

No-take Reserve Networks:

Sustaining Fishery Populations and Marine Ecosystems

By Steven N. Murray, Richard F. Ambrose, James A. Bohnsack, Louis W. Botsford, Mark H. Carr, Gary E. Davis, Paul K. Dayton, Dan Gotshall, Don R. Gunderson, Mark A. Hixon, Jane Lubchenco, Marc Mangel, Alec MacCall, Deborah A. McArdle, John C. Ogden, Joan Roughgarden, Richard M. Starr, Mia J. Tegner, and Mary M. Yoklavich

ABSTRACT

Improved management approaches are needed to reduce the rate at which humans are depleting exploited marine populations and degrading marine ecosystems. Networks of no-take marine reserves are promising management tools because of their potential to (1) protect coastal ecosystem structure and functioning, (2) benefit exploited populations and fisheries, (3) improve scientific understanding of marine ecosystems, and (4) provide enriched opportunities for non-extractive human activities. By protecting marine ecosystems and their populations, no-take reserve networks can reduce risk by providing important insurance for fishery managers against overexploitation of individual populations. Replicated reserves also foster strong scientific testing of fishery and conservation management strategies. Reserve networks will require social acceptance, adequate enforcement, and effective scientific evaluation to be successful. Processes for reserve establishment should accommodate adaptive management so boundaries and regulations can be modified to enhance performance. However, even well-designed reserve networks will require continued conservation efforts outside reserve boundaries to be effective. Establishing networks of no-take reserves is a process-oriented, precautionary management strategy that protects functional attributes of marine ecosystems. As an addition to fishery management practices and other conservation efforts, no-take reserve networks may improve the status of exploited populations while conserving marine resources for future generations.

Few of the world's coastal regions remain undisturbed by human activities (GESAMP 1991; NRC 1995; Vitousek et al. 1997). During the past century, America's coastal ecosystems have been changed by inputs of pollutants, modifications of watersheds, destruction of habitats, invasions of exotic species, and extractions of living resources (Suchanek 1994; Lubchenco et al. 1995; NRC 1995). Despite good intentions, existing efforts to manage and protect marine resources frequently are inadequate.

Many marine ecosystems show reduced biodiversity and other signs of degradation (Suchanek 1994; Lubchenco et al.

1995; NRC 1995). Moreover, many populations of exploited fish and invertebrates are declining in numbers and average size despite the

efforts of fishery managers (FAO 1995; Roberts 1997; NRC 1999). In the United States, the tradition of open access and a lack of political



A sign posted at the shore entrance near the Asilomar Conference Center in the Monterey Bay National Marine Sanctuary indicates that fishing is allowed even though "all" marine animals and plants are protected. Regulations for national marine sanctuaries often do not limit or restrict fishing; commercial and recreational fishing is allowed in all national marine sanctuaries established in waters off California (McArdle 1997).

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will to change management strategies have inhibited implementation of effective measures to protect marine resources. Even marine ecosystems believed to be protected strongly, including many of those contained within U.S. marine sanctuaries and national parks, allow commercial and recreational fishing (Dugan and Davis 1993; McArdle 1997). Clearly, improved management approaches are required to sustain fisheries and effectively protect U.S. marine ecosystems and the goods and services they provide. Here, we discuss the potential of networks of no-take marine reserves to protect fishery populations and marine ecosystems.

Fisheries

Globally, the use of marine fish stocks is at or near a sustainable limit, and many populations are currently overexploited (NRC 1999). More than 40% of the world's marine fishery populations is heavily to fully exploited, and 25% is classified as overexploited, depleted, or recovering (NRC 1999). In the last decade, this high exploitation rate has led to the partial or complete collapse of many of the world's fisheries, and new, unexploited populations are no longer available to replace depleted stocks (Vitousek et al. 1997). Even in countries with active fishery management, the regulatory process has not prevented overfishing of many stocks. For example, in the United States, 36% of fishery stocks with known status under federal purview was classified as overutilized based on 1992-1994 data, and only 20% was underutilized with the potential to be fished more heavily (NMFS 1996).

Fishing activities also harm more than targeted populations. Many individuals of nontargeted species are killed incidentally as bycatch or discards and through the ghost-fishing of abandoned gear (NRC 1999). Global bycatch and discards between 1988 and 1990 amounted to approximately one-third of total landed biomass (Alverson et al. 1994), making the ecological consequence of bycatch and discard mortality a serious problem of modern fisheries management (Dayton et al. 1995; NRC 1999). Fishing also can change the genetic structure of exploited populations (Ricker 1981; Smith et al. 1991; Law et al. 1993). The selective removal of certain species by fishing can modify species interactions and result in changes that cascade throughout marine communities (Dayton et al. 1995; Hixon and Carr 1997; NRC 1999). Other fishing activities such as trawling and dredging disturb and alter seafloor habitats, and can modify the structure and diversity of benthic communities (Auster et al. 1996; Collie et al. 1997; Thrush et al. 1998).

Examples: New England and Pacific groundfish

Overfishing has been implicated in collapses of fisheries off the Atlantic coasts of New Eng-

land, Canada, and elsewhere (Safina 1995; Myers et al. 1997; Fogarty and Murawski 1998). Overexploitation, first by distant-water fleets and then by domestic fishing, resulted in depletion of valuable groundfish and other fishery stocks in the Georges Bank ecosystem off New England and Nova



J. B. Phillips Collection, Maritime Museum of Monterey

Rockfish fishers work in a skiff off the Point Sur, California, coast in the late 1930s. Rockfishes and other West Coast groundfish stocks are vulnerable to overfishing.

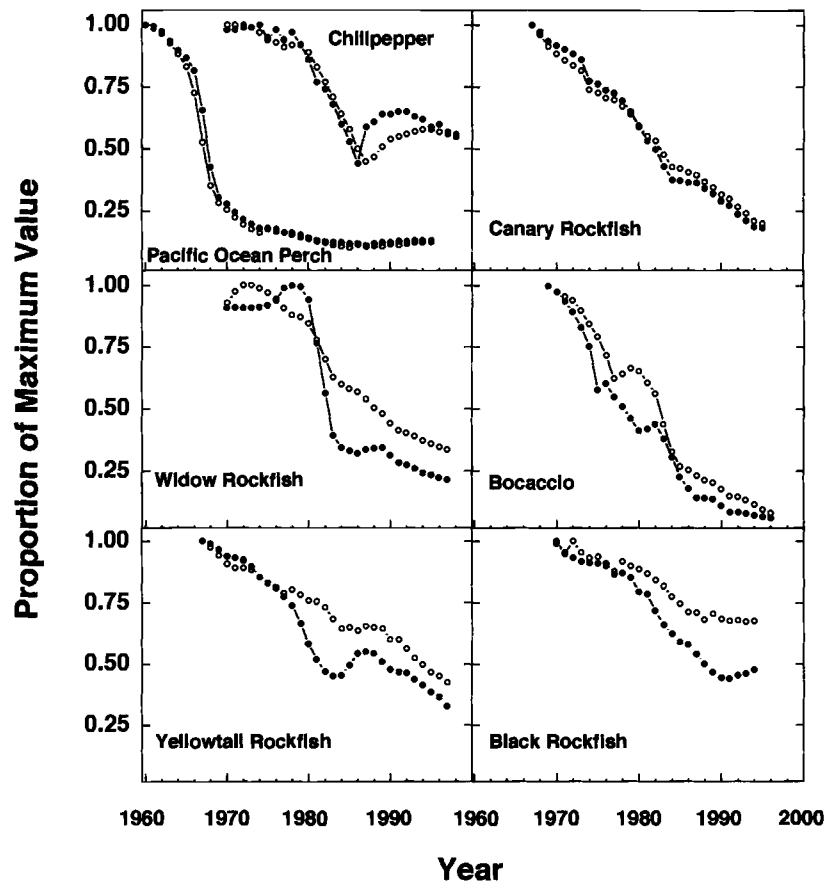


Figure 1. Precipitous declines in seven stocks of Pacific rockfish (*Sebastes* spp.) during the last 20 to 30 years. Plotted are trends in exploitable biomass (open circles) and spawning output (closed circles). Redrawn from Ralston (1998).

Scotia (Fogarty and Murawski 1998; NRC 1999). Despite warnings from fishery scientists, groundfish exploitation rates in the 1990s surpassed recommended levels, and the biomass of valuable Atlantic cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), yellowtail flounder (*Limnada ferruginea*), and other species dropped sharply, eventually resulting in the closure of once highly productive fishing grounds (Fogarty and Murawski 1998). In addition to depleting groundfish populations, fishing and fishing activities changed species composition, altered the food web structure, and damaged important benthic habitats on Georges Bank (Collie et al. 1997; Fogarty and Murawski 1998; NRC 1999). Currently, approximately 30% of Georges

Bank is closed to all fishing gear capable of catching groundfish as part of a stock recovery plan (Fogarty and Murawski 1998).

Similarly, many groundfish stocks are in jeopardy on the West Coast of North America (Figure 1). Off Washington, Oregon, and California, groundfish have been intensely fished, beginning with the large catches made by foreign fleets in the late 1960s and early 1970s (King 1990) and continuing with high domestic removals in the 1980s and 1990s (Pacific Fishery Management Council 1995).

Rockfishes, a large component of the West Coast groundfish fishery, are live-bearers, and several species mature slowly (>5-10 yr) and have long life spans (50-140 yr) (Archibald et al. 1981; Wyllie Echeverria 1987). Additionally, most rockfishes experience sporadic recruitment associated with variable oceanographic conditions (Ralston and Howard 1995; Ralston 1998). These characteristics make rockfishes particularly vulnerable to fishing and slow to recover from overexploitation (Beverton 1992; Leaman 1991; Gunderson 1997a). For example, stocks of Pacific ocean perch (*Sebastes alutus*) have yet to recover from the mid-1960s to early 1970s, when they were reduced to almost 10% of their unfished biomass (Ralston 1998). More recently, bocaccio (*S. paucispinis*) populations have declined to the point where they are now regarded as critically endangered by the World Conservation Union, and canary (*S. pinniger*) and widow (*S. entomelas*) rockfish are only 20%-30% of their unfished biomass (Pacific Fishery Management Council 1995; Ralston 1998). Several other rockfishes subsist at dangerously low levels, and many other populations also have been depleted (Gunderson 1997b). Even species that currently are abundant or that have life histories allowing for faster recovery are susceptible to overexploitation given today's fishery practices. Without intervention, existing management strategies probably will lead to serial depletion of the least-resilient species.

Examples: California's abalone and sea urchin fisheries

Valuable nearshore invertebrate fisheries also have recently collapsed. In the 1950s and 1960s, five abalone species (*Haliotis* spp.) supported hundreds of commercial fishers and hundreds of thousands of sport divers in California (Cox 1962; Dugan and Davis 1993). However, abalone stocks have been serially depleted, and the California fishery has collapsed (Figure 2). Today, only the recreational fishery for red abalone (*H. rufescens*) survives, and it is restricted to an area north of San Francisco where a de facto depth refugium

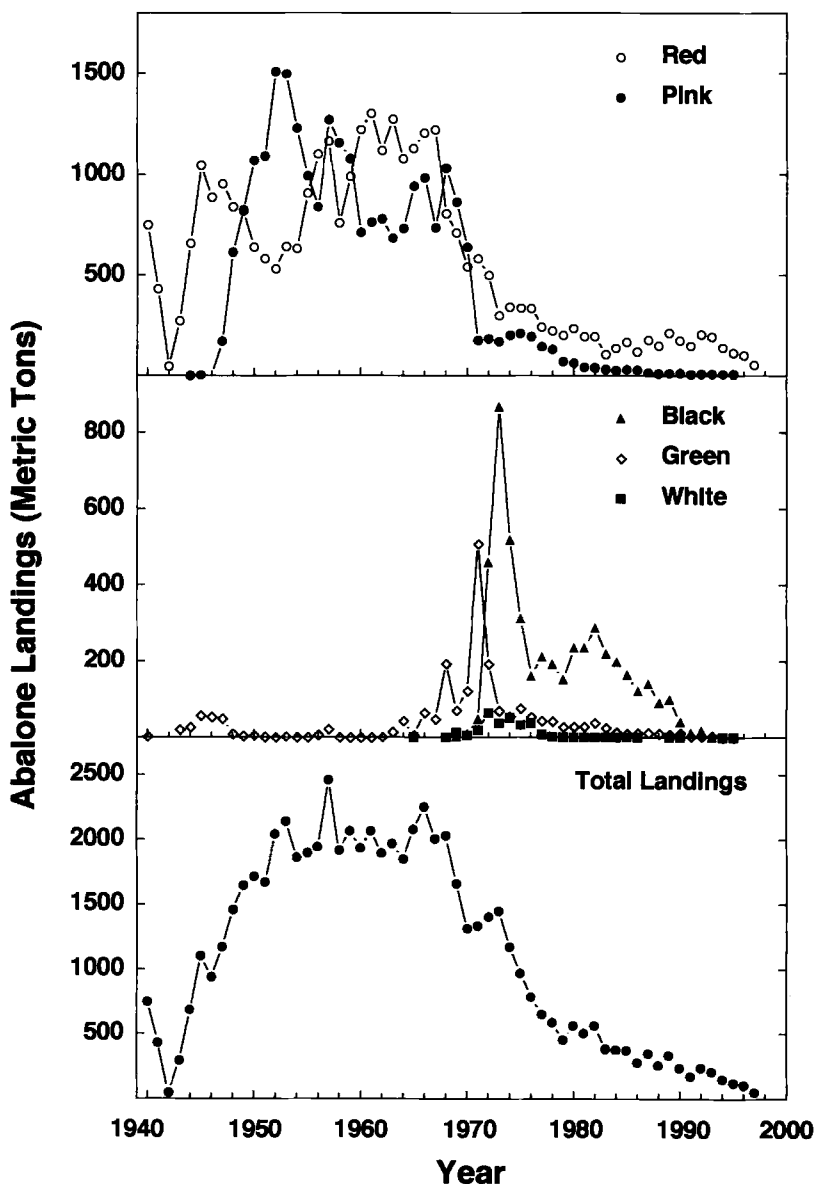


Figure 2. Sequential depletion of California abalone populations that once supported a commercial fishery. Data obtained from landing records compiled by the California Department of Fish and Game. Red abalone (*Haliotis rufescens*), pink abalone (*H. corrugata*), white abalone (*H. sorenseni*), green abalone (*H. fulgens*), and black abalone (*H. cracherodii*). Data provided by Ian Taniguichi, California Department of Fish and Game.

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has sustained an annual take of 1,000 mt (Tegner et al. 1992). The white abalone (*H. sorenseni*) supported a commercial fishery in the early 1970s, but its numbers declined rapidly following intense fishing pressure to levels where the white abalone has now been declared a candidate for the federal endangered species list and may become the first marine invertebrate known to be fished to extinction (Davis et al. 1996; Tegner et al. 1996).

A red sea urchin (*Strongylocentrotus franciscanus*) fishery developed when abalone populations were depleted in the 1970s (Parker and Kalvass 1992), and by 1992 urchins were California's most valuable marine fishery (Dugan and Davis 1993; McWilliams and Goldman 1994; Kalvass and Hendrix 1997). In the last decade, however, sea urchin landings have fallen, recruitment has declined in some locations, and the California urchin fishery is now considered by the NMFS (1996) to be fully exploited.

Abalones and sea urchins, like many commercially important benthic invertebrates, are broadcast spawners where gamete concentrations are quickly diluted upon release and fertilization success is density-dependent. Consequently, reductions in density can affect reproductive success and lead to further population declines. Allee effects, together with intense exploitation, have been responsible for the extinction of giant clams (*Tridacna gigas*) in Fiji, Guam, New Caledonia, and the Northern Marianas (Wells 1997). Such issues are important considerations for maintaining populations of exploited sea cucumbers (Conand 1997), bivalves such as scallops (Caddy 1989), and other invertebrates that depend on external fertilization.

Fishery management

Clearly, improved fishery management practices are needed to prevent overfishing and the serial depletion of exploited populations. Management of most fisheries is still based on single-species models despite the fact that multiple species are caught in almost every fishery (Mangel et al. 1996; Roberts 1997; NRC 1999). Existing single-species population models require a reliable time series of survey and catch-at-age data to reconstruct trends in stock biomass and exploitation rates. However, it is seldom possible to develop accurate models because of inadequate data, difficulties in estimating critical model parameters,

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and problems in accounting for environmental variability and uncertainty. Although increasingly promoted by fishery scientists and managers, multispecies models require even more information than single-species models and still

are subject to problems of parameter estimation and in accounting for large, unexpected disturbances (NRC 1999). Thus, it is difficult to model exploited populations, to evaluate the risk involved in any fishery management decision, and to know when management actions are truly working to sustain fishery stocks. This can be true even for well-studied fisheries with seemingly stable populations (Gordon and Munro 1996; Hall 1998; Lauck et al. 1998).

Consequently, fishery managers need to allow for uncertainties and to use caution when establishing sustainable catch levels to protect against overfishing (Mangel et al. 1996; Hall 1998; Lauck et al. 1998). Because over-exploitation often takes years to detect, the mid-course corrections in catch or effort needed to sustain targeted stocks may not be implemented soon enough if landings are set too high (Dayton 1998). Current practices usually place the burden of proof on fishery scientists by requiring overwhelming evidence of resource damage before limitations are placed on fisheries (Garcia 1994; Mangel et al. 1996; Botsford et al. 1997). However, even when the scientific evidence suggests that a fishery resource is being depleted, the political will to take a precautionary approach and restrict fishing is often lacking. Existing management practices also make it difficult to regulate new fisheries such as the commercial live-fish fishery off California, where fishing effort has increased ten-fold but catches only four-fold in the 1990s (Hardy 1996). Without immediate restrictions, this live-fish fishery may deplete many shallow-water West Coast fishes. Moreover, the removal of urchin-consuming California sheephead (*Semicossyphus pulcher*), a principal target of the live-fish fishery in southern California, could lead to destructive overgrazing by unfished urchin species in kelp forest communities (Dayton et al. 1998).

Other threats to marine ecosystems

Human activities other than fishing also threaten marine ecosystems. Land-based activities of an expanding human population harm marine ecosystems through the discharge of sediments, pesticides, sewage, industrial pollutants, and high concentrations of nutrients (Lubchenco et al. 1995; Agardy 1997; Vitousek et al. 1997). Nearly 40% of the world's population is concentrated within 100 km of the sea (Cohen et al. 1997). In the United States, almost half of the population can be found in coastal regions that account for only 5% of the land, and this population is growing by more than 1% each year (Culliton et al. 1990; NOAA 1990). The development of U.S. waterfront property has led to extensive destruction and modification of natural coastal habitats, including more than 70% of the original wetlands in Maryland and Connecticut, and 90% in California (Dahl et al. 1991). With greater coastal population densities, more people visit the shore for educational and recreational activities such as fishing, tidepool exploring, swimming, diving, and collecting organisms. Evidence is accumulating that these activities can harm coastal ecosystems (Hawkins and Roberts 1992; Keough et al. 1993; Brosnan and Crumrine 1994) and that existing management practices need to be reconsidered.

Marine reserves

Restricting fishing in nursery and spawning grounds or closing areas to rebuild depleted stocks has long been part of fishery management practices (Fogarty 1999). The establishment of no-take reserves, and specifically no-take reserve networks, however, has not received much attention despite the potential of reserves to improve fishery stocks and to support fisheries and fishery management. Marine reserves encompass less than one-quarter of 1% of the world's oceans, and only a fraction of these protected areas has been designated no-take reserves (McAllister 1996). Few no-take marine reserves exist in the United States. Planned networks of no-take reserves have not been instituted in North America until recently, when a set of no-take reserves was established in the Florida Keys National Marine Sanctuary (Bohnsack 1998a). Even in Florida, however, the combined area of the reserves comprising the network consists of less than 0.5 % of the sanctuary's waters (Ogden 1997). In California, no-take reserves protect only 0.2 % of state waters (McArdle 1997, 1998), and planned reserve networks do not exist.

Few no-take marine reserves exist in the United States.

Knowledge of requirements for effective marine reserves is less well-developed compared with terrestrial reserves, where a working theoretical framework exists for design and management (Simberloff 1988; Barrett and Barrett 1997). Because marine and terrestrial systems differ substantially, many of the management principles derived from terrestrial experiences are not applicable to marine reserves (Agardy 1997; Allison et al. 1998). Understanding the factors that determine population and community dynamics in marine systems is much more difficult than on land (Caley et al. 1996; Hixon 1998). For example, humans commercially exploit mostly plants and herbivores in terrestrial systems, whereas in the ocean predators are frequently targeted (Hixon and Carr 1997; Steneck 1998). Also, marine ecosystems are influenced to a much greater extent by variable, unpredictable physical processes (Agardy 1997; Botsford et al. 1997) and are more likely to experience decadal-scale shifts in physical conditions compared with their terrestrial counterparts (Steele 1991, 1998).

Moreover, because ocean currents transport organisms and materials great distances, marine sites are exposed to much broader regional influence than sites on land. Because many marine populations depend on larval recruitment from distant sources for replenishment (Roughgarden et al. 1994; Botsford et al. 1994; Palmer et al. 1996), sites providing sources of larvae and eggs need to be connected hydrographically to recipient sites to ensure the maintenance of local populations (Roberts 1998). The dependence of many marine populations on other areas for recruitment strongly underscores the need for multiple reserves that protect populations over regional scales (Ballantine 1995, 1997; Roberts 1998).

Benefits of no-take reserve networks

Protect ecosystem structure and functioning

Self-sustaining networks of marine reserves can potentially protect ecosystems by protecting habitats and communities from extractive activities that can lead to significant loss of biodiversity and changes in species interactions (Dayton et al. 1995; Boehlert 1996; Hixon and Carr 1997). Individual reserves can vary in design and management objectives (Agardy 1997), but effective networks that protect ecosystem structure and functioning should consist of a core of no-take reserves in which extraction of all living organisms is prohibited. In the absence of effective protection, many populations of predatory fish and other pelagic and continental shelf species already have been reduced to levels so low that they no longer perform their former ecological roles (Dayton et al. 1995, 1998; Pauly et al. 1998). Networks of no-take marine reserves can (1) help recover fishery populations; (2) eliminate mortality of nontargeted species within protected areas due to bycatch, discards, and ghost fishing; (3) protect reserve habitats from damage by fishing gear; and (4) increase the probability that rare and vulnerable habitats, species, and communities are able to persist.

Increase scientific understanding

Networks of no-take marine reserves can serve as sites for increasing scientific knowledge and understanding of marine ecosystems and their management. Without unexploited areas against which to measure change, scientists have little ability to fully evaluate the true impacts of fishing or other forms of human disturbance on marine populations and communities (Roberts 1997; Dayton et al. 1998). No-take reserve networks provide the required benchmark sites for separating effects of extractive human activities from those caused by natural shifts in physical regimes. This is important because natural oceanographic variability can significantly affect marine systems (NRC 1999) but can almost never be evaluated in the presence of cumulative effects of anthropogenic disturbance without benchmark sites (Dayton et al. 1995, 1998; Botsford et al. 1997). Baseline data from unfished stocks also can vastly improve estimates of population parameters for harvested species (Smith et al. 1999). The opportunity to improve understanding of marine ecosystems is particularly critical since modifications of physical, chemical, and biological systems by human activities are proceeding in new ways, at faster rates, and over larger spatial scales than ever before (Lubchenco 1998).

Enhance non-extractive human activities

No-take marine reserves create social and economic opportunities that otherwise would be impossible by supporting human activities dependent on minimally disturbed sites. These include activities such as wilderness experiences, ecotourism, scientific research, and advanced marine education. Other nonextractive activities also might be enhanced by no-take reserves, including diving, underwater photography, cultural and aesthetic uses, and

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environmental education. Many of these activities have substantial social and economic benefits that in some regions may even exceed the extractive uses of marine reserves (Dixon and Sherman 1990; Brock 1994; U.S. Department of Commerce 1996).

Benefit fishery populations

No-take reserve networks can directly and indirectly benefit exploited marine populations and fisheries. It has been repeatedly shown that the abundances, average sizes, and spawning biomass of exploited populations will rebound in no-take reserves (Rowley 1994; Bohnsack 1995; Roberts et al. 1995). These demographic changes are a predicted outcome of reserve protection because many fish and invertebrates live longer, reach greater body size, and produce significantly more eggs and larvae in the absence of fishing mortality (Bohnsack 1992, 1995; Roberts and Polunin 1993). No other form of fishery management provides the opportunity for a segment of a fishery stock to realize its full ecological and demographic potential.

No-take marine reserves have the potential to enhance exploited populations and benefit fisheries by

- (a) Dispersing larvae that replenish fishing grounds removed from reserve source populations (Carr and Reed 1993; Rowley 1994; Bohnsack 1998b); however, the degree of augmentation will depend on the species, existing oceanographic conditions, and the magnitude of fishing mortality outside protected areas (Carr and

Reed 1993; Sladek Nowlis and Roberts 1999);

- (b) Exporting biomass to adjacent fishing grounds in the form of emigrating juveniles and adults (Russ and Alcala 1989; Rowley 1994; Bohnsack 1998b); and
- (c) Protecting portions of exploited stocks from genetic changes, altered sex ratios, and other disruptions caused by selective fishing mortality (Ricker 1981; Law et al. 1993; Bohnsack 1992, 1998b).

Support fisheries and fishery management

No-take marine reserves also can support and benefit fisheries and fishery management. Sound fisheries management must allow for effects of changing environmental conditions and uncertainty or inaccuracies in stock assessment and projected sustainable catch levels (Roberts 1997; Dayton 1998; Lauck et al. 1998). Refugia provided by sufficiently large, no-take reserve networks can

- (a) Decrease the likelihood of stock collapse because reserves can act as regional buffers against unanticipated fishing mortality, unforeseen management errors, or environmental changes (Bohnsack 1998b). Hence, reserve networks that partition targeted species into exploited and unexploited populations can be used as a bet-hedging strategy to reduce risk to fishery managers over regional scales (Roberts 1997; Dayton 1998; Lauck et al. 1998);
- (b) Accelerate the rate of recovery of overexploited populations because of the increased spawning stock located in reserves (Bohnsack 1998b);

Table 1. Guidelines for developing functional reserve networks that link ecological processes (extended from Ballantine 1995, 1997).

- (1) Reserves should have clearly identified goals, objectives, and expectations.
 - (a) Clearly identify and describe the purposes of each reserve.
 - (b) Clearly identify the species, communities, and habitats to be protected.
 - (c) Clearly identify the projected role and contribution of each reserve to the network.
- (2) Reserves should represent a wide variety of environmental conditions.
 - (a) Locate reserves in each biogeographic region, in the path of major currents, and in major upwelling cells.
 - (b) Distribute reserves across latitudinal and depth clines in each biogeographic region.
 - (c) Design reserves to match the scale of ecological and oceanographic processes.
 - (d) Include representative habitat types and biotic communities.
 - (e) Consider habitat quality inside and outside each reserve.
 - (f) Establish reserves in areas with high and low levels of human disturbance.
- (3) Reserves should be replicated within each biogeographic region.
 - (a) Replicate reserves to protect similar habitats and biotic communities to maximize effectiveness and to guard against excessive damage from catastrophic events.
 - (b) Replicate reserves to ensure effective designs for experimental and monitoring studies.
- (4) Reserves should accommodate adaptive management.
 - (a) Develop flexible management practices to enable science-based revisions of reserve regulations and boundaries.
 - (b) Develop scientific research and monitoring programs to evaluate biological and social performance.
 - (c) Plan reserves to meet current and expected future needs.
- (5) Reserves should be of sufficient size to be self-sustaining.
 - (a) Design reserve networks so coverage is large enough to sustain populations after local catastrophic events.
 - (b) Make individual reserves large enough to limit deleterious edge effects and to facilitate enforcement.

- (c) Theoretically decrease variability in annual catches by augmenting some fishery stocks, especially when reserves are large, and fishing mortality is high outside reserve boundaries (Sladek Nowlis and Yoklavich 1998; Sladek Nowlis and Roberts 1999);
- (d) Serve as sites for collecting valuable fishery-independent data and for conducting fishery research that cannot be carried out in exploited areas (Lindeboom 1995); and
- (e) Prevent modification and degradation of critical marine habitat caused by fishing practices (Dayton et al. 1995; Allison et al. 1998).

Designing effective reserve networks

Certain guidelines apply to the design of any marine reserve network regardless of its geographic location (Table 1). First, the goals, objectives, and expectations of each reserve in the network should be specified together with the species, communities, and habitats targeted for protection. Individual reserves can have different goals, but a reserve network should form a protective system that connects ecosystem functioning over regional scales. Thus, reserves forming the network should be distributed along latitudinal, depth, or other environmental gradients, and protect representative species and habitat types found in different biogeographic regions. For example, reserve networks in California should include habitats such as nearshore coastal waters, offshore islands, the edges of the continental slope, submarine canyons, and seamounts off the coast, whereas those in Florida should contain mangroves, seagrass beds, and coral reefs.

The design of reserve networks should be based on knowledge of the natural systems, species' life cycles and habitat requirements, and existing conditions such as the

Reserve sites should be chosen based on available historical data and expected ecological benefits.

degree of degradation or integrity of targeted habitats and populations. Individual reserve placement should take into account oceanographic conditions and major currents to maximize biological exchange among reserves and between adult and nursery habitats (Carr and Reed 1993; Carr and Raimondi 1998). For example, Pacific Coast reserves should include major upwelling cells that occur along the coast approximately every 100 km (Starr 1998) because the proximity of spawning adults to upwelling jets may be an important factor for dispersal and recruitment of several fish species, including rockfishes (Yoklavich et al. 1996; Morgan and Botsford 1998). In addition, eddies or counter currents near upwelling jets may enhance recruitment of invertebrates (Wing et al. 1995; Alexander and Roughgarden 1996; Bjorkstedt and Roughgarden 1997).

The type, distribution, and quality of habitats inside and outside reserve boundaries should be considered

when locating individual marine reserves. Realizing the goal of improving fishing outside reserves requires suitable and sufficient habitat to support populations inside reserve boundaries, and the availability of appropriate habitat in adjacent fishing grounds where stocks are to be extracted (Carr and Reed 1993; DeMartini 1993). Reserve sites should be chosen based on available historical data and expected ecological benefits. They can include regions that have been subjected to both high and low

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levels of human disturbance. Whereas pristine areas and lightly exploited populations often are regarded as excellent candidates for protection, highly degraded systems also offer opportunities to restore marine ecosystems (Agardy 1997; Roberts 1998). In fact, highly exploited areas such as those adjacent to urban population centers may show stronger responses to reserve designation (Sladek Nowlis and Roberts 1997), but their success will depend on protection against other forms of human disturbance (Allison et al. 1998).

Replication of reserves is important for risk management because multiple reserves can serve as a hedge against isolated catastrophic events that affect populations or destroy habitat. Moreover, given the spatial and temporal variation of environmental processes that influence larval survival, protection of similar habitats in multiple locations can increase the chances that reserves will improve recruitment of individual species (Roberts 1998; Starr 1998). Reserves also must be replicated over appropriate regional scales to facilitate the scientific research and monitoring programs needed to provide accurate biological and social feedback on performance (NRC 1995; Ballantine 1997). Replication strengthens statistical inference and is important for rigorously testing hypotheses on reserve functions. Hence, the availability of replicated reserves is crucial for science-based improvement of reserve design and for increasing knowledge of fundamental processes in changing marine systems.

The common approach of establishing small, isolated reserves compromises the ability to achieve most conservation objectives, including enhancing fishery populations and improving fisheries (Roberts 1998). Whereas individual reserves can differ in size depending on their purpose (Carr et al. 1998), to be self-sustaining, an effective network must include reserves of sufficient size and number to protect key habitats and species' populations regardless

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of what happens outside reserve boundaries. Effective networks could include (1) large reserves that protect a substantial portion (e.g., 20%-50%) of the spawning stock of a vulnerable species (e.g., Mangel 1998; Sladek Nowlis and Yoklavich 1998; Sladek Nowlis and Roberts 1999), (2) reserves that protect typical habitats and communities (e.g., 10%-20% of habitat coverage; Plan Development Team 1990), and (3) small reserves that protect critical, sensitive, or unique habitats, areas, or species.

Although more information about reserve size and the optimal distances for spacing reserves is needed to design networks that meet many management objectives, the best way to gather this information is to implement reserve systems and study how they function. Therefore, initial attempts to establish reserve sizes and locations must be based on reserve goals and the best available scientific data and models. Better guidance for reserve design will be possible when results from research performed in reserves become available, and when new scientific data on critical parameters such as recruitment and dispersal are obtained for populations targeted for protection. In the interim, the previously described lines of reasoning provide a strong rationale for significantly expanding the

Effective scientific research and monitoring programs must be developed together with the establishment of reserve networks.

small, insufficient amount of marine habitat now being protected by no-take reserves if the goal is to enhance fishery populations (NRC 1999). Additionally, estimates of the habitat and home-range requirements for protecting spawning stocks (Bohnsack 1994; Starr 1998), and models of adult spillover (Polacheck 1990; DeMartini 1993) and larval export (Quinn et al. 1993; Sladek Nowlis and Roberts 1997, 1999) consistently support the need for a sizeable increase in reserve areas that exclude fishing.

To be effective in the long term, reserve networks must be founded on adaptive resource management, where design modifications can be made using feedback loops between science and management (Agardy 1997; Allison et al. 1998). Improved scientific understanding of network function can lead to changes in the boundaries, locations, and regulations of individual reserves in an effort to better attain reserve goals. Therefore, effective scientific research and monitoring programs must be developed together with the establishment of reserve networks.

Reserve evaluation

To achieve desired goals, reserves and reserve networks must be both properly designed and evaluated (Carr and Raimondi 1998). Improper evaluation or misunderstanding

of reserve goals can lead to inaccurate perceptions of reserve performance. For example, well-designed reserves might make important contributions to the larval replenishment of exploited populations, but flawed methods of evaluation (e.g., poor measures of recruitment, measurements at inappropriate temporal or spatial scales, and low statistical power to detect changes) can fail to demonstrate their posi-

Misperceptions of reserve protection might lead to resource collapse and environmental degradation if other management strategies have been relaxed...

tive effects. Similarly, reserves also may protect some species but not others such as abalone and sea urchins in the presence of sea otters (Parker and Kalvass 1992; Karpov and Tegner 1992) or some fish populations under heavy predation by pinnipeds (Schmitt, et al. 1995). If the status of such a species forms the foundation for reserve evaluation, reserve performance may be perceived as unsatisfactory when, in fact, reserves have protected ecosystem functioning and increased regional abundances of other fishery stocks and populations. Timely and rigorous evaluation of reserve performances is essential if reserves are to function as effective management tools. If a reserve fails to yield expected results, and this failure is not detected in a timely manner, a false sense of insurance can be imparted to managers, user groups, and society. This mistaken security may jeopardize the future not only of an individual reserve, but also of regional policy, when reserve failure is ultimately detected (Carr and Raimondi 1998). For example, misperceptions of reserve protection might lead to resource collapse and environmental degradation if other management strategies have been relaxed or if fishing intensity has been allowed to expand or intensify outside reserve boundaries.

Strong scientific evaluation of reserve performance can be challenging because of difficulties in implementing rigorous statistical procedures to detect reserve effects over a large range of spatial and temporal scales. The inherent variability of marine systems can hinder the ability to detect, for example, a statistically significant increase in fish abundance within a reserve relative to reference areas, or reserve contributions to the larval recruitment of fishery stocks outside reserve boundaries. This problem emphasizes the need to develop stronger empirical and analytical approaches for evaluating reserve success. Modeling approaches to reserve evaluation will encounter many of the same problems that make parameter estimation difficult when employing typical models for assessing fishery stocks. Clearly, much greater scientific attention will be required to develop successful models (and model parameterization).

Social considerations

Social attitudes, economic concerns, institutional structures, and political processes must be considered to establish effective marine reserve networks. The potential for reserve networks to serve as successful resource management tools will be limited if the ways people value and use resources associated with reserves are not taken into account (Fiske 1992). This is because resource users frequently resist establishment of marine reserves or other conservation measures that restrict human activities. Part of this resistance is because the goals and economic and social benefits of marine reserves often are not well articulated by those promoting reserve protection or well understood by users who resist reserve establishment.

Restriction, termination, or displacement of activities such as fishing, oil development, and pollutant discharge involve real and perceived socioeconomic costs that must be weighed against the expected benefits of creating

reserves. Other issues that must be considered when assessing the potential benefits of reserve networks include the uncertainties of traditional fishery manage-

Restriction, termination, or displacement of activities... involve real and perceived socioeconomic costs that must be weighed against the expected benefits of creating reserves.

ment; the magnitude of human impact on ocean ecosystems; and the importance of intact, functioning marine ecosystems. Because a critical goal of no-take reserve networks is to protect and sustain ecosystem functioning, the

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No-take reserve networks offer a range of benefits for species such as the canary rockfish (*Sebastes pinniger*) that are greatly affected by environmental variation and that are experiencing population declines despite active fishery management.

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value of such functions must be recognized before benefits can be fully appreciated. However, a societal problem is the failure to appreciate the importance of ecosystem goods and services (Peterson and Lubchenco 1997), in part because most user groups focus only on extracting tangible marine products over short time scales. Moreover, a mismatch between operative time scales for ecological, socioeconomic, and political processes can result in inaccurate expectations of the time-course for reserve outcomes to be realized. For example, considering the longevity and erratic recruitment of many rockfishes, it might be decades before reserve benefits to rockfish stocks outside reserve areas can be demonstrated (Yoklavich 1998). Such a lag would be perceived as too long for most fishers whose social and economic well-being is contingent on shorter schedules. Distinguishing real from perceived costs and weighing short- against long-term costs and benefits are issues that must be addressed when a reserve network is being established.

Knowledge of human systems can be used to anticipate potential support and opposition to establishing marine reserve networks or locating individual reserve sites. Recognition of the need for reserves, particularly in more remote settings, often comes from outside local communities (Wells and White 1995), but sociopolitical inertia can be difficult to overcome without adequate local support. Local individuals, groups, and institutions can greatly assist efforts to design and manage reserves (Johannes 1982; Fiske 1992; Walters and Butler 1995). Additionally, local or "traditional" knowledge of natural conditions can complement scientific knowledge and often provide otherwise unavailable and important information (Inglis 1993; Neis 1995). Institutional planning and coordination also are essential among local, state, and federal agencies (Agardy 1997).

Too often, U.S. reserves have been initiated by the public or special interest groups in response to a perceived opportunity or threat and created in the absence of a larger, regional plan. In California, this bottom-up tradition has resulted in a poorly designed, fragmented collection of individual reserves with unmatched or unclear objectives and weakly defined management goals (McArdle 1997, 1998). To develop effective reserve networks, better planning and adequate governmental mechanisms for creating functional reserves must be achieved, including structures that facilitate coordination among U.S. agencies with overlapping jurisdictions.

The success of no-take reserves depends on compliance with regulations (e.g., Causey 1995; Ticco 1995; Proulx 1998), yet too often reserve management and enforcement practices have been weak (Beatley 1991; Alder 1996). Reserves may create incentives for some to break rules, especially if social or legal institutions are inadequate. This is because poaching can have high payoffs when reserves successfully protect valuable fishery populations such as abalone (Tegner et al. 1992, 1996). Compliance can be voluntary but in many cases may occur only with realistic levels of enforcement by responsible agencies and the threat of

meaningful penalties for poaching. For example, in southern California, where most rocky shores are easily accessible, unlawful collecting and poaching of intertidal organisms have been widespread in existing reserves because enforcement has been virtually nonexistent (Murray 1998).

Granting exceptions to restrictions can compromise the performance of no-take reserves or reserve networks. Fishers frequently resist plans to establish reserves that eliminate fishing and often cite a lack of evidence in support of reserve benefits. However, the burden of proof should be shifted, with fishing exemptions granted only in certain cases (e.g., fishing for migratory species, subsistence fishing by indigenous peoples using traditional or equivalent gear) where it can be shown that extractive activities will not prevent reserves from achieving their conservation goals. In some cases, it even may be necessary to restrict or limit nonextractive recreational activities. Because marine reserves can attract human visitors, increases in nonextractive use also can damage resources and potentially compromise reserve performance (Broome and Valentine 1993).

Conclusions

Impacts of human disturbance on marine ecosystem services and sustainability, including overfishing, are well documented (NRC 1995, 1999; Vitousek et al. 1997). Changes in ecosystem structure and functioning, and declines in exploited marine populations become even more likely as the pressures of fishing and other human activities increase. Moreover, fisheries and environmental managers are being challenged by marine systems that are changing in new and unpredictable ways, ranging from broad climatic changes (NRC 1999) to the more-regional cumulative impacts of human activities (Lubchenco 1998). Declining trends in the health of America's fishery populations and marine ecosystems need to be offset by improved management approaches. Continued depletion of many exploited populations and reductions in marine biodiversity are likely outcomes if existing practices are maintained as the principal vehicles for managing fisheries and protecting marine ecosystems (Ludwig et al. 1993; Boehlert 1996). Improvements in fishery data and models, and the advocacy of more precautionary approaches toward establishing sustainable catch levels are needed, but alone they may be insufficient to significantly improve the status of many exploited populations.


Marine reserves are receiving increasing attention and have been identified as a viable management strategy for promoting the sustainable use of ocean resources (Costanza et al. 1998; NRC 1999). No-take reserve networks offer opportunities to improve the status of exploited populations, benefit fisheries management, and increase understanding of marine ecosystems. By protecting resident populations and ecosystem functioning, networks of no-take reserves provide a precautionary approach for managing wild resources. Reserve populations ensure against inaccuracies and inherent uncertainties in fishery models as well as unpredictable fluctuations in fishery stocks (Hall 1998; Lauck et al. 1998). No-take reserve networks might

enhance and make more stable the landings of many fishery populations throughout the long term compared with existing practices (Sladek-Nowlis and Roberts 1997). Besides directly benefitting exploited stocks, effective reserves add an ecosystem-based management tool that focuses on processes and functioning, and extends fishery and conservation benefits beyond individual targeted populations (Agardy 1997; Roberts 1998; NRC 1999).

The degree to which no-take reserve networks can improve a fishery will be difficult to predict but will be based on characteristics of the species being protected and the network design. Nevertheless, a sufficient theoretical framework now exists for designing reserve networks in the United States. The short-term negative socioeconomic effects of implementing no-take reserve networks should be less than the long-term repercussions of overfishing, including the disruptions that result from stock collapses. Short-term reductions in fishery landings, and the resulting social and economic adjustments required by fishers, may be mitigated partially by phasing in reserves to distribute the loss of fishing grounds and related catches throughout several years. During this period the benefits obtained from reserves may begin to offset losses due to displacement of fishing activities (Sladek Nowlis and Roberts 1997).

By protecting targeted and untargeted populations from extractive activities, no-take reserve networks also provide areas with intact ecosystems that enhance opportunities to build scientific understanding of complex marine processes. Without no-take reserve networks, fewer opportunities will be available to investigate and understand marine ecosystem functioning and to use this knowledge to improve fisheries management and conservation measures. Public access to reserves can increase the types and quality of many important non-extractive human activities that require minimally disturbed areas such as education, ecotourism, photography, recreational diving, fish watching, cultural activities, and wilderness enjoyment (Bohnsack 1998b). The economic and social benefits of non-extractive uses of a reserve in many cases can exceed its extractive value (Dixon and Sherman 1990; Brock 1994; U.S. Department of Commerce 1996). Although high levels of nonextractive use can significantly affect coastal populations (Brosnan and Crumrine 1994; Addressi 1995; Keough and Quinn 1998), these effects can be offset where necessary (e.g., easily accessible urban shores and popular shallow-water reefs) by restricting or limiting public access and through public education. Public acceptance, a requirement for reserve success, can be strong with local support, education, direct experience, and adequate enforcement (Fiske 1992; Wolfenden et al. 1994; Ballantine 1995).

No-take reserve networks can complement existing management practices, improve efforts to interrupt declining trends in fishery populations, and help preserve marine ecosystems for future generations. However, reserve networks can only supplement other management policies because ocean currents move across reserve boundaries (Allison et al. 1998), and on-site managers can-

not control characteristics of reserve waters or recruitment of reserve populations dependent on sources outside reserve boundaries. Individual reserves or reserve networks cannot alone produce desired fishery and conservation outcomes (Roberts 1998; NRC 1999). The effectiveness of even well-designed reserve networks must depend on conservation and fishery management efforts undertaken outside reserve boundaries (Agardy 1997; Allison et al. 1998; Fogarty 1999). 

Steven N. Murray is a professor of biology, Department of Biological Science, California State University, Fullerton, CA 92834-6850. Richard F. Ambrose is director, Environmental Science and Engineering Program, University of California, Los Angeles. James A. Bohnsack is a research fishery biologist, NOAA/NMFS, Miami, Florida. Louis W. Botsford is a professor of wildlife and fisheries biology, Department of Wildlife, Fish, and Conservation Biology, University of California, Davis. Mark H. Carr is an assistant professor, Department of Biology, University of California, Santa Cruz. Gary E. Davis is senior scientist, Channel Islands National Park, Ventura, California. Paul K. Dayton is a professor of marine ecology, Scripps Institution of Oceanography, University of California, San Diego. Dan Gotshall, of Sea Challengers in Monterey, is a senior marine biologist who retired from the California Department of Fish and Game. Don R. Gunderson is a professor, School of Fisheries, University of Washington, Seattle. Mark A. Hixon is a professor of marine ecology, Department of Zoology, Oregon State University (OSU), Corvallis. Jane Lubchenco is the Wayne and Gladys Valley professor of marine biology and distinguished professor of zoology, OSU. Marc Mangel is a professor of environmental studies and marine sciences, Department of Environmental Studies, University of California, Santa Cruz. Alec MacCall is chief, Groundfish Analysis Branch, NMFS, Tiburon Laboratory, California. Deborah A. McArdle is a marine advisor, University of California Sea Grant Extension Program, Santa Barbara. John C. Ogden is director, The Florida Institute of Oceanography, St. Petersburg. Joan Roughgarden is a professor of population biology, Biological Science, Stanford University, California. Richard M. Starr is a marine advisor, University of California, Sea Grant Extension Program, Moss Landing. Mia J. Tegner is a research marine biologist, Scripps Institution of Oceanography, University of California, San Diego. Mary M. Yoklavich is a research fishery biologist, NMFS, Pacific Fisheries Environmental Laboratory, Pacific Grove, California.

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References

- Addressi, L. 1995. Human disturbance and long-term changes on a rocky intertidal community. *Ecol. Appl.* 4:786-797.
- Agardy, M. T. 1997. Marine protected areas and ocean conservation. Academic Press, San Diego, California.
- Alder, J. 1996. Costs and effectiveness of education and enforcement, Cairns Section of the Great Barrier Reef Marine Park. *Environ. Manag.* 20:541-551.
- Alexander, S. E., and J. Roughgarden. 1996. Larval transport and population dynamics of intertidal barnacles: a coupled benthic/oceanic model. *Ecol. Monogr.* 66:259-275.
- Allison, G. W., J. Lubchenco, and M. H. Carr. 1998. Marine reserves are necessary but not sufficient for marine conservation. *Ecol. Appl.* 8(Supplement):S79-S92.
- Alverson, D. L., M. H. Freeberg, S. A. Murawski, and J. G. Pope. 1994. A global assessment of fisheries bycatch and discards. Fisheries Tech. Pap. No. 339. Food and Agriculture Organization, Rome.
- Archibald, C., W. Shaw, and B. M. Leaman. 1981. Growth and mortality estimates of rockfishes (Scorpaenidae) from B.C. coastal waters 1977-1979. *Can. Tech. Rep. Fish. Aquat. Sci.*, No. 1048.
- Auster, P. J., R. J. Malatesta, R. W. Langton, L. Watling, P. C. Valentine, C. L. S. Donaldson, E. W. Langton, A. N. Shepard, and I. G. Babb. 1996. The impacts of mobile fishing gear on seafloor habitats of the Gulf of Maine (Northwest Atlantic). Implications for conservation of fish populations. *Rev. Fisheries Sci.* 4:185-202.
- Ballantine, W. J. 1995. Networks of "no-take" marine reserves are practical and necessary. Pages 13-20 in N. L. Shackel and J. H. M. Willison, eds. *Marine protected areas and sustainable fisheries. Science and Management of Protected Areas Association*, Wolfville, Nova Scotia.
- _____. 1997. 'No-take' marine reserve networks support fisheries. Pages 702-706 in D. A. Hancock, D. C. Smith, A. Grant, and J. P. Beumer, eds. *Developing and sustaining world fisheries resources: the state and management*. 2nd World Fisheries Congress, Brisbane, Australia.
- Barrett, N. E., and J. P. Barrett. 1997. Reserve design and the new conservation theory. Pages 236-251 in S. T. A. Pickett, R. S. Ostfeld, M. Shachak, and G. E. Likens, eds. *The ecological basis of conservation: heterogeneity, ecosystems, and biodiversity*. Chapman and Hall, New York.
- Beatley, T. 1991. Protecting biodiversity in coastal environments. *Coast. Manag.* 19:1-19.
- Beverton, R. J. H. 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *J. Fish Biol.* 41:137-160.
- Bjorkstedt, E., and J. Roughgarden. 1997. Larval transport and coastal upwelling: an application of HF radar in ecological research. *Oceanography* 10:64-67.
- Boehlert, G. W. 1996. Biodiversity and the sustainability of marine fisheries. *Oceanography* 9:28-35.
- Bohnsack, J. A. 1992. Reef resource habitat protection: the forgotten factor. *Marine Recreational Fisheries* 14:117-129.
- _____. 1994. How marine fishery reserves can improve reef fisheries. *Proc. Gulf Caribb. Fish. Inst.* 43:217-241.
- _____. 1995. Maintenance and recovery of reef fishery productivity. Pages 283-313 in N. V. C. Polunin, and C. M. Roberts, eds. *Management of reef fisheries*. Chapman and Hall, London.
- _____. 1998a. Marine reserves: lessons from Florida. Pages 89-99 in M. M. Yoklavich, ed. *Marine harvest refugia for West Coast rockfish: a workshop*. NOAA-TM-NMFS-SWFSC-255, La Jolla, California.
- _____. 1998b. Application of marine reserves to reef fisheries management. *Aust. J. Ecol.* 23:298-304.
- Botsford, L. W., C. L. Moloney, A. Hastings, J. L. Largier, T. M. Powell, K. Higgins, and J. F. Quinn. 1994. The influence of spatially and temporally varying oceanographic conditions on meroplanktonic metapopulations. *Deep-Sea Res.* 41:107-145.
- Botsford, L. W., J. C. Castilla, and C. H. Peterson. 1997. The management of fisheries and marine ecosystems. *Science* 277:509-515.
- Brock, R. E. 1994. Beyond fisheries enhancement: artificial reefs and ecotourism. *Bull. Mar. Sci.* 55:1181-1188.
- Broome, G., and P. Valentine. 1993. Principles of social impact assessment and its application to managing the Great Barrier Reef. (Cooperative Research Centres) Reef Research Centre, Townsville, Australia.
- Brosnan, D. M., and L. L. Crumrine. 1994. Effects of human trampling on marine rocky shore communities. *J. Exp. Mar. Biol. Ecol.* 177:79-97.
- Caddy, J. F. 1989. A perspective on the population dynamics and assessment of scallop fisheries, with special reference to the sea scallop *Placopecten magellanicus* Gmelin. Pages 559-574 in J. F. Caddy, ed. *Marine invertebrate fisheries: their assessment and management*. John Wiley and Sons, New York.
- Caley, M. J., M. H. Carr, M. A. Hixon, T. P. Hughes, G. P. Jones, and B. A. Menge. 1996. Recruitment and the local dynamics of open marine populations. *Ann. Rev. Ecol. Syst.* 27:477-500.
- Carr, M. H., and P. T. Raimondi. 1998. Concepts relevant to the design and evaluation of fishery reserves. Pages 27-31 in M. M. Yoklavich, ed. *Marine harvest refugia for West Coast rockfish: a workshop*. NOAA-TM-NMFS-SWFSC-255, La Jolla, California.
- Carr, M. H., and D. C. Reed. 1993. Conceptual issues relevant to marine harvest refuges: examples from temperate reef fishes. *Can. J. Fish. Aquat. Sci.* 50:2019-2028.
- Carr, M. H., L. Ziobro, T. Hourigan, D. Ito, D. McArdle, L. Morgan, W. Palsson, R. Parrish, S. Ralston, P. Reilly, J. Sladek Nowlis, and R. Starr. 1998. Working group II. Science-based design considerations. Pages 143-148 in M. M. Yoklavich, ed. *Marine harvest refugia for West Coast rockfish: a workshop*. NOAA-TM-NMFS-SWFSC-255, La Jolla, California.
- Casey, B. D. 1995. Enforcement in marine protected areas. Pages 119-148 in S. Gubbay, ed. *Marine protected areas. Principles and techniques for management*. Chapman and Hall, London.
- Cohen, J. E., C. Small, A. Mellinger, J. Gallup, and J. Sachs. 1997. Estimates of coastal populations. *Science* 278:1211-1212.
- Collie, J. S., G. A. Escanero, and P. C. Valentine. 1997. Effects of bottom fishing on the benthic megafauna of Georges Bank. *Mar. Ecol. Progr. Ser.* 155:159-172.
- Conand, C. 1997. Are holothurian fisheries for export sustainable?

- Pages 2,021-2,026 in H. A. Lessios and I. G. MacIntyre, eds. Proceedings of the Eighth International Coral Reef Symposium. Smithsonian Tropical Research Institute, Balboa, Panama.
- Costanza, R., F.**, and 15 coauthors. 1998. Principles for sustainable governance of the oceans. *Science* 281:198-199.
- Cox, K. W.** 1962. California abalones, family Haliotidae. Fish Bulletin No. 118. The Resources Agency of California, Department of Fish and Game, Sacramento.
- Culliton, T. J., M. A. Warren, T. R. Goodspeed, D. G. Remer, C. M. Blackwell, and J. MacDonough.** 1990. Fifty years of population change along the nation's coast. Second report of the coastal trend series. Office of Oceanography and Marine Assessment, National Oceanic and Atmospheric Administration, Washington, DC.
- Dahl, T. E., C. E. Johnson, and W. E. Frayer.** 1991. Status and trends of wetlands in the coterminous United States mid-1970's to mid-1980's. U.S. Department of Interior, U.S. Fish and Wildlife Service, Washington, DC.
- Davis, G. E., P. L. Haaker, and D. V. Richards.** 1996. Status and trends of white abalone at the California Channel Islands. *Trans. Amer. Fish. Soc.* 125:42-12,548.
- Dayton, P. K.** 1998. Reversal of the burden of proof in fisheries management. *Science* 279:821-822.
- Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman.** 1995. Environmental effects of marine fishing. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 5:205-232.
- Dayton, P. K., M. J. Tegner, P. B. Edwards, and K. L. Riser.** 1998. Ghost communities and the problem of reduced expectation in kelp forests. *Ecol. Appl.* 8:309-322.
- DeMartini, E. E.** 1993. Modeling the potential of fishery reserves for managing Pacific coral reef fishes. *Fish. Bull.* 91:414-427.
- Dixon, J. A., and P. B. Sherman.** 1990. Economics of protected areas: a new look at benefits and costs. Island Press, Washington DC.
- Dugan, J. E., and G. E. Davis.** 1993. Applications of marine refugia to coastal fisheries management. *Can. J. Fish. Aquat. Sci.* 50:2029-2042.
- FAO (Food and Agriculture Organization).** 1995. The state of world fisheries and aquaculture. United Nations FAO, Rome.
- Fiske, S. J.** 1992. Sociocultural aspects of establishing marine protected areas. *Ocean Coast. Manag.* 17:25-46.
- Fogarty, M. J.** 1999. Essential habitat, marine reserves, and fishery management. *Trends Ecol. Evol.* 14:133-134.
- Fogarty, M. J., and S. A. Murawski.** 1998. Large-scale disturbance and the structure of marine systems: fishery impacts on Georges Bank. *Ecol. Appl.* 8(Supplement):S6-S22.
- Garcia, S. M.** 1994. The precautionary principle: its implications in capture fisheries management. *Ocean Coast. Manag.* 22:99-125.
- GESAMP (Group of Experts on the Scientific Aspects of Marine Pollution)** 1991. The state of the marine environment. Blackwell Scientific Publications, Oxford.
- Gordon, D. V., and G. Munro,** eds. 1996. Fisheries and uncertainty: a precautionary approach to resource management. University of Calgary Press, Calgary.
- Gunderson, D. R.** 1997a. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. *Can. J. Fish. Aquat. Sci.* 54:990-998.
- _____. 1997b. Spatial patterns in the dynamics of slope rockfish stocks and their implications for management. *Fish. Bull. U.S.* 95:219-230.
- Hall, S. J.** 1998. Closed area for fisheries management—the case consolidates. *Trends Ecol. Evol.* 13:297-298.
- Hardy, R.** 1996. Management and assessment of rockfish resources in Central California. Annual performance report. Federal Aid in Sport Fish Restoration Act. California Department of Fish and Game, Marine Resources Division, Monterey, California.
- Hawkins, J. P., and C. M. Roberts.** 1992. A direct test of the effects of protective management on abundance and yield of tropical marine resources. *J. Conseil Int. l'Explor. Mer* 47:40-47.
- Hixon, M. A.** 1998. Population dynamics of coral-reef fishes: controversial concepts and hypotheses. *Aust. J. Ecol.* 23:192-201.
- Hixon, M. A., and M. H. Carr.** 1997. Synergistic predation, density dependence, and population regulation in marine fish. *Science* 277:946-949.
- Inglis, J.,** ed. 1993. Traditional ecological knowledge: concepts and cases. International Program on Traditional Ecological Knowledge: International Development Research Centre, Ottawa.
- Johannes, R. E.** 1982. Traditional conservation methods and protected marine areas in Oceania. *Ambio* 11:258-261.
- Kalvass, P., and J. Hendrix.** 1997. The California red sea urchin (*Strongylocentrotus franciscanus*) fishery: catch, effort and management trends. *Mar. Fish. Rev.* 59:1-20.
- Karpov, K. A., and M. J. Tegner.** 1992. Abalones. Pages 33-36 in W. S. Leet, C. M. Dewees, and C. W. Haugen, eds. California's living marine resources and their utilization. California Sea Grant Extension Publication UCSGEP-92-12, Davis, California.
- Keough, M. J., G. P. Quinn, and A. King.** 1993. Correlations between human collecting and intertidal mollusc populations on rocky shores. *Conserv. Biol.* 7:378-390.
- Keough, M. J., and G. P. Quinn.** 1998. Effects of periodic disturbances from trampling on rocky intertidal algal beds. *Ecol. Appl.* 8:141-161.
- King, K. A.** 1990. Foreign and joint venture fishing operations off Washington, Oregon, and California. National Marine Fisheries Service, North West Region Report. Seattle, Washington.
- Lauck, T., C. W. Clark, M. Mangel, and G. R. Munro.** 1998. Implementing the precautionary principle in fisheries management through marine reserves. *Ecol. Appl.* 8(Supplement):S72-S78.
- Law, R., J. M. McGlade, and T. K. Stokes,** eds. 1993. The exploitation of evolving resources: proceedings of an international conference held at Julich, Germany, 3-5 September 1991. Lecture notes in biomathematics, Volume 99. Springer-Verlag, Berlin.
- Leaman, B. M.** 1991. Reproductive styles and life history variables relative to exploitation and management of *Sebastes* stocks. *Environ. Biol. Fish.* 30:253-271.
- Lindeboom, H. J.** 1995. Protected areas in the North Sea: an absolute need for future marine research. *Helgoländer Meeresunters.* 49: 591-602.
- Lubchenco, J.** 1998. Entering the century of the environment: the need for a new social contract for science. *Science* 279:491-497.
- Lubchenco, J., G. W. Allison, S. A. Navarrete, B. A. Menge, J. C. Castilla, O. Defeo, C. Folke, O. Kissakin, T. Norton, and A. M. Wood.** 1995. Coastal systems. Pages 370-381 in United Nations Environmental Programme, ed. Global biodiversity assessment. Cambridge University Press, Cambridge.
- Ludwig, D., R. Hilborn, and C. Walters.** 1993. Uncertainty, resource exploitation, and conservation: lessons from history. *Science* 260:17-18.
- Mangel, M.** 1998. No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. *Ecology Letters* 1:87-90.
- Mangel, M.,** and 41 coauthors. 1996. Principles for the conservation of wild living resources. *Ecol. Appl.* 6:338-362.
- McAllister, D. E.** 1996. The status of the world ocean and its biodiversity. Ocean Voice International, Ottawa.

PERSPECTIVE

- McArdle, D. A.** 1997. California Marine Protected Areas. Publication No. T-039. California Sea Grant College System, La Jolla, California.
- McArdle, D. A.** 1998. The status of California marine protected areas. Pages 74-85 in O. T. Magoon, H. Converse, B. Baird, and M. Miller-Henson, eds. California and the world ocean '97. Taking a look at California's ocean resources: an agenda for the future. American Society of Civil Engineers, Reston, VA.
- McWilliams, B., and G. Goldman.** 1994. Commercial and recreational fishing in California: their impact on the state's economy. University of California, Berkeley, CA.
- Morgan, L. E., and L. W. Botsford.** 1998. The influence of larval transport and retention zones on recruitment patterns and the design of harvest refugia for rockfish. Pages 41-49 in M. M. Yoklavich, ed. Marine harvest refugia for West Coast rockfish: a workshop. NOAA-TM-NMFS-SWFSC-255, La Jolla, California.
- Murray, S. N.** 1998. Effectiveness of marine life refuges on southern California shores. Pages 1,453-1,465 in O. T. Magoon, H. Converse, B. Baird, and M. Miller-Henson, eds. California and the world ocean '97. Taking a look at California's ocean resources: an agenda for the future. American Society of Civil Engineers, Reston, Virginia.
- Myers, R. A., J. A. Hutchings, and N. J. Barrowman.** 1997. Why do fish stocks collapse? The example of cod in Atlantic Canada. *Ecol. Appl.* 7:91-106.
- NMFS (National Marine Fisheries Service).** 1996. Our living oceans. The economic status of U.S. fisheries, 1996. U.S. Dept. Commerce, NOAA Tech. Memo. NMFS F/SPO-22. Silver Spring, Maryland.
- NOAA (National Oceanic and Atmospheric Administration).** 1990. Estuaries of the United States: vital statistics of a national resource base. National Ocean Service, National Oceanic and Atmospheric Administration, Washington, DC.
- NRC (National Research Council).** 1995. Understanding marine biodiversity: a research agenda for the nation. National Academy Press, Washington, DC.
- _____. 1999. Sustaining marine fisheries. National Academy Press, Washington, DC.
- Neis, B.** 1995. Fishers' ecological knowledge and marine protected areas. Pages 265-272 in N. Shackell, and J. H. M. Willison, eds. Marine protected areas and sustainable fisheries. Science and Management of Protected Areas Association, Wolfville, Nova Scotia.
- Ogden, J. C.** 1997. Marine managers look upstream for connections. *Science* 278:1,414-1,415.
- Pacific Fishery Management Council.** 1995. Status of the Pacific Coast groundfish fishery through 1995 and recommended biological catches for 1996: stock assessment and fishery evaluation. Pacific Fishery Management Council, Portland, Oregon.
- Palmer, M. A., J. D. Allan, and C. A. Butman.** 1996. Dispersal as a regional process affecting the local dynamics of marine and stream benthic invertebrates. *Trends Ecol. Evol.* 11:322-326.
- Parker, D., and P. Kalvass.** 1992. Sea urchins. Pages 41-43 in W. S. Leet, C. M. Dewees, and C. W. Haugen, eds. California's living marine resources and their utilization. California Sea Grant Extension Publication UCSEGP-92-12, Davis, California.
- Pauly, D., V. Christensen, J. Dalsgaard, R. Froese, and F. Torres, Jr.** 1998. Fishing down marine food webs. *Science* 279:860-863.
- Peterson, C. H., and J. Lubchenco.** 1997. Marine ecosystem services. Pages 177-194 in G. Daily, ed. Nature's services: societal dependence on natural ecosystems. Island Press, Washington, DC.
- Plan Development Team.** 1990. The potential of marine fishery reserves for reef fish management in the U.S. southern Atlantic. NOAA Tech. Mem., NMFS-SEFC-261. U.S. Department of Commerce, Washington, DC.
- Polacheck, R.** 1990. Year around closed areas as a management tool. *Natural Resource Modeling* 4:327-353.
- Proulx, E.** 1998. The role of law enforcement in the creation and management of marine reserves. Pages 74-77 in M. M. Yoklavich, ed. Marine harvest refugia for West Coast rockfish: a workshop. NOAA-TM-NMFS-SWFSC-255, La Jolla, California.
- Quinn, J. F., S. R. Wing, and L. W. Botsford.** 1993. Harvest refugia in marine invertebrate fisheries: models and applications to the red sea urchin, *Strongylocentrotus franciscanus*. *Amer. Zool.* 33:537-550.
- Ralston, S.** 1998. The status of federally managed rockfish on the U.S. West Coast. Pages 6-16 in M. M. Yoklavich, ed. Marine harvest refugia for West Coast rockfish: a workshop. NOAA-TM-NMFS-SWFSC-255, La Jolla, California.
- Ralston, S., and D. F. Howard.** 1995. On the development of year-class strength and cohort variability in two northern California rockfishes. *Fish. Bull.* 93:710-720.
- Ricker, W. E.** 1981. Changes in the average size and average age of Pacific Salmon. *Can. J. Fish. Aquat. Sci.* 38:1636-1656.
- Roberts, C. M.** 1997. Ecological advice for the global fisheries crisis. *Trends Ecol. Evol.* 12:35-38.
- _____. 1998. Sources, sinks, and the design of marine reserve networks. *Fisheries* 23(7):16-19.
- Roberts, C. M., W. J. Ballantine, C. D. Buxton, P. Dayton, L. B. Crowder, W. Milon, M. K. Orbach, D. Pauly, and J. Trexler.** 1995. Review of the use of marine fishery reserves in the U.S. southeastern Atlantic. NOAA Tech. Memo. NMFS-SEFSC 376, Miami, Florida.
- Roberts, C. M., and N. V. C. Polunin.** 1993. Marine reserves: simple solutions to managing complex fisheries? *Ambio* 22:363-368.
- Roughgarden, J., S. Pennington, and S. Alexander.** 1994. Dynamics of the rocky intertidal zone with remarks on generalization in ecology. *Phil. Trans. Roy. Soc. London B.*, 343:79-85.
- Rowley, R. J.** 1994. Marine reserves in fisheries management. *Aquat. Conserv. Mar. Freshw. Ecosyst.* 4:233-254.
- Russ, G. R., and A. C. Alcala.** 1989. Effects of extreme fishing pressure on an assemblage of coral reef fishes. *Mar. Ecol. Prog. Ser.* 56:13-27.
- Safina, C.** 1995. The world's imperiled fish. *Sci. Amer.* 273:46-53.
- Schmitt, C. C., S. J. Jeffries, and P. J. Gearin.** 1995. Pinniped predation on marine fish in Puget Sound. Pages 630-637 in Puget Sound Research '95, proceedings. Puget Sound Water Quality Authority, Olympia, Washington.
- Simberloff, D.** 1988. The contribution of population and community ecology to conservation science. *Ann. Rev. Ecol. Syst.* 19:473-512.
- Sladek Nowlis, J., and C. M. Roberts.** 1997. You can have your fish and eat it, too: theoretical approaches to marine reserve design. Pages 1907-1910 in H. A. Lessios and I. G. MacIntyre, eds. Proceedings of the Eighth International Coral Reef Symposium, Volume 2. Smithsonian Tropical Research Institute, Balboa, Panama.
- _____. 1999. Fisheries benefits and optimal design of marine reserves. *Fish. Bull.* 97:604-616.
- Sladek Nowlis, J., and M. Yoklavich.** 1998. Design criteria for rockfish harvest refugia from models of fish transport. Pages 32-40 in M. M. Yoklavich, ed. Marine harvest refugia for West Coast rockfish: a workshop. NOAA-TM-NMFS-SWFSC-255, La Jolla, California.
- Smith, P. J., R. I. C. C. Francis, and M. McVeagh.** 1991. Loss of genetic diversity due to fishing pressure. *Fish. Res.* 10:309-316.

- Smith, B. S., L. W. Botsford, and S. R. Wing.** 1999. Estimation of growth and mortality parameters from size frequency distributions lacking age patterns: the red sea urchin (*Strongylocentrotus franciscanus*) as an example. *Can. J. Fish. Aquat. Sci.* 55:1236-1247.
- Starr, R. M.** 1998. Design principles for rockfish reserves on the U.S. West Coast. Pages 50-63 in M. M. Yoklavich, ed. *Marine harvest refugia for West Coast rockfish: a workshop*. NOAA-TM-NMFS-SWFSC-255, La Jolla, California.
- Steele, J. H.** 1991. Can ecological theory cross the land-sea boundary? *J. Theor. Biol.* 153:425-436.
- _____. 1998. Regime shifts in marine ecosystems. *Ecol. Appl.* 8(Supplement):S33-S36.
- Steneck, R. S.** 1998. Human influences on coastal ecosystems: Does overfishing create trophic cascades? *Trends Ecol. Evol.* 13:429-430.
- Suchanek, T. H.** 1994. Temperate coastal marine communities: biodiversity and threats. *Amer. Zool.* 34:100-114.
- Tegner, M. J., J. D. Martini, and K. A. Karpov.** 1992. The California red abalone fishery: a case study in complexity. Pages 370-383 in S. A. Shepherd, M. J. Tegner, and S. A. Guzmán del Pr o, eds. *Abalone of the world*. Blackwell Scientific Publications, Oxford.
- Tegner, M. J., L. V. Basch, and P. K. Dayton.** 1996. Near extinction of an exploited marine invertebrate. *Trends Ecol. Evol.* 11:278-280.
- Thrush, S. F., J. E. Hewitt, V. J. Cummings, P. K. Dayton, M. Cryer, S. J. Turner, G. A. Funnell, R. G. Budd, C. J. Milburn, and M. R. Wilkinson.** 1998. Disturbance of the marine benthic habitat by commercial fishing: impacts at the scale of the fishery. *Ecol. Appl.* 8:866-879.
- Ticco, P. C.** 1995. The use of marine protected areas to preserve and enhance marine biological diversity: a case study approach. *Coast. Manag.* 23:309-314.
- U.S. Department of Commerce.** 1996. Appendix M: Assessment of the potential costs and benefits of the final management plan regulations. Pages M1-M34 in *Florida Keys National Marine Sanctuary: Final Management Plan/Environmental Impact Statement, Vol. III. Sanctuaries and Reserves Division, National Oceanic and Atmospheric Administration, Washington, DC.*
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo.** 1997. Human domination of Earth's ecosystems. *Science* 277:494-499.
- Walters, B. B., and M. Butler.** 1995. Should we see lobster buoys bobbing in a marine park? Pages 205-213 in N. Shackell, and J. H. M. Willison, eds. *Marine protected areas and sustainable fisheries. Science and Management of Protected Areas Association, Wolfville, Nova Scotia.*
- Wells, S. M.** 1997. Giant clams: status, trades, and mariculture, and the role of CITES in management. World Conservation Union. International Union of the Conservation of Nature Communications Division, Gland, Switzerland.
- Wells, S., and A. T. White.** 1995. Involving the community. Pages 61-84 in S. Gubbay, ed. *Marine protected areas. Principles and techniques for management*. Chapman and Hall, London.
- Wing, S. R., L. W. Botsford, J. L. Largier, and L. E. Morgan.** 1995. Spatial variability in settlement of benthic invertebrates in an intermittent upwelling system. *Mar. Ecol. Progr. Ser.* 128:199-211.
- Wolfenden, J., F. Cram, and B. Kirkwood.** 1994. Marine reserves in New Zealand: a survey of community reactions. *Ocean Coast. Manag.* 25:31-51.
- Wyllie Echeverria, T.** 1987. Thirty-four species of California rockfishes: maturity and seasonality of reproduction. *Fish. Bull.* 85:229-250.
- Yoklavich, M. M., ed.** 1998. *Marine harvest refugia for West Coast rockfish: a workshop*. NOAA-TM-NMFS-SWFSC-255, La Jolla, California.
- Yoklavich, M. M., V. J. Loeb, M. Nishimoto, and B. Daly.** 1996. Nearshore assemblages of larval rockfishes and their physical environment off Central California during an extended El Niño event, 1991-1993. *Fish Bull.* 94:766-782.