule sources for a given local population. Ellipses represent isolated adult populations (pop.). Bold lines indicate high recruitment rates within or between isolated adult populations. Broken lines indicate low recruitment rates. (A) Short-distance dispersal/single source, or self-replenishment pattern; (B), short-distance/multiple source, or limited-distance pattern; (C), long-distance dispersal/single-source pattern; and (D), long-distance/multiple-source pattern. Adapted from Carr and Reed (1993).

vide sites as ecological benchmarks against which anthropogenic perturbations can be measured. Finally, reserves can provide important educational, recreational, and economic opportunities (Ballantine 1991, Agardy 1994, Kenchington and Bleakley 1994, Gubbay 1995).

LIMITATIONS OF MARINE RESERVES

All uses of reserves imply a fundamental assumption: Reserves protect the populations within their boundaries. However, the potential effectiveness of reserves to protect populations is limited by many processes that are unique to marine systems. Hydrographic circulation patterns and episodic events such as El Niño–Southern Oscillations (ENSOs) can span thousands of kilometers; biological processes entrained in such patterns similarly have very large-scale components. Consequently, patterns of organism dispersal and migration can span huge geographic distances. Thus, the most important reason that biological effectiveness of reserves is limited is that scales of fundamental processes in marine systems are often much larger than scales that reserves can encompass. We address a few of the facets of these large-scale implications, including patterns of population replenishment and anomalous climatic effects.

Patterns of population replenishment

Reserves, by themselves, cannot guarantee protection or replenishment of populations of many species. Many marine species have a pelagic phase in their life history that necessarily expands the spatial scale of effective biological populations. Kenchington (1990) points out that there are classes of species for which reserves will have little use, specifically those with both planktonic larvae and planktonic or pelagic adults. The organisms in this class range from most phytoplankton and zooplankton species to pelagic fishes with large home ranges. However, other species with planktonic larvae or large adult ranges may have a stage that is dependent on nursery areas, spawning sites, or calving sites. Such species may be protected by reserves if the critical areas can be identified, assuming of course that other life stages that are not site-dependent are not overexploited. However, even for species that are predominantly sessile or of limited mobility, reserve effectiveness will be highly dependent on the replenishment pattern for those benthic populations. Understanding the range of dispersal patterns within marine systems is critical to assessing reserve effectiveness.

Carr and Reed (1993) distinguish four patterns of population replenishment that will have different implications for reserve design and effectiveness (Fig. 1). These four patterns can be organized on two axes: distance of propagule transport relative to the scale of reserves and the number of propagule sources for population replenishment. Species that fit into the short dispersal/single source pattern (Fig. 1A) are those such as invertebrates with direct development and crawl-away juveniles, live-bearing fish, tunicates, and many seaweeds. Populations of such species can be considered self-replenishing at the scale of most reserves. Limited-distance dispersers such as abalone (McShane et al. 1988, Tegner 1993, Sasaki and Shepherd 1995) and shallow-dwelling rock fish may disperse beyond reserve boundaries, but mostly to areas immediately adjacent to the reserve (Fig. 1B). Thus, reserve pop-

ulations of these species may be replenished from more than one nearby source. Some species (Fig. 1C) with longer dispersal may have only one or a few populations actively reproducing ("source populations") and the remaining populations, though apparently thriving, are dependent on the source populations for replenishment (Pulliam 1988). For example, strong predominant current patterns (Blot et al. 1990) or episodic events such as ENSOs (Cowen 1985) may select some populations over others as sources. In some cases, the range of a species may naturally fluctuate greatly because populations at the edges of the range depend on rare recruitment events (Vermeij et al. 1990). In the fourth pattern, larvae of some species are in the water column for so long that populations tend to supply larvae to a broad larval pool and the population to which the larvae settle is essentially random (Fig. 1D). Thus, dispersal is a regional process that will affect local populations (Palmer et al. 1996). Potential examples of this pattern are some rockfishes of the genus *Sebastes* (Moser and Boehlert 1991); the urchin, *Strongylocentrotus purpuratus* in the Northeastern Pacific (Palumbi 1995); and the Australian lobster along Western Australia (Phillips et al. 1979). Modeling efforts have demonstrated how the open nature of these latter patterns can have dramatic implications for local population stability (e.g., Roughgarden et al. 1985, Botsford et al. 1994, reviewed by Caley et al. 1996). While these four conceptual patterns represent relatively discrete states, real systems will lie along a continuum between the patterns and will likely vary in space and time.

Effective design of fishing refugia will be highly dependent on the replenishment pattern of the species to be protected and the goal of a reserve (Carr and Reed 1993). For example, the goal of regional replenishment from fishing refugia makes little sense for populations closed at the scale of the refugium (Fig. 1A) because there would be no effective dispersal out of the reserve and nearby populations would be unaffected by the protection offered by a reserve (DeMartini 1993). Further, the location of the reserve within a regional pattern of replenishment can be very important. An obvious example is the single-source/long-distance dispersal pattern. In Fig. 2A, the box represents a reserve that protects the source population and, therefore, protects replenishment of other populations as well. However, a reserve in a different area (Fig. 2B) protects no reproductive population. Thus, another key consideration relative to population replenishment is the predominant water flow and transport direction and, consequently, what activities are allowed "upstream" from a reserve. Selection of the location of reserves and the management outside them must consider oceanographic patterns as well as biological patterns.

Further, reserves must protect not only critical or special habitats, but also enough habitat. For instance,

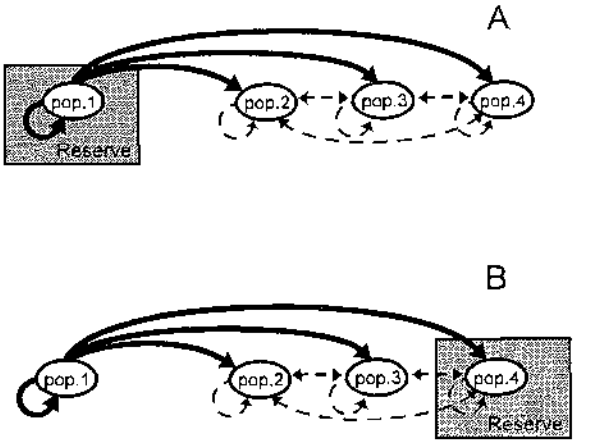

FIG. 2. Importance of reserve placement to reserve effectiveness. Single reserve (shaded box) established on a single-source pattern. (A) Reserve protects the reproductive source population (pop.) for many populations; (B) reserve protects no reproductive self-sustaining population. See Fig. 1 for explanation of symbols.

for species with a multiple source pattern (Fig. 1D), the most appropriate approach would be to spread a network of reserves throughout a significant portion of the range of the larval pool. Such a design would separate reserves sufficiently to spread the risk of a single reserve being affected by a local or even a larger scale perturbation (Plan Development Team 1990, Ballantine 1991, Quinn et al. 1993, Castilla and Fernández 1996)

However, if the goal of a reserve is to protect a broad range of species instead of a single target species, determining an appropriate design becomes complex because every community has a mix of these different dispersal patterns. Fig. 3 shows the range of planktonic-stage durations for some common intertidal invertebrate species in the Northeastern Pacific. The distance individuals will disperse is expected to be roughly correlated with the duration of the planktonic stage. Note that these durations range from no planktonic period (crawl-away juveniles) to several months. Because optimal reserve design for a species is dependent upon dispersal distance (Quinn et al. 1993), a reserve designed for some species in an area may be useless to others in the same area (Carr and Reed 1993, DeMartini 1993). While the species in Fig. 3 are indicative of the range of larval duration possible within a site, little is known about the frequency distribution of the dispersal distances of species to extrapolate the predominant patterns of population replenishment.

Episodic climatic events and climatic change

Another fundamental challenge to the design of effective reserves is presented by episodic climatic events that can overwhelm populations within reserves. For example, large-scale environmental fluctuations associated with ENSO events can change dominant cur-

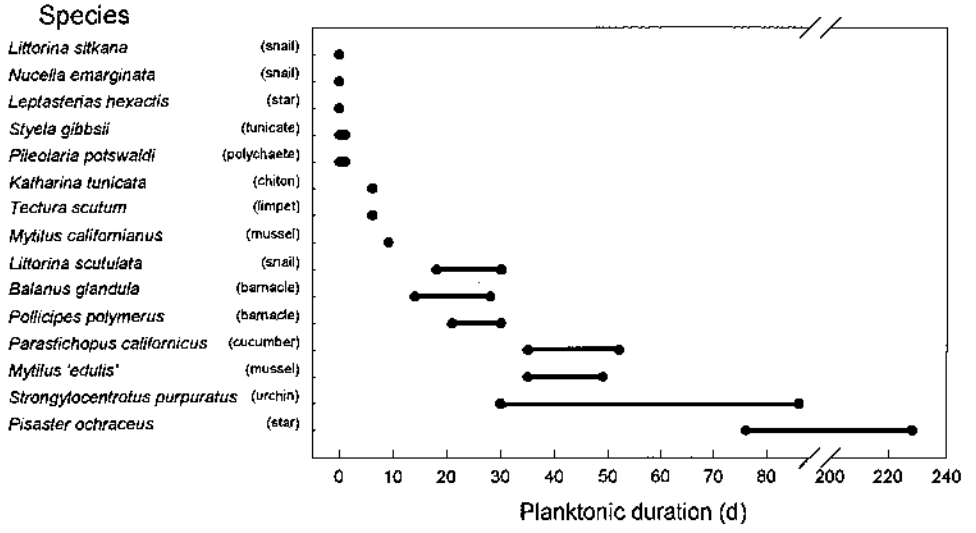

FIG. 3. Planktonic duration for some common intertidal invertebrates in the northeastern Pacific of the United States. These data are summarized from Strathmann (1987), mostly from laboratory studies of the time that larvae spend in the plankton before they settle. This time is expected to be roughly correlated with the dispersal distance of a larva. For some species, a range of planktonic durations was available, but for others only a single value was given. Species near the top of the graph either are direct developers or have a very short larval duration in the plankton. Species near the bottom are in the plankton for ≥1 mo, implying an extensive dispersal potential.

rent patterns, water temperatures, storm regimes, and upwelling conditions (Bakun 1990) and subsequently change the holopelagic and benthic communities (McGowan 1985, Pearcy et al. 1985, Smith 1985, Warwick et al. 1990, Castilla and Camus 1992). The 1982–1983 El Niño event affected the entire area now encompassing the Monterey Bay National Marine Sanctuary on the central California coast, a large MPA by most standards. Such events can dramatically increase recruitment (Castilla and Camus 1992) or, more often, disrupt benthic populations and their reproductive success (Fiedler et al. 1986, Tegner and Dayton 1987, Brown and Suharsono 1990). For example, mortality on many coral reefs exceeded 95% in the 1982–1983 ENSO event (Glynn and Colgan 1992). Paleosedimentary records suggest that such large variation is typical (McCall 1986). Populations in reserves the designs of which depend solely on self-replenishment can be severely reduced by such changes. With such drastic reductions, rare long-distance dispersal events may be important (Scheltema 1986, Reed et al. 1988) and therefore even short-distance dispersers may be dependent on nonreserve sources of replenishment.

Because reserves are usually meant to be permanent, the design must be effective even under conditions that may be very different than current conditions. In particular, reserves are likely to become ineffective if their designs do not account for *increasing* human pressure outside the reserve and any likely directional climate change (Peters and Darling 1985). For example, the size necessary for a fishing refugium depends on the intensity of fishing outside the refugium (Carr and Reed 1993, Quinn et al. 1993) and reserves designed for current fishing pressures may be inadequate in the future. Similarly, if recent predictions of climate change (Houghton et al. 1995, Watson et al. 1995) and their suggested consequences (Bakun 1990, Fields et al. 1993, Barry et al. 1995, Houghton et al. 1995, Roemmich and McGowan 1995*a*, Watson 1995) are accurate, reserves may experience altered current and upwelling regimes (and therefore dispersal patterns), average temperatures and temperature variability, productivity, and quite possibly species composition and abundance. Roemmich and McGowan (1995*a*, *b*) document large changes in primary and secondary productivity throughout the Southern California Bight between 1951 and 1993, potentially caused by a rise in water temperature. Holbrook and Schmitt (1996) describe corresponding declining trends in the abundance, richness, and structure of reef fish assemblages within the Bight over much of the same period. Reserve goals and design under such considerations become more complicated. Because no single reserve can protect against such large-scale climatic events, perhaps a series of reserves spread across latitudes would allow species to shift their distribution among reserves in response to such changes.

Finally, there are some types of threats to marine systems for which reserves will offer no direct protection: threats that are also dispersed on a large scale. For example, reserves are likely to be inadequate to protect local populations from highly dispersive pollutants (e.g., Jarman et al. 1992, Loganathan and Kannan 1994), disease epidemics (e.g., Rasmussen 1977,

Lessios 1988, Steinbeck et al. 1992, Littler and Littler 1995) or the spread of exotic species (e.g., Carlton et al. 1990, Trowbridge 1995).

Where Reserves Will Be Directly Effective

The conditions under which properly designed reserves will be directly effective are a function of (1) how potentially controllable the threat is, that is, the ability to manage the spread or the intensity of the threat and (2) the spatial scale of the threat. When the spatial scale of a threat is small, and the threats are manageable at the reserve scale, reserves are potentially effective for protecting populations within the reserve. For example, reserves provide the ability to control an intensive localized fishing pressure. However, when the threat is large-scaled, even though that threat is potentially controllable, reserves cannot be effective without coordination with other forms of management. Simply, the only successful control is where the scale of management is as large as the scale of the threat. For instance, reserve restrictions may be able to control the discharge of highly dispersed pollutants such as oil, pesticides, or polychlorinated biphenyls (PCBs) in or near reserves, but they cannot control the transport of those compounds into a reserve from distant sources. Further, even though the spatial scale of the threat may be local, some threats are not likely to be manageable. An exotic species that is introduced near a reserve, either accidentally or intentionally, will spread into a reserve regardless of reserve boundaries or regulations.

For these reasons, even for threats for which reserves can be potentially effective, their actual effectiveness will depend upon the protection provided outside reserve boundaries (Carr and Reed 1993, Agardy 1994, Kenchington and Bleakley 1994). We offer three design guidelines to help integrate the protections offered by reserves with those that will be required external to the reserves. For reserves to protect the populations within them, these questions must be addressed:

1) Will reserve populations be able to persist despite greater fishing pressure outside of the reserve?

2) Will reserve populations be able to persist despite episodic climatic events and directional climate change?

3) Will reserve populations be able to persist despite increases in threats from pollution, species introductions, and disease spread?

Addressing these questions clearly requires reserve designers to assess the significance and trends of human-induced threats and natural fluctuations both inside and outside reserves, as well as to account for patterns of population replenishment. While it is unlikely any of these questions can be completely answered, attempts to maximize population persistence in the face of important threats and the political, social, and economic constraints of reserves should increase the biological effectiveness of the reserve.

Filling Knowledge Gaps

Although reserves can, and should be established using existing information, design and effectiveness can be improved with a better understanding of relevant biological, ecological, oceanographic, economic, and social processes. In some cases, this improved understanding can be gained from existing or newly designed reserves using the principles of adaptive management (Walters and Holling 1990, Lee 1993). Indeed, reserves treated as experiments may be the most effective method of filling some of the knowledge gaps.

Increasing understanding of fundamental processes

A priority should be the identification of patterns of population replenishment for target species or those species deemed essential to the functioning of the community in need of protection. One impediment to accomplishing this has been the poor understanding of the patterns of currents, eddies, and local areas of mixing within 5 km of the shore (Menge 1992). When adequately documented, such knowledge can be very useful in the prediction of larval movement (Olson 1985, Sammarco and Andrews 1989, Botsford et al. 1994, Wing et al. 1995). Direct approaches, such as determining the actual parental source of recruits, are usually impractical with all but very short-distance dispersers (Olson 1985, Cohen 1990, Stoner 1992). In special cases, mark and recapture studies may be applicable for adults (Attwood and Bennett 1994) and perhaps some larvae (Levin 1990). Indirect methods of inferring dispersal patterns from population genetic structure can yield some important insights about the geographical extent of larval pools of more broadly dispersing species (Waples 1987, Waples and Rosenblatt 1987, Blot et al. 1990, Doherty et al. 1995, Palumbi 1995, Shulman and Bermingham 1995). Currently, however, such studies usually cannot precisely locate source populations. These molecular techniques hold much promise and deserve extensive development. Modeling (e.g., Botsford et al. 1994) can fill critical gaps in our knowledge that cannot be addressed experimentally or with short-term observations. The development of detailed knowledge of larval life histories (e.g., Strathmann 1987) and organismal distributions will be helpful to understanding replenishment patterns. Until more powerful methods become available, the identification of source populations may require a combination of many of these methods. Moreover, the implications of temporal and spatial variation in source populations should be explored (Botsford et al. 1994, Rogers-Bennett et al. 1995).

Improved understanding of how large-scale anomalies such as ENSO affect coastal systems and populations (McGowan 1985, Smith 1985, Lough 1994,

Holbrook and Schmitt 1996) would help determine how well reserves will accommodate such effects. Predicting effects of directional climate change (Peters and Darling 1985, Ray et al. 1992, Fields et al. 1993, Lubchenco et al. 1993) will facilitate evaluation of the long-term effectiveness of a reserve.

Further, greater understanding is needed about the demographic consequences of different exploitation strategies and how reserves might act to ameliorate those consequences. Many fishing practices modify the structure of populations by severely reducing the overall biomass of a population (e.g., Alcala 1988, Roberts 1995), decreasing age and size at sexual maturity (Plan Development Team 1990, Rijnsdorp 1993, Harmelin et al. 1995), and altering sex ratios and genetic structure (Ryman et al. 1995). Reserves may counter some of these changes if they export older individuals and supply propagules to surrounding populations. However, reserve populations may experience their own selection pressures. For example, if fishing pressure outside a reserve is strong enough, reserve populations may be selected for shorter dispersal (Rowley 1992).

The design and effectiveness of reserves will also benefit greatly from a better understanding of the sources, fates, and impacts of contaminants in the sea. Critical to this is our ability to predict the likelihood and magnitude of contamination within reserves generated from external sources. Such predictions will be based on accurate estimates of the origin, dispersal, and longevity of contaminants and the response of reserve inhabitants to potential levels of contamination.

Improving designs

To improve the effectiveness of marine reserves, the appropriate criteria for selecting the location, size, and number of reserves must be clarified. In terrestrial conservation, because of the profound effects of habitat loss and fragmentation, much theoretical work has necessarily focused on isolated populations because ". . . virtually all natural habitats or reserves are destined to resemble islands . . . becom[ing] small isolated fragments of formerly much larger continuous natural habitat" (Wilcox 1980:95). For instance, this "insular ecology" has developed methods to determine the minimum population size required for the persistence of self-replenishing populations over numerous generations (Shaffer 1981, Lande 1988, 1995). Reserve designers may use the criteria of minimum viable population size to select appropriate populations to protect. Thus, designing a reserve for a typical self-replenishing population must consider one "worst-case" scenario whereby the reserve population is isolated and completely independent of other propagule sources (Fig. 4A). However, for a large proportion of marine species, populations are much more "open" and more highly "mixed." For such species, the most appropriate criteria for reserve selection may be areas with minimum

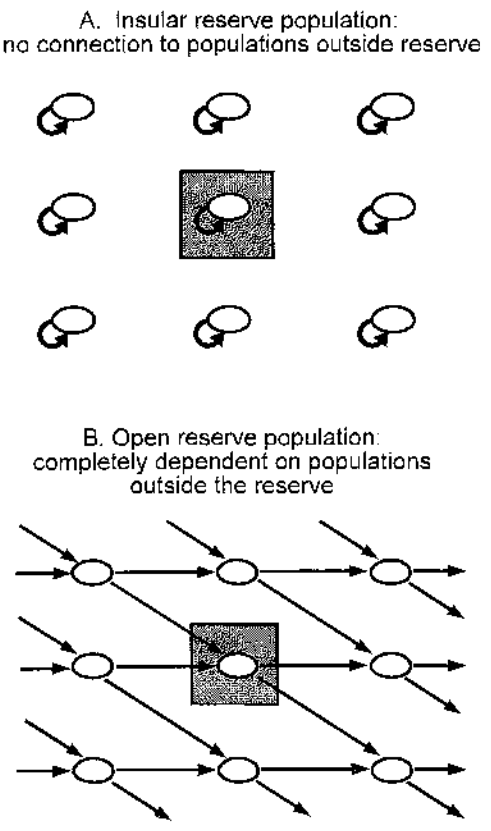

FIG. 4. Contrasting "worst-case" scenarios to consider when designing a reserve for (A) a self-replenishing population and for (B) a highly open population. The shaded box refers to a proposed reserve. In (A), populations are isolated from other propagule sources and thus must be of a sufficient size to allow persistence of that population. In (B), populations in the reserve are completely dependent upon replenishment from external, non-protected sources. See Fig. 1 for explanation of symbols.

viable population *flow*, that is, areas that receive consistent influx of propagules sufficient to sustain the local population. Thus, the design of an open-population reserve must account for a very different "worst-case" scenario whereby the reserve population is completely dependent on the matrix of interconnected and unprotected populations external to the reserve (Fig. 4B). Currents that transport organisms from one site to another may be similar to terrestrial "corridors," although the former would be much more spatially dynamic. Modeling efforts by Roughgarden and co-workers (Roughgarden et al. 1985, Roughgarden and Iwasa 1986, Possingham and Roughgarden 1990) and others (e.g. Botsford et al. 1994) have explored the implications of "open" population structure on population dynamics, but much work is still necessary to provide practical guidelines for reserve designs.

Whether many small reserves or a few large reserves will protect more species has been addressed in very few marine systems (but see McNeill and Fairweather

1993). For some reserve goals, biological considerations may make several small reserves more effective. A fishing refugium design may be best served by many reserves so that the interaction among populations in protected areas and those in unprotected areas can be maximized (Dugan and Davis 1993, Quinn et al. 1993). But for reserves designed to protect biodiversity "hot spots" in regions of high human impact, it may be more important to isolate the hot spot from threats as much as possible. In such cases, a single large reserve may be more appropriate to minimize the interaction with heavily used areas. Indeed, the goals of biodiversity reserves and fishing refugia may be mutually exclusive for that reason.

Networks of reserves have been advocated by numerous researchers (Salm and Clark 1989, Ballantine 1991, Dyer and Holland 1991, Bohnsack 1992, Quinn et al. 1993, Castilla and Fernández 1996) as a potentially effective solution to large-scale reserve coverage while applying restrictions to only a small fraction of exploited areas. Researchers propose that such networks, properly designed, could provide several replicate source populations, reduce region-wide risk of anomalous effects on a single reserve and increase the potential benefits to nonreserve areas by increasing the connectance between protected and nonprotected areas. Such proposals deserve extensive exploration because, even under ideal conditions, the persistence of a given population cannot be assured (Mangel and Tier 1994) and multiple, spatially separate reserves may be the best solution. Determining the best design for a limited total area available for protection deserves critical attention.

Judging effectiveness

Evaluating a reserve's effectiveness is essential to increasing conservation potential (McNeill 1994) but, without a methodology to explicitly evaluate reserves, few improvements will be made. It may seem trivial to assert that for the effectiveness of reserves to be judged, the goals must be explicit. Nevertheless, the assertion is necessary because a large proportion of currently established marine reserves have no management plans (Kelleher et al. 1995*a*).

There are, however, a number of confounding factors that demand serious attention if reserve effectiveness is to be judged critically. The problem of statistical replication is severe. Within-site replication is pseudoreplication (Hurlbert 1984) and cannot be used to increase statistical power. Even in networks, reserves are often implemented one at a time (Ballantine 1991). Therefore, analyses that allow tests of nonreplicated designs such as BACI analysis (Underwood 1991, Stewart-Oaten et al. 1992, several chapters in Schmitt and Osenberg 1996), alternative methods (Carpenter et al. 1989, Carpenter 1990) or Bayesian approaches (Reckhow 1990) are probably most appropriate. Most of these analyses depend on sufficient monitoring before the policy is implemented, but it is still rare that areas to be protected are monitored before protections are in place (Bennett and Attwood 1991, McNeill 1994). Furthermore, BACI designs require appropriate "controls." However, the location of reserves are often chosen because they offer some unique characteristics such as high diversity or because they are spawning grounds (Salm and Clark 1989, Kelleher and Kenchington 1992). Finding areas similar to reserves will often be difficult but necessary. Unless suitable controls are found, monitoring can provide only correlative evidence, not direct causal evidence.

Furthermore, monitoring of reserves faces the generic difficulties of detailed research in the marine environment: limited access time and visibility with SCUBA and the high cost of research with submersibles. Such constraints force limited monitoring that may yield only coarse indications of trends between treatments. These constraints, as well as artifacts in reserves such as the modified behavior of fish in response to divers (Cole 1994), may limit the ability to detect biologically significant differences between protected and nonprotected areas (Cole et al. 1990). Therefore it is essential that optimal monitoring programs be developed that collect data best suited to evaluate reserve effectiveness. This will require that reserve goals (e.g., maximizing reserve population densities, maximizing sustainable yield outside of the reserve, or maximizing reserve biodiversity) are explicit.

Finally, monitoring can be used for more than documenting long-term changes in populations. Research within the reserve could be geared toward determining what ecological processes could be managed within the reserve (i.e., manifestations of post-settlement processes or locally closed populations) vs. those that cannot (i.e., externally driven processes such as larval supply or water-borne toxicants). Also, collaborative research programs that integrate long-term monitoring studies (conducted by management personnel with long-term funding) with short-term academic investigations directed at understanding the mechanisms responsible for producing for any long-term patterns would yield a greater understanding than such research performed in isolation.

Conclusions

We have addressed only biological issues of reserves. Many other factors such as funding, local participation, and political feasibility and commitment (Kenchington and Agardy 1990, Kenchington and Bleakley 1994, Gubbay 1995) are critical to the success of reserves. However, ignoring important biological issues or severely compromising design or implementation because of nonbiological issues will jeopardize the original conservation goals.

Marine protected areas offer not only potential for

conservation gains, but also the opportunity to expand conservation theory and to integrate human uses of marine resources with their protection. For reserves to meet this broad conservation potential, an important challenge is to develop shortcuts for a given reserve to determine, from the long list of potentially important factors, which factors will be critical for reserve effectiveness under the constraints of limited budgets and data, but heavy human pressure on systems. However, these challenges are ripe for productive research, which could elevate marine reserves into a more defensible and effective stage.

The issues presented herein are rarely addressed adequately in marine reserve design and implementation. Further, marine conservation and marine reserves have received relatively little attention within the broad conservation community (Irish and Norse 1996, Murphy and Duffus 1996). The issues and problems presented here would benefit greatly from the consideration by that community. Marine reserves are a critical component of a conservation strategy but must be coupled with other, complementary efforts.

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