

# Design and Designation of Marine Reserves

JOSHUA SLADEK NOWLIS AND  
ALAN FRIEDLANDER

Marine reserves represent a complex biological and social phenomenon. Any given marine reserve is likely to encompass a unique mixture of species, habitats, and ecosystems, and these combinations as well as their broader distributions will help to determine the best design principles. The social and political atmosphere will also vary from one reserve to the next, with different levels of support, sense of need, and even goals and objectives for the reserve or reserve network. An effective marine reserve designation process should follow advice based on local biological and ecological characteristics, but should also provide flexibility to address the social and political atmosphere. This process should include plenty of opportunity for interaction between technical advisers and the general public, with an open invitation to members of the public to propose designs and a chance for scientists to inform and review these proposals.

Marine reserves provide a valuable and powerful tool to help meet the multiple goals and address the complex challenges facing managers in many areas, but are clearly not the best tool for all purposes. In assessing their use, it is important to keep in mind what makes reserves different from other management tools, and ultimately what their relative strengths and weaknesses are. Four properties make reserves stand out from other management measures. First, reserve boundaries are simpler to enforce and thus more difficult to circumvent than other regulations. It is easier to see whether a boat is fishing in an area than to board it and examine its catch or gear for compliance. Second, reserves allow fish to grow large and realize their full reproductive potential. Third, reserves protect an entire area from many major human impacts, letting nature

flourish and effectively manage itself. In this manner, they represent a form of effective ecosystem-based management even when we do not understand the details of how the ecosystems work (Buck 1993). Finally, reserves provide lightly affected areas that we can use as a reference to understand the effects of human activities and how to control them in the future (see also chapters 4, 8, and 10 for examples and discussion).

## DESIGN CRITERIA

Ecological considerations are important in marine reserve design, but it is imperative to view them in the broader context of a designation process. We begin with this broader view, then discuss some general design principles and conclude with a detailed discussion of several design elements.

### Ecological Dimensions in Context

Ecological considerations are an important part, but only one part, of an effective process to establish marine reserves (Table 5.1). The ocean is a public resource and as such its management should reflect the desires of society, whether those desires are for sustainable fishing, conservation, nonconsumptive uses, or some combination of these. Enforcement considerations should also influence reserve design to ensure that goals are actually met. These considerations can usually be addressed through a set of general criteria that may be satisfied with a wide range of possible designs.

If no-fishing zones are regularly violated, reserves will only benefit the poachers. Enforcement can be aided through the selection of appropriate shapes, sizes, and locations for reserves. However, the most important factor in achieving compliance is often broad community-level support, including acceptance by fishers—the people most likely to be excluded from marine reserves (Proulx 1998). If they are involved early on in the process, exposed to and educated about scientific deliberations, and ultimately held responsible for proposing and modifying reserve designs, local communities and fishers are more likely to take ownership of reserves and assist in both compliance and enforcement. Where reserves have been established without broad public support, they may be vulnerable to dismantling when politics shift (e.g., Russ and Alcala 1999; see also chapters 4 and 8) or in danger of never being created in the first place.

Stakeholder input is also a means to collect and consider invaluable in-

Table 5.1 Recommended Marine Reserve Designation Process

- 
1. Goals
    - a. Representatives of the general public specify goals for the management area.
    - b. Scientific and enforcement advisers work with these representatives to clarify goals and specify measurable objectives.
  2. Design criteria
    - a. Scientific and enforcement advisers determine appropriate design criteria for a reserve or reserve network in the management area—including recommendations for overall percent inclusion in the reserve; habitat types to consider; critical areas for inclusion; and the size, shape, and configuration of individual reserves within a network—based on the management goals.
    - b. If requested, advisers illustrate their criteria by drawing examples on maps.
  3. Drafting alternatives
    - a. Representatives of the general public draft alternative network designs, taking socioeconomic and cultural impacts into consideration.
    - b. Scientific and enforcement advisers work with the general public representatives to ensure their alternatives reflect the general design criteria.
    - c. The public submits alternatives along with descriptions of the socioeconomic and cultural ramifications to the government agency or working group. Advisers provide formal reviews of each alternative and its capacity to meet stated goals.
  4. Selecting alternatives
    - a. The government group drafts a final list of alternatives, taking into account the public's values, scientific and enforcement reviews, and any potential short-term socioeconomic or cultural impacts.
    - b. The public comments on draft alternatives.
    - c. The government group chooses a preferred alternative.
    - d. More public comments are made.
    - e. The government group makes a final choice.
- 

formation about the biology and socioeconomic properties of ocean use (Johannes 1997). Some cultures have studied and fished local waters for centuries, and even shorter-lived fishing traditions can provide a wealth of knowledge for effective reserve design, as discussed further in chapter 7. Stakeholder input will be best represented and included if stakeholders are exposed to the development of scientific and enforcement criteria and then encouraged to develop reserve design proposals that meet these criteria.

#### Act Now? or Study the Problem?

One key question in developing marine reserves is whether to act quickly to establish reserves or wait for more study. Several authors have made the point that reserves seem to work for most species even when they are set up with little or no scientific guidance and, consequently, we needn't wait for more study (e.g., Roberts 1998). Other authors have used simple models to illustrate

the potential pitfalls of establishing reserves in poor locations (e.g., Crowder et al. 2000). *Sources* are areas that produce more fish than they contain, some of which move to other areas at some point in their life cycle. By contrast, *sinks* are areas that produce fewer fish than live there and are only sustained because they are supplemented from source areas. Crowder et al. developed a model in which areas were either sources or sinks and showed that managers could actually do more harm than good if they created a marine reserve network that encompassed more sinks than sources.

A major flaw with the preceding argument, though, is the assumption that sources and sinks are static—that they do not change with the establishment of marine reserves. In fact, strong evidence supports the fact that reserves usually become sources by creating an area with many fish producing lots of offspring (Appeldoorn 2001). As a result, it is an incorrect simplification of reality to assume that all sinks will remain so if they are designated as marine reserves. Very strong sinks may not be overcome by marine reserves, but these areas are likely to be poor enough in quality that they aren't identified as useful areas from the start. More subtle sinks, on the other hand, are more likely to become sources after reserves result in the buildup of high abundance and reproductive potential within them. In this manner, the concern over sinks is similar to that of poor habitat in general. Reserves may not function well if placed in poor quality habitats, whether because of unrecoverable degradation, source-sink issues, or low natural productivity.

To avoid these potential pitfalls, there are some pieces of information that may be worth taking the time to collect, depending on how readily they might be available. Traditional knowledge of crucial areas—spawning grounds for example—and other key life history traits may be readily available from experienced fishers in the area (Johannes 1978). It also may be possible, depending on the ecosystems and budgets involved, to make at least rough maps showing habitat distributions throughout the management area. Habitat mapping is more achievable than ever with the advent of technologies that can discern habitats remotely, as discussed in chapter 7. Finally, there may be a wealth of scientific information already collected from the area that can be instructive once it is compiled. These sorts of information may add substantially to the effectiveness of marine reserve design without long delays. For most other types of information, though, the benefits gained by learning them would not be worth the time it takes to do so. If important discoveries are made during or after reserve implementation, they may justify a reevaluation of the reserve design. For example, a black grouper spawning aggregation was discovered less

than 100 meters outside a newly designated marine reserve in the Florida Keys (Eklund et al. 2000). It is a challenge to provide sufficient flexibility to allow rapid response to discoveries such as these while providing enough process to maintain public support.

### The Designation Process

The process for designating marine reserves will be more effective if it is driven by well-defined goals (Ballantine 1997), which could include the conservation of healthy natural ecosystems, insurance of fisheries against collapse due to management errors, or many other possibilities. The process should clearly specify how it will address public values, ecological, socioeconomic, and enforcement considerations, and the input of fishing communities and other stakeholders. General processes have already been proposed for developing marine reserve networks (Hockey and Branch 1997; Roberts et al. 2003a). These processes score potential reserve areas relevant to the specified goals, engineer a set of biologically adequate alternatives, and select among those according to socioeconomic criteria.

We contend that the most successful site selection and designation processes will rely on the same basic philosophy but be driven less by government agencies or scientists and more by the public (see Table 5.1). While a top down approach may work well in some settings, a bottom up approach is ultimately the most likely to produce long-lasting site designations. However, top-down interest and pressure can provide a broader context for individual site designations and a cohesive national policy can provide a framework for developing a stronger network or system approach, especially if it includes bottom-up input. Regardless, it is valuable to set up several working groups that interact extensively from the start. One should represent the public at large, another should consist of informed and objective scientists with relevant biological and social expertise, a third should consist of enforcement experts, and in situations where multiple agencies have overlapping jurisdiction, a fourth may be required consisting of representatives of those agencies.

Goal setting is a crucial first step. Marine reserves can help to achieve many societal goals, ranging from fisheries enhancements to conservation of natural environments for economic and intrinsic reasons (NRC 2001). Since no single reserve design will satisfy all goals equally it is important to specify goals as the first step in a designation process (Murray et al. 1999). At the same time, efforts should be made to ensure that the reserve design is capable of meeting a range

of goals (Roberts et al. 2003a). These goals should incorporate the desires of local people, and their enumeration is an opportunity to involve stakeholders early in the reserve creation process. When establishing goals, it should be clear to what area they apply (Roberts et al. 2003a). It is important that these goals are communicated clearly to a group of scientific advisers in a manner that is amenable to their asking relevant questions. To facilitate this process, we recommend that draft goals be shared with the science group who can then provide feedback to the public group, who may choose to revise the stated goals for clarity, specificity, or both.

Once goals are clearly defined, the science and enforcement groups can develop relevant design criteria. The criteria should state acceptable ranges for several design elements and highlight how choices of one element may affect how other elements are addressed. Scientific criteria will most constructively address several elements:

- The total size of the reserve or reserve network
- The habitat types to consider
- Critical areas for inclusion
- The size, shape, and configuration of individual reserves within a network

Enforcement criteria will most constructively address:

- The size, shape, and location of individual reserves

If requested, advisers should illustrate criteria by drawing examples on maps. In our experience, examples are better received when several quite different options are presented. Single examples tend to be construed as detailed recommendations even if they are meant only to serve as an illustration of how to achieve general design criteria.

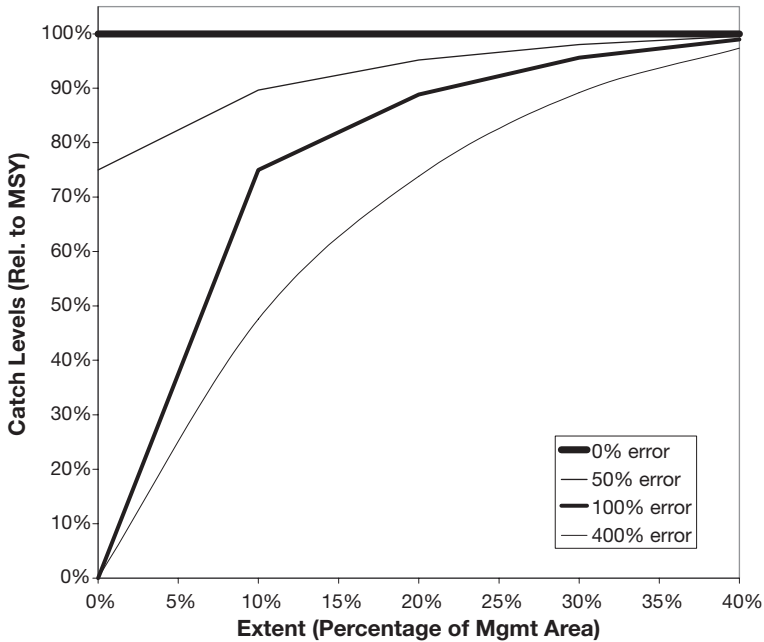
Extensive communication with the public helps to inform them of the design criteria and prepare them to draft alternatives for the design of the reserve or reserve network. Although all members of the public deserve the opportunity to present alternatives, special attention should be paid to those stakeholders that spend the most time on or in the water, including fishers. The opinions of stakeholders with extensive on-the-water experience are especially important because of their knowledge of local ocean life and fisheries, their vulnerability to short-term negative impacts if they are displaced by marine reserves, and the crucial role their opinions play in achieving compliance and assisting with enforcement. Scientific and enforcement experts should provide constructive critiques of proposed alternatives, including suggestions of how

to make the alternatives fit better with the general design criteria. This step can be formal or informal but will have the greatest impact if it is done in an interactive manner. Modified alternatives should then be submitted to the government agency or working group along with descriptions of how the alternatives were devised, what their short- and long-term socioeconomic and cultural ramifications may be, and the rationale for excluding specific other areas. Scientific and enforcement advisers can then provide analysis of how effective each alternative is likely to be at meeting the stated goals. The government agency or group then drafts a final list of alternatives, taking into account the public's values, ecological and enforcement reviews, and any potential socioeconomic or cultural impacts. They should aim to include a suite of alternatives that covers the range of realistic possibilities and addresses the desires and concerns of a broad cross section of the public. The public should have a chance to comment on the alternatives to help inform the government's choice of a draft preferred alternative, and be granted another chance for comment before a final selection is made.

This process may be more time consuming than a more autocratic one and less rigorous than a more scientifically driven one. But, it is worth the time investment and loss of some scientific rigor to involve the general public deeply in the process. If the general design criteria are done well, they should ensure that the reserve or reserve network will be effective enough. This process emphasizes public involvement because there are far greater dangers for failure due to lack of public acceptance than due to poor design.

## Goals

Marine reserves can help to achieve many societal goals, which can generally be lumped into four categories: (1) ecosystem protection, (2) improved fisheries, (3) expanded knowledge and understanding of marine systems, and (4) better nonconsumptive opportunities (NRC 2001). There has been a disconnect in the ways in which design criteria have been addressed for each goal. Whereas optimality models—which predict the design that will maximize reserve performance—have been the norm when addressing fishing benefits, especially the maximization of yields (NRC 2001), risk minimization models and other methods to predict the minimum necessary design have been the norm for other goals. The reason for this disconnect is simple: the optimal solution for addressing conservation and nonconsumptive goals would be to close the entire ocean to fishing and other major human impacts, while our scientific



**FIG. 5.1 Risk Minimization Overrides Other Design Considerations.** This graph shows sustained catch levels, relative to maximum sustainable yields (MSY), as a function of reserve size and error level. Marine reserves, or another method of setting aside a protected population, maintain productive fisheries even if managers are making large errors. Reserves increase catches under all circumstances when management errors lead to overfishing, with more dramatic increases under larger errors. Note that maximum sustainable yields can be achieved with large reserve networks even if errors are large. Also note that the use of reserves does not necessarily cost any yield—without errors, maximum sustainable yields can be achieved with or without reserves. Source: Adapted from Sladek Nowlis and Bollermann 2002.

understanding would be best served by having an extensive reserve network with smaller scale experimental fishing areas.

How do we find balance given this dichotomy? It depends on societal values but, more often than not, marine reserves should be viewed in terms of risk minimization for all benefits rather than optimality for fishing benefits. This conclusion follows two important observations. First, risk minimization is an underlying goal for all four of the categories. Unless we conserve the entire ecological and socioeconomic system with some minimal network of marine reserves, none of the other goals can be assured (Appeldoorn and Recksiek 2000). Research has shown that setting aside populations free from risk of fishing makes the populations as a whole much more robust and resilient to inadvertent management errors (Fig. 5.1; Sladek Nowlis and Bollermann 2002).



Second, models have generally predicted that risk minimization requires larger and more ambitious marine reserves or reserve networks than maximizing fishing benefits (see NRC 2001 for overview of goal-oriented design criteria), and maximum fishing yields can still be achieved with large reserves (Sladek Nowlis and Roberts 1995, 1999). Since the more ambitious design based on risk minimization can satisfy optimal fishing opportunities but not vice versa, it has to take precedence. However, this approach should not be viewed as the conservation alternative. Instead it rests on the philosophy that we should allow as much fishing as possible without risking the future of the fish, fishery, or ecosystem. As such, it represents responsible ocean management where conservation goals are achieved by stacking the odds toward long-term success for both ecosystems and fisheries. Consequently, design criteria based on risk minimization should serve as minimum standards, and larger reserves may be desirable, depending on the goals of the reserve or reserve network.

### General Design Principles

A substantial effort has gone into developing design principles for conservation areas on land, and much can be learned about marine reserve design from them. These efforts have examined and illuminated a wide range of concepts, including (1) minimum viable population sizes, (2) effective population sizes, (3) biodiversity hotspots, and (4) landscape processes. The first two of these concepts are aimed at ensuring any protected area is sufficiently large to contain a viable population. For many land species and a few ocean ones, an area may need to be very large to maintain a viable population, often considered to require at minimum an effective population size of 200 (Gilpin and Soulé 1986).

The latter two concepts are aimed at identifying priority areas for protection and represent two very different approaches. Under the hotspot approach, scientists map out the ranges of any and all species of interest. They then analyze those maps to identify hotspots that contain particularly large numbers of species. Ideally, areas should be chosen so that all species are represented in at least one conservation area. This approach offers the potential to find and use complementary areas to achieve broader conservation goals, but it also raises some concerns. Species ranges are not static and may change with developmental stages, seasons, and ecological succession—the natural process of recovery of an area to natural or human disturbance. Moreover, concern has been raised that areas of high species diversity may in fact be poor quality habi-

tat for many of them (Araújo and Williams 2001). In contrast, the landscape process approach looks at systems in a more dynamic way. Including an entire watershed as part of a protected area (marine or terrestrial) is one simple illustration of this sort of thinking since upstream activities can impact a downstream conservation area (Pickett et al. 1997). On land, this approach has led to such ideas as providing corridors to link networks of protected areas (Noss 1987; Simberloff and Cox 1987).

We should heed the lessons learned on land, but with care to avoid overgeneralizing them. One fundamental difference between ecosystems on land and in the sea is their status. Although marine ecosystems have suffered badly (Jackson et al. 2001; Myers and Worm 2003), they are generally not as badly degraded as those on land. One important implication of this difference is that we still rely on the ocean to a greater degree for wild-caught food. The design of parks on land, where much habitat has already been urbanized or farmed, often focuses on keeping as much of the biota inside as possible—an island of nature amidst human development. The greatest threat to land-based biodiversity has gradually shifted from overexploitation to habitat destruction, in part because many of the great natural food sources have been hunted to unproductive levels. In the sea, there are still widespread habitats that have the potential to perform their natural ecological functions if managed appropriately. As a result, we can think of marine reserves in the context of wild fish production to sustain outside fishing areas (NRC 2001). Another difference that contributes to the capacity of marine reserves to produce food is the relative openness of ocean systems. The fluidity of the ocean makes it inevitable that many species will disperse beyond reserve boundaries. These differences all favor the use of the landscape process concept over hotspots as a guiding principle for designing networks of marine reserves.

Scientists have already identified some guiding principles for designing marine reserves or reserve networks and we will build on these. Ballantine (1995, 1997) identified three important concepts:

- Representation of all habitats
- Replication of reserve units to avoid losing too much from the occasional poor quality area
- Networking the reserve units in a self-sustaining manner

He suggested that the network should encompass 20 to 30 percent of the total management area. Roberts et al. (2003b) added a few additional rules of thumb. They recommended prioritizing sites to most efficiently achieve the greatest

result. Specifically, they recommended preferentially including four site categories:

- Sites that include vulnerable habitats
- Sites that contain vulnerable life history stages
- Sites that are capable of supporting exploited species or rare species
- Sites that provide ecological services

The services include coastal barriers and water purification but might also include places that have special nonconsumptive value, like a popular diving spot (see chapter 4 for more detail on other ecological services). These authors also recommended avoiding sites with very high threats from human or natural disasters. We agree with avoiding sites under high threat of human catastrophes and also those highly vulnerable to natural disasters if reserves are going to be sparse. However, if a reasonably large reserve network is going to meet the other general rules of thumb, then it will be important to include areas that are frequently disturbed naturally. We believe they should simply be treated as one more habitat type to be included in a representative and replicated manner.

This landscape-level approach is being used more frequently. Sala et al. (2002) showed that biodiversity in the Gulf of California, Mexico, was not random. Instead it showed organization corresponding to latitude and depth. Friedlander et al. (2003a) took a similar broad look at the pattern of diversity around Old Providence and Santa Catalina Islands in the Seaflower Biosphere Reserve, Colombia. They found strong similarities in the full assemblages and bottom-dwelling reef communities within habitat types they had previously defined, differences among habitat types generally, and additional differences between sites near the island and those on a long shallow bank that extended to the north. Once these distinctions were recognized, they were incorporated into the design process by ensuring that each distinct type was represented.

### Crucial Factors

Although a number of different factors can influence marine reserve design, two stand out as especially important: the fluidity of the ecosystems involved and the extent of damaging activities outside the reserve. Not coincidentally, these two factors underlie our ability to rely on the sea for wild-caught food. The fluidity is a crucial factor because reserves will be more effective the better they retain adults, although some degree of export of reproduction is de-

sirable (PDT 1990; Sladek Nowlis and Roberts 1999). The extent of damaging activities is important because it determines the extent to which reserves have to accomplish all management objectives. For example, high yields can be achieved from many fisheries in the absence of marine reserves if fishing is at relatively low levels, carefully controlled, or both. In contrast, very large reserves may be necessary to achieve similar fishery yields if fishing activity is high in the remaining fishing grounds (Sladek Nowlis and Roberts 1999).

### *Movement to and from Reserves*

Marine reserve design will be influenced a great deal by the degree of interaction across space in the ocean. Most marine species, particularly those targeted by fishing efforts, have planktonic larvae, which generally spend from a week to several months in the water column (Boehlert 1996). These lengthy larval periods provide great potential for long-distance dispersal. It has been demonstrated that, if larvae drift passively on surface currents, they may move hundreds of kilometers during their larval phase (Roberts 1997). Reinforcing this evidence of high dispersal potential, genetic studies have shown surprisingly high homogeneity in marine populations across entire ocean basins, suggesting that populations mix genetically over these broad ranges (e.g., Lacson 1992). However, work in population genetics has also shown that very little mixing, on the order of a few individuals per generation, need take place to maintain this homogeneity among otherwise distinct populations (Slatkin 1987).

Not all organisms can disperse so far. Tunicates, for example, generally produce large larvae with limited dispersal ability. Larvae of the tunicate *Lissoclinum potella* are visible to the naked eye in field conditions and can be followed from parent to settlement (e.g., Olson and McPherson 1987). The lack of dispersal capability can influence tunicate biodiversity patterns, with extremely limited distributions for some species (e.g., the Chilean tunicate *Pyura praeputialis*, Clarke et al. 1999). Though tunicates are not a traditional target for exploitation most places in the world, there is growing interest in previously nonexploited groups, including tunicates, by the aquarium and pharmaceutical industries. Other exploited species also show limited dispersal patterns (e.g., the bull kelp *Durvillea antarctica*, Castilla and Bustamente 1989), but these species are exceptions to the general rule of high dispersal potential among exploited species.

However, larvae might not disperse as far as surface currents on the open ocean would suggest. Small-scale coastal oceanography can play a major role

in larval dispersal and recruitment (Caselle and Warner 1996) and can lead to local retention of larvae (Black 1993; Wolanski and Sarsenski 1997). Larval behavior can also play an important role in dispersal (e.g., Jenkins et al. 1999; Katz et al. 1994). Together, local oceanography and larval behavior can lead to significant amounts of local retention (e.g., Cowen et al. 2000). These patterns can be accentuated by differential survival of newly settled individuals. Even if larvae manage to move far away from parents, the chances of discovering suitable habitat decrease with increasing distance. If they do not find suitable habitat, they are more likely to die—making the dispersal ultimately ineffective.

These discoveries are backed by growing evidence that there are genetic gradients, which indicate relatively low exchange through dispersal (Palumbi 2003). Collectively, the body of work on larval dispersal suggests that many coastal marine populations retain larvae locally but also allow some larvae to disperse large distances. Perhaps not coincidentally, this strategy of mixed dispersal ranges has been shown to have profoundly positive ecological and evolutionary benefits in terrestrial and freshwater systems (Cohen and Levin 1987). The interactions among larger-scale oceanographic processes, smaller-scale coastal oceanography, and larval behavior are still poorly understood and remain a great mystery of marine ecology.

Reserves provide an opportunity to learn more about larval dispersal patterns. Reserves create a buildup of biomass, and therefore potential reproductive output, within their borders. To the extent that larvae are retained locally, this phenomenon should be observable as gradients of larval abundance, decreasing as one moves away from the reserve. Only a few studies have attempted to document a larval gradient, or any phenomenon, outside of reserve boundaries, but they offer promising results. In one reservelike experiment, Tegner (1992) reintroduced green abalone (*Haliotis fulgens*) into an area off of California. Green abalone were depleted to very low levels at the time of reintroduction from heavy overfishing, so the reintroduced abalone served as a reserve of sorts. The author demonstrated higher than expected recruitment in the general area of the reintroduction, with apparent recruitment enhancement up to 8 km away. Additional studies like this one offer potential to gain a better understanding of larval dispersal and the links between adult biomass and new recruitment into a population.

Like larval dispersal, postsettlement movements by juveniles and adults may contribute to the openness of marine systems. Marine species can be classified into three general categories: benthic, pelagic, and demersal. Benthic species are associated with bottom substrate as adults, and thus have extremely lim-

ited adult dispersal capabilities. There are some benthic species that have been shown to move substantial distances as adults (e.g., spiny lobsters, Acosta 1999) but most are physically attached to the bottom with minimal movement capabilities. Incidentally, benthic species may be most capable of benefiting from reserve protection because their limited movement capabilities can make them susceptible to reproductive failure if density is too low (Levitan 1991). Pelagic species form the other extreme, being associated almost exclusively with the water column. Demersal species fall in between, typically associated with bottom structure but with capabilities to swim in the water column. Reserve studies and reserve efforts have generally focused on benthic and especially demersal species (Halpern 2003) because pelagic species may be less likely to benefit from reserves (Bohnsack 1996; but see Guenette and Pitcher 1999).

Although postsettlement movement in demersal species is easier to study than larval dispersal, it is nearly as poorly understood. Studies have examined movement patterns of both tropical and temperate demersal species both indirectly and directly, albeit with a bias toward reef-associated fish.

Reserves provide the majority of indirect evidence about postsettlement movement. For example, Russ and Alcala (1996) showed higher densities of adult fish close to the border of a reserve on Apo Island, Philippines, than farther from it, suggesting the possibility that fish move across the border but not too far. Similar results were found at the border of a marine reserve on Barbados (Rakitin and Kramer 1996). Johnson et al. (1999) demonstrated that, in addition to a buildup of biomass within a Florida reserve, some fish moved in and out, and a number of world record trophy fish were caught in the area. Additional direct evidence comes from observable phenomena like spawning aggregations where high abundances concentrated in space and time could only be explained by movements to and from the aggregation.

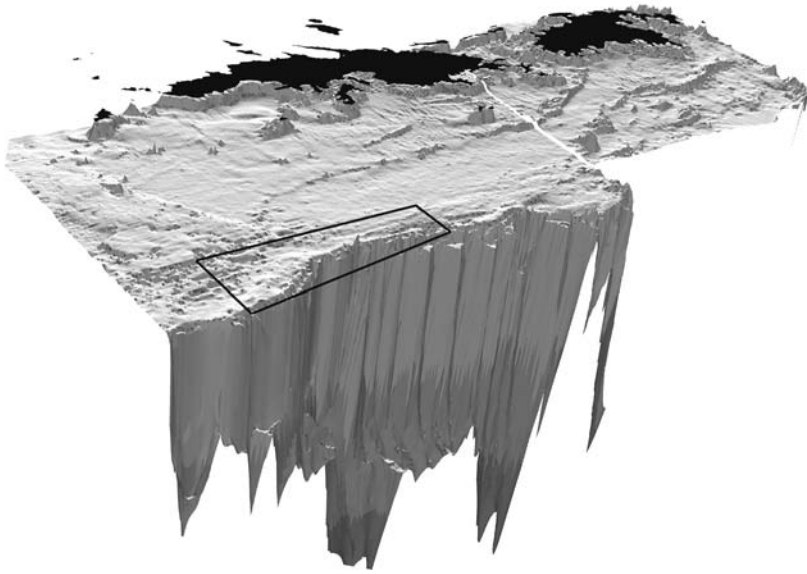
Direct evidence consists of tagging experiments, where tagged fish are retrieved by fishers or by underwater visual observation, and tracking experiments, where fish are equipped with an acoustic device that can be tracked using a hydrophone from the surface. Tagging experiments provide a coarse-scale picture of movement, showing the limits over longer periods of time. Tracking experiments provide the fine-scale picture, showing detailed movement patterns over short time frames.

Although juvenile and adult fish movement patterns are still poorly understood, a picture is emerging that includes specialized movements tied to particular life history events with less frequent and often habitat-limited movement patterns at other times.

Many species of fish and marine invertebrates utilize different habitats as they grow and mature, typically moving from shallow inshore habitats, to deeper offshore habitats (Roberts 1996). In some cases, these movement patterns through development will vary depending on whether appropriate habitats are adjacent, and may be inhibited by habitat types that act as a barrier to dispersal (e.g., Acosta 1999). These sorts of movements can also occur on a daily basis. Juvenile grunts in the Caribbean undergo predictable movements between daytime resting and nighttime feeding areas (Ogden and Ehrlich 1977).

Numerous species of fish aggregate to spawn, requiring long-distance movements for some. Tropical species like groupers and snappers are particularly well known for this phenomenon. Larger groupers and snappers can migrate great distances to specific sites and form spawning aggregations of hundreds or thousands of individuals at specific times of the year (Domeier and Colin 1997). Long-term persistence of these aggregations at specific sites (e.g., Colin and Clavijo 1978) makes these species extremely susceptible to fishing pressure (Sadovy 1993). Several grouper and snapper species have been greatly overfished throughout the world, largely due to extreme exploitation of spawning aggregations. Despite the recognition of this behavior and great importance to conservation, only a small, but growing, number of spawning aggregations have been closed to fishing, and a paucity of scientific information exists on the details of spawning aggregations, especially the potentially important habitat characteristics of spawning aggregation sites (Fig. 5.2; and see chapters 9 and 10). It is not surprising that fish seek this complex habitat while spawning because the complexity offers shelter for the large number of fish that gather, and it may also influence the dispersal of offspring so that some are retained within the complex habitat structure whereas others are effectively dispersed longer distances (Wolanski and Sarenski 1997).

Many temperate adult fishes show similar patterns (Cushing 1995). Fish tend to be found in higher concentrations on spawning grounds compared to feeding grounds and thus are more susceptible to fishing pressure in these locations. The spawning grounds for plaice in the Southern Bight in the southern North Sea have remained in the same location since the grounds were discovered in 1921 (Harding et al. 1978). Between 1921 and 1967, the mean peak date of spawning for these fish was January 19 with a standard deviation of less than one week (Cushing 1969). Plaice spawning therefore exhibits a high degree of predictability in both space and time. Cod tagged in five regions on the Canadian Shelf tended to return to their grounds of first spawning, with a low emigration rate (distant recaptures/all recaptures) of 0.0375, which would



**FIG. 5.2 Complex Habitat at a Spawning Aggregation Site (NOAA/NOS/NCCOS/CCMA-Biogeography Program unpublished data).** The Red Hind Bank Marine Conservation District, St. Thomas, U.S. Virgin Islands, was established to protect spawning aggregations of red hind (*Epinephelus guttatus*), a Caribbean reef fish, and other species. Not coincidentally, red hind and other groupers utilized a site with complex habitat, providing refuge for spawners (see Beets and Friedlander 1999 for more detail).

promote a relatively high rate of gene flow between each group (Thompson 1943) but relatively little mixing from a standpoint of stock productivity.

Despite the ability to migrate large distances and the propensity of some species to do so at specific stages of their life history, most reef-associated fishes appear to be rather sedentary and possess relatively small home ranges. Holland et al. (1993) found that a population of *weke* (white goatfish, *Mulloidichthys flavolineatus*) in Hawaii showed high site fidelity, with 93 percent of recaptures occurring at the release site. In a trapping and tagging study conducted in Hanalei Bay, Kauai, Friedlander et al. (1997) recaptured or resighted 85 percent of all tagged individuals of twenty-three species within 50 meters of their release site. The limited range of dispersal of recaptured *omilu* (blue trevally, *Caranx melampygus*) (75.5 percent within 0.5 km of the release site) and strong site fidelity observed from sonically tagged fish suggest that dispersal is much less than might be predicted for a highly mobile, piscivorous species (Holland et al. 1996). *Kumu* (whitesaddle goatfish [*Parupeneus porphyreus*]), a Hawaiian endemic goatfish and important fisheries species, were acoustically tracked around the Coconut Island refuge for periods up to ninety-



three hours (Meyer et al. 2000). The home ranges of all fish were within the boundaries of the Coconut Island reserve. This small reserve (less than 1 km<sup>2</sup>) was capable of protecting both large juveniles and some spawning size individuals (Meyer et al. 2000). *Kala* (blue spined unicornfish [*Naso unicornis*]) were acoustically tracked for periods of up to twenty two days in the shallow high-energy fringing reef habitat in the Waikiki Marine Life Conservation District (Meyer and Holland 2001). The home ranges of all of the *kala* tracked were completely encompassed by the boundaries of the Waikiki Marine Life Conservation District. However, more mobile species, such as jacks and goatfishes, ranged over an area slightly larger than 1 km<sup>2</sup> (Meyer 2003). Even this limited movement exceeded the 0.32 km<sup>2</sup> size of the Waikiki Marine Conservation District and left these fish vulnerable to fishing. Caribbean reef fish showed similarly restricted movements in and near a marine reserve on Barbados, with most species rarely showing much movement away from the site of first capture (Chapman and Kramer 2000). However, some species (e.g., horse-eye jacks [*Caranx latus*] and bar jacks [*C. ruber*]) did appear to move frequently from the study area. Moreover, even sedentary species showed relatively more movement when the reef habitat was uninterrupted than when it was fragmented.

These results suggest considerable site fidelity on the part of a number of species. They also suggest that an association exists with a particular locality of rather limited size. Short-term (e.g., day-to-day) movements may be common, but tag recovery data and telemetry data indicate that if these fishes make such movements, most of them return to the home locality. Although different species have widely different movement patterns these results are generally consistent with existing ideas about the limited normal range of movements of many demersal, reef habitat-associated species.

Nevertheless, some evidence suggests that marine systems are open and thus vulnerable to impacts unless marine protected areas are very large. Friedlander and DeMartini (2002) identified twice the fish biomass in the large, remote, and lightly fished Northwestern Hawaiian Islands than in small, fully protected marine reserves in the main Hawaiian Islands (Sladek Nowlis and Friedlander, 2004). Large apex predators made up the majority of fish by weight in the Northwestern Hawaiian Islands but were virtually absent from reefs in the main Hawaiian Islands, even those protected from fishing. The marine reserves themselves contained more than twice the fish biomass of areas that received partial or no special protections within the main Hawaiian Islands (Friedlander et al. 2003b). Nevertheless, the reserve effect was not adequate to reestablish fully functioning ecosystems, most likely because of the small extent of

marine reserves as a whole and the heavy fishing pressure surrounding them. Although many benefits can be reaped from small reserves, larger ones may be necessary to sustain fully functioning ocean ecosystems.

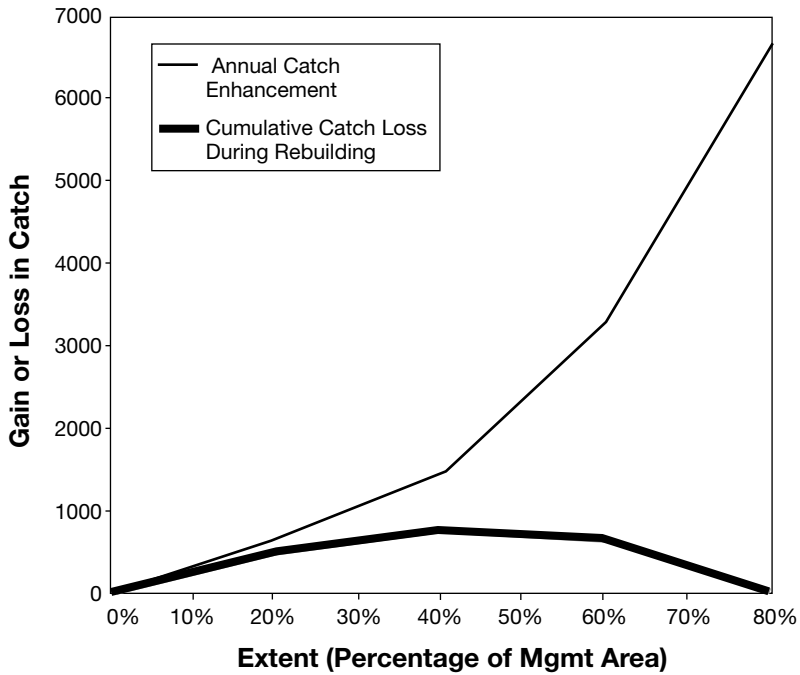
### *Outside Impacts*

The second crucial marine reserves design factor is the degree of outside impacts. For example, models have shown consistently that maximum yields can be obtained over a range of reserve sizes depending on the intensity of fishing outside of the reserve (Sladek Nowlis and Roberts 1995, 1999). If impacts are light and strictly controlled outside of reserves, marine reserves may not be necessary. However, experience suggests that fishing rates rarely stay light and are even less frequently under strict control of managers (e.g., Myers and Worm 2003).

In addition to modeling reserve design based on the scales of outside impacts, managers may wish to reduce the magnitude of outside impacts on reserves. One way in which managers can do so is by integrating reserves with coastal zone, ecosystem, or broader ocean zoning management plans. Another way is through the creation of linked land–sea protected areas that protect adjacent terrestrial and marine areas. Reserve designations can help to protect the designated area from fishing, point-source pollution, and other directed human impacts, but may not offer protection from non–point source runoff. As a result, it may be desirable to locate marine reserves downstream from terrestrial protected areas, or at least to enact stricter controls on upstream development if a reserve is put in place. In some cases, though, it may be necessary to scale up the size of marine reserves to account for major disturbances such as oil spills or hurricanes (Allison et al. 2003).

### Total Extent of Reserves or Reserve Network Coverage

The hottest debate regarding marine reserves usually surrounds their extent of coverage through the management area in question. A recommendation of 20 percent (PDT 1990) created uproar along the southeastern Atlantic coast of the United States, whereas a recommendation of 30 to 50 percent (Airamé et al. 2003) caused a similar stir in the Channel Islands of California. Total extent is a key design consideration because it is arguably the most important for achieving goals but also has the greatest influence on what the short-term costs are likely to be for displaced stakeholders (Fig. 5.3). Costs can be significant if large marine networks are created (Sladek Nowlis and Roberts 1997). Fortu-



**FIG. 5.3 Extent of Reserves: More Benefits, More Costs.** A population model of the white grunt (*Haemulon plumieri*), a Caribbean reef fish, experiencing heavy overfishing initially. The creation of a marine reserve or reserve network enhances catches in the long term but also generates short-term costs. Source: Adapted from Sladek Nowlis 2000.

nately, those costs are expected to be offset by reserve benefits clearly and quickly when fisheries are most depleted, and can be deferred under any circumstances by phasing in reserves (Sladek Nowlis and Roberts 1997). It is also worth noting that for most overfished fisheries—ones that have been depleted to the point where they have lost productivity potential—reserves often impose smaller opportunity costs than other more conventional management techniques while offering the greatest chance of achieving rebuilding to more productive levels (Sladek Nowlis 2000).

A number of scientists have examined the question of how much area to include in a marine reserve or reserve network (reviewed in NRC 2001). The recommendations depend on a number of factors, foremost among them being the goals and objectives for the reserve or reserve network. A number of studies have examined the extent of reserve that will maximize fishery yields (e.g., Sladek Nowlis and Roberts 1999) and even these studies found a wide range of possible extents, from none to sizable, depending on several circumstances. On the other hand, there are also many nonconsumptive benefits one might achieve from marine reserves, and most of these benefits will be maximized by

having very large extents. Consequently, the percentages discussed following here should be viewed as minimum standards rather than optimal recommendations. To move forward on this complex issue, we focus on risk minimization. While this is not the only goal one might have for a marine reserve or reserve network, it is fundamentally important because without it managers are gambling with the future of the ecosystem and the people that rely on it for sustenance.

Scientific results suggest that reserve networks need to protect a population consisting of 30 to 50 percent of its pristine size to ensure against collapses (Mangel 1998; Sladek Nowlis and Bollermann 2002). This level of insurance reduces the tremendous uncertainties that surround fisheries management. For example: in the United States, where more resources are available than almost anywhere else on the planet for fisheries management and science, over three quarters of all federally managed fish populations (some species are managed as separate populations across their range) were of unknown abundance, had unknown levels of fishing pressure, or both, in the year 2000 (NMFS 2001). State managed fisheries may do even worse. A 2002 California report indicated that 85 percent of all nearshore species (the ones most likely to be State managed) were of unknown status (CDFG 2002). If we cannot even identify the status of fish, we surely cannot manage them with certainty. Scientific studies clearly indicate that uncertainty can be countered most effectively by maintaining a portion of a fished population as off limits from all fishing (e.g., Sladek Nowlis and Bollermann 2002).

Closing 30 percent of an area will not necessarily protect 30 percent of the fished population from fishing, nor will it necessarily reduce catches by 30 percent. If especially productive areas are chosen, the effects may be amplified. On the other hand, two factors will cause a smaller portion of the population to be protected than reserves might suggest.

1. Marine systems vary tremendously in their openness, and some reserve benefits will be diluted the more individuals move across reserve boundaries. Openness can be minimized by using relatively fewer large reserve units within a network because large reserves will leak less than smaller ones (Diamond 1975). However, it is likely that systems with high fluidity will need a greater extent of reserve coverage to counteract this fluidity. As such, reserves are a more obvious choice for less open systems—including most coastal ocean ecosystems—than more fluid systems, like open-ocean pelagic ecosystems. It is also possible to address this issue by selecting areas with high habitat diver-

sity since many species move among different habitats daily (Holland et al. 1993) or throughout their life cycles, and may need to move shorter distances if several habitat types are in close proximity (Appeldoorn et al. 1997, 2003).

2. Ecological disasters will also tend to increase the extent of reserve coverage necessary to minimize risks. Natural and human-caused ecological disasters may disrupt equilibrium processes inside reserves and in doing so make them less effective at meeting management goals. However, natural ecological disasters are part of natural cycles and we should not harbor a static view of the world. When habitats are disturbed, the natural process of succession gradually restores mature living communities; for example, old-growth forests or coral reefs. Succession is an important process in ecology. It is through this process that early successional, fast-growing, and widely dispersing organisms coexist with the hardier, slower-growing species that ultimately outcompete them in an undisturbed site. Retaining the natural cycles of disturbance is important for maintaining ecological balance. When damaging human activities are added to natural forms of disturbance, the results depend on their relative magnitudes and frequencies. In an environment with little natural disturbance, even small amounts of human impacts can disrupt the ecosystem. By contrast, in an environment with high rates of natural disturbance, relatively high rates of human impacts may not noticeably affect the ecosystem. If human impacts do degrade certain areas more than the natural cycle of disturbance, reserve coverage will need to be scaled up to account for the degradation. For example, it has been determined that along the California coastline reserve coverage needs to be scaled up by 20 to 80 percent to address oil spills (Allison et al. 2003).

A number of scientists have identified 20 percent reserve coverage as a minimum societal goal (e.g., Ballantine 1997; PDT 1990). This percentage was originally proposed based on overfishing definitions that suggested fished populations should be maintained at levels that on average allowed individuals to achieve 20 percent of their expected reproductive output (Goodyear 1993). Since that time, overfishing definitions have been overhauled, often to far more conservative levels (e.g., 40 percent for rockfish, Clark 1993). Recent recommendations have focused on broad concepts of insurance rather than on single-species management. These approaches have identified that reserve coverage of as little as 10 to 20 percent can help sustain a fishery, whereas 30 to 50 percent may be necessary to ensure high, long-term abundance and catch levels (Sladek Nowlis and Bollermann 2002). Depending on the scale of impacts out-

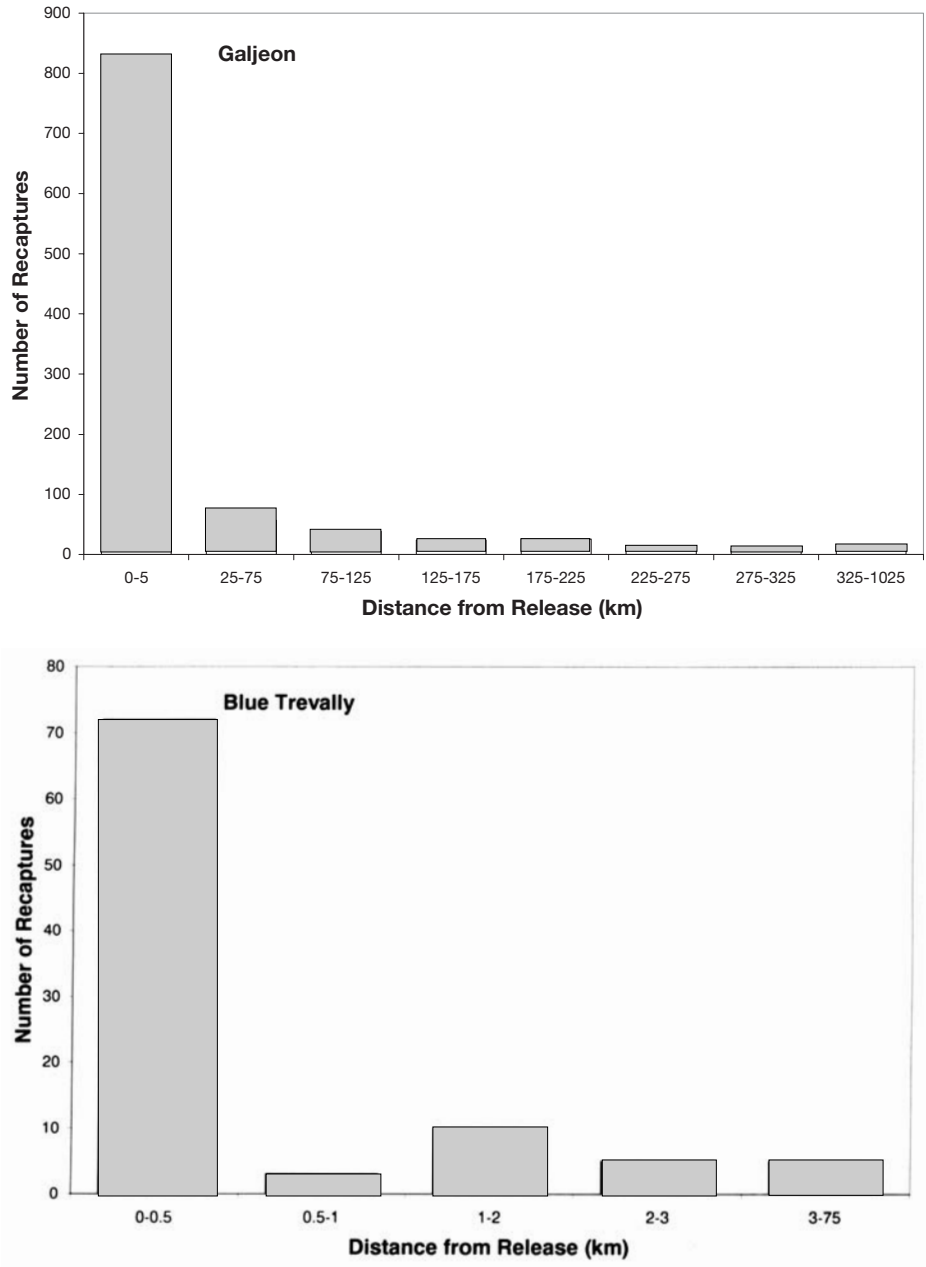
side, the openness of the system, and the rate and extent of ecological disasters, reserve extents may need to be modified to encompass the desired proportion of the unfished abundance. And these recommendations should be viewed as minimum standards rather than optimal recommendations because there are many nonconsumptive benefits that may also be important in the designation of marine reserves.

### Size and Shape of Individual Reserves

Scientists have actively debated the size and shape of conservation areas on land since the 1970s and developed some general principles. Their debate was based on the presumption that resources would limit the total coverage of land conservation areas and, as such, a key decision would be how to parcel out the coverage. Coined the single-large-or-several-small (SLOSS) debate, a general consensus emerged that few larger reserves were generally better than several small because they were more likely to contain functional ecosystems within their borders and to suffer less from outside effects (Diamond 1975).

In the sea, the size and shape of individual reserves can have important effects on ecological and socioeconomic performance as mediated by the fluidity of the system and scale of impacts in outside areas. Whether goals are to enhance fishing opportunities or conservation of natural ecosystems, it will be desirable to design marine reserves so that adults stay inside them while some of their offspring disperse out (PDT 1990; Sladek Nowlis and Roberts 1999). There is one fairly minor exception to this rule. In a few cases (e.g., recreational trophy fisheries) there will be far greater value placed on the catch of a few very large individuals. In these cases, it may be desirable to have a small amount of adult movement across reserve boundaries (Johnson et al. 1999). But even this minor motivation to have leaky reserves should be tempered for a couple of reasons. First, too much leakiness will prohibit fish from growing large enough to provide the trophy opportunities. Second, because of the wide range of movement patterns exhibited by different species and sometimes even different members of the same species (as discussed following here), most sizes and shapes that maintain most adults within reserve borders will also foster enough spillover of some species to provide trophy fishing opportunities.

Keeping adults in marine reserves will be easier in some systems than in others. Given new studies that show relatively low rates of adult movement in coastal environments (e.g., Attwood and Bennett 1994; Holland et al. 1996; Fig. 5.4), relatively small marine reserves may adequately protect adults near



**FIG. 5.4 Movement Tendencies and Capabilities.** Both the (a) galjeon, a southern African shoreline fish, and (b) blue trevally, a Hawaiian shallow-water predator, showed remarkable dispersal potential, yet the vast majority of individuals stayed very close to home (see Attwood and Bennett 1994 and Holland et al. 1996 for more detail).

the coast. In fact one reserve on the Caribbean island of St. Lucia was highly effective despite measuring only 150 by 175 meters (Roberts and Hawkins 1997). The shape of a reserve could help if it accounts for connectivity among

habitat types. Since fish may use more than one habitat type throughout the day or their life cycle, it is usually preferable to include multiple habitat types within the same reserve (Appeldoorn et al. 1997). There is no single best shape for doing so, although swaths stretching from shore into deep water are more likely to contain a diversity of habitats than reserves without as much depth range (e.g., PDT 1990), and may encompass common natural migrations from shallower, land-associated to deeper habitats (Appeldoorn et al. 2003; Davis and Dodrill 1989; Love 1996).

For highly mobile species like the bluefin tuna, reserves might need to be extremely large if they are going to protect a substantial portion of adults. Instead, these species might gain more realistic protection from reserves located in areas where large groups of animals come together to feed or reproduce (Hyrenbach et al. 2000). Complementary regulations will be especially important for highly mobile species to address uncertainty. These could include size limits (Myers and Mertz 1998) or quota systems (Sladek Nowlis and Bollermann 2002). Regardless, we find relatively sedentary species in virtually every part of the ocean, particularly associated with bottom habitats. Given increasing fishing efforts targeting deepwater species and the impacts this can have on bottom habitats (Dayton et al. 1995), it makes sense to consider all areas of the ocean when designing networks of marine reserves.

Enforcement can also be enhanced through the shape of individual reserves. Both enforcement and compliance will be greatly aided if reserve borders are straight lines running north–south and east–west or utilizing other obvious navigational reference points. Enforcement will also generally be easier if there are relatively few large rather than many small reserves. However, the size issue has enough ecological and socioeconomic implications that enforcement considerations may be secondary in this respect.

### Site Selection

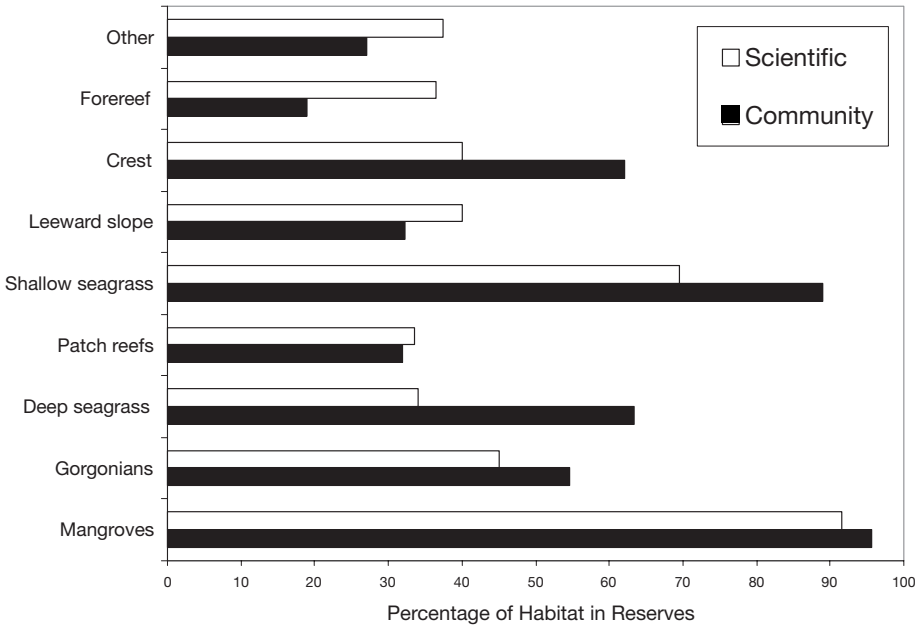
Marine reserve networks have the greatest chance of including all species, life stages, and ecological linkages if they encompass representative portions of all ecologically relevant habitat types in a replicated manner (Ballantine 1995, 1997). Studies indicate that habitats are a good surrogate for species, so that a system of protected areas that incorporates all habitat types is also likely to provide refuge for most species. In fact, habitats are generally a better focus for protected area design than species because they are easier to map and are more closely tied to the ecological processes whose conservation should be the



ultimate goal. As a precursor to including habitat types in a protected area, it will be necessary to define habitat types in an ecologically relevant manner and map out their distributions. Let us consider an example.

We have performed extensive surveys of the coastal ocean environments around Old Providence and Santa Catalina islands (in close proximity to each other) in the Archipelago of San Andrés, Old Providence, and Santa Catalina, Colombia, which were recently designated the Seaflower Biosphere Reserve (Friedlander et al. 2003a). We used preexisting habitat maps (Díaz et al. 1996) and surveyed a wide range of habitat types for ecological differences as identified by distinct fish assemblages and communities of organisms living on the seafloor. Based on these surveys, we were able to lump several habitat types into a few simple yet distinct categories and identify ecological connections among these habitats. We also identified a major difference between otherwise similar appearing habitats based on their proximity to land (Appeldoorn et al. 2003). The shelf extends approximately 20 kilometers north of the islands but only a short distance south. Our surveys showed distinct differences in fish assemblages for all habitat types depending on whether the survey site was close to the island or on the northern bank. This finding confirmed the importance of links between coral reefs and other nearshore habitats, like mangrove lagoons and sea grass beds (Ogden 1988), which serve as nursery grounds for a number of species. The bank habitats were nevertheless valuable and worthy of protection because of their differences (some species thrive in the absence of the ones that start life in mangroves or sea grass beds), but it was helpful to identify them as different from otherwise similar looking habitats near the islands.

It is important to represent all habitats, but some may have greater conservation value than others. It is especially important to identify limiting habitat types and ensure that these are preferentially included in no-fishing or no-entry zones. These habitats fall into three categories: rare habitats, especially vulnerable habitats, and habitats where fish are especially vulnerable to overfishing. Habitats may be rare because they only develop under limited ecological conditions or because they have been disproportionately impacted by previous activity. For example, coastal wetlands exist in a narrow band at the water's edge and have been targeted heavily by coastal development (Rosenberg et al. 2000). Vulnerable habitats would include those that are especially likely to be impacted by fishing activity. Structurally complex habitats are especially vulnerable to the impacts of bottom trawling, for example (Dayton et al. 1995; Watling and Norse 1998). Habitats where fish are especially vulnerable primarily include places where fish gather to feed or reproduce. When they are



**FIG. 5.5 Overrepresentation of Sensitive Habitats in Reserve Networks.** Scientists working in the Seaflower Biosphere Reserve, San Andrés Archipelago, Colombia, developed recommendations for the percent of each habitat type to include in well-designed marine reserve networks around Old Providence Island. These targets were 36 percent inclusion for most habitat types, but higher for those habitats known to be rare and vulnerable, including mangrove lagoons and spawning aggregations (see Friedlander et al., 2003a, for more detail). The scientists also provided examples of how reserves might be designed to achieve these target percentages. The percent of each habitat type included in the scientists' examples (white bars) is contrasted here with the percent of each habitat type included in proposals made by stakeholders for such a reserve network (black bars).

gathered together, fish are easier to catch en masse. Moreover, they may selectively choose structurally complex, and thus vulnerable, habitat for shelter during these aggregations (Beets and Friedlander 1999). At the same time, there may be some areas that are of particular value because they contain or are in close proximity to all the habitats necessary to support a productive ecosystem. These areas, along with those that are rare or vulnerable, such as spawning aggregation sites, should receive particular attention (Fig. 5.5).

Another question with respect to habitat inclusion is whether it is acceptable or desirable to include degraded habitats within a reserve. From a socio-economic perspective, a site may be desirable if it was impacted at some point in the past and is now no longer of great utility. Sites like this could be acceptable reserves if the source of degradation is identified and eliminated, and if the system appears to have the capacity to recover its former productivity

in a reasonable timeframe. For example, overfished locations may be perfectly acceptable as long as the habitat or target species have not suffered too severely. In fact they may be ideal candidates for another reason—their ability to recover quickly. Studies predict that the most heavily fished areas are most likely to recover quickly (Sladek Nowlis and Roberts 1997). In doing so, they have great potential to solidify support for marine reserves. It has been our experience that, especially among fishers, seeing an area recover quickly after designation as a marine reserve removes doubt about the effectiveness of this management tool. In part, this reaction is due to the visible evidence that fishing was keeping the fish populations down, but it also appears to arise from a contagious enthusiasm at seeing fish at higher abundance than many thought possible. Not all degraded areas are good candidates, though. For example, an embayment that receives untreated sewage is probably not a good candidate unless the sewage effluent is going to be redirected and studies indicate the bay has not been impacted to the extent that recovery is unlikely.

The tolerance for including impacted habitats should increase with greater extent of reserve coverage. If reserves will encompass a substantial portion of an entire management area, it might actually be desirable to include habitats in varying conditions (while avoiding severely degraded habitats) to learn whether and to what extent habitats can recover. However, greater damage will require higher coverage to ensure that reserves minimize risk of collapse since it will take some time before they are capable of providing resilience to the region's marine ecosystems.

We therefore recommend that stakeholders lead site selection with support and guidance from technical advisers. The ecological, socioeconomic, and enforcement design criteria should be conveyed to stakeholders, with continuing discussion and feedback as stakeholder groups create and collaborate on proposals. To the extent that stakeholder groups can agree on a single proposal that meets the basic scientific criteria, we recommend that such a proposal be adopted.

## Regulations

A common question when designating marine reserves is whether a little fishing is acceptable if conducted by some group that might cause relatively light impacts. On the one hand, there are some examples where certain kinds of fishing are likely to have little effect on the species of concern. In one studied case, pelagic fishing (for fish in the water column) seemed compatible with the recovery of a bottom-dwelling scallop and some groundfish populations

on Georges Bank off the northeastern United States (Murawski et al. 2000). However, this result should not be taken as typical. This region has greater management capacity than almost any other place on the planet, and enforcement was carried out using satellite-based vessel monitoring systems. It would be difficult to replicate this scenario in most places in the world.

On the other hand, allowing some fishing in an area can open up a host of enforcement and ecological difficulties. In contrast to the Georges Bank example, most studies of partially protected marine protected areas (MPAs) show they fare poorly, most likely because of the difficulty in enforcing the ban on certain kinds of fishing when other fishing activity with similar appearance is allowed (Reed 2002; see also New Zealand Poor Knight's discussion in chapter 11). Wallace (1999) examined northern abalone abundance in several sites around southern Vancouver Island, British Columbia, Canada. Abalone collection was banned in all of the study sites and throughout the region, but sites varied in their other regulations. Five sites were open to other types of fishing, and all had extremely low abalone abundance—suggesting poaching. Three other sites were closed to all fishing. One was a designated ecological reserve, a second was a prison site where fishing was prohibited close to shore, and the third was near a military installation. The military site had the highest abundance of abalone, probably owing to high levels of enforcement. The prison site and the ecological reserve had fewer abalone, suggesting that some poaching may have taken place, but both had substantially more abalone than the five partially protected sites. More impressively, the ecological reserve had as many abalone as the prison site, suggesting that compliance within the reserve matched the prison site. These results indicate that allowing some fishing can create a real enforcement challenge.

In a larger study, Friedlander et al. (2003b) surveyed sixty sites around the main Hawaiian Islands. These sites varied in their fishing regulations. Some sites were open to all forms of fishing, others were MPAs that allowed some forms of fishing but not others, a few were managed using traditional Hawaiian methods and light overall fishing pressure, and still others were no-take marine reserves. Results indicated that open and partially protected sites were quite similar both in their fish assemblages and in the amount of fish they contained. These sites were distinct in both respects from marine reserves and from lightly fished sites managed using traditional Hawaiian practices, which had similar characteristics to each other. These results would indicate that most exceptions were deleterious to any benefits partial protection might provide, with the possible exception of light fishing using traditional methods in a culture

where these methods have evolved over centuries and management responsibility was delegated to the local community.

Allowing some forms of fishing also threatens an area with ecological effects that cascade through an ecosystem. Certain species have been identified as key players in ecosystems. Their removal can trigger changes throughout the entire ecosystem. For example, the loco (*Concholepas concholepas*), a predatory snail, plays a central role in keeping mussels from dominating the Chilean rocky intertidal zone. It is also a prized food source and has been depleted throughout Chile. Protected areas have not only allowed the loco to recover, but at more natural abundance levels it restores the Chilean rocky intertidal environments to more natural conditions (Castilla and Durán 1985; Durán and Castilla 1989). There are many other examples of similar key species in marine environments (Pinnegar et al. 2000; see also examples in chapters 4, 8, and 11). If an MPA were closed to all other forms of fishing but allowed collection of these important species, the MPA would not contain an ecosystem in natural ecological balance. These types of ecological interactions are especially important to be aware of because we know relatively little about ecological interactions in the ocean, and these types do appear fairly often.

To assure that a number of fishery and conservation goals are achieved, a core network of true marine reserves is necessary. However, these reserves could fit naturally within a broader zoning plan that includes a full range of MPAs and other management zones. Such a zoning approach would also enable managers to address a broad range of threats to and conflicts about protection and use of marine resources. Conservationists and fishers do not monopolize conflict about use of the ocean. There are also rifts between commercial, recreational, and subsistence fishing; between motorized and nonmotorized water sports; and between fishing and oil drilling, just to name a few. Zoning provides an opportunity to reduce all of these conflicts by designating areas where each activity is allowed.

In a broader zoning approach marine reserves should lie at the core of larger marine protected areas (NRC 2001). Doing so can buffer the reserves from outside impacts and reduce the impact of leaky reserves. Buffer zones might be compatible with such uses as light fishing using traditional practices and other forms of tightly regulated commercial and recreational fishing.

## CONCLUSIONS

Reserves should be designed using a process that clearly defines the role of the general public, scientific and enforcement advisers, and fishing communities.

The aim of the process should not be one of compromising scientific advice with the will of fishers, but instead achieving mutually agreed upon goals related to sustaining fish, fisheries, and ocean ecosystems into the foreseeable future. Toward this end, scientific and enforcement advice should play a key role in shaping designs, but the task of selecting actual reserve sites is ideally left to a public process that engages key stakeholders, including fishers and the broader public, as long as those sites are compatible with the agreed to and stated goals for the reserve and the expert advice about their ability to meet them.

There are some useful rules of thumb for designing marine reserves or reserve networks. While different goals could result in different designs, it is worth paying special attention to minimizing the risk of collapsing fished populations and the fisheries and ecosystems they support. Given our lack of knowledge, we would need marine reserves or other tools that kept 10 to 20 percent of all fish off limits to fishing to assure persistence, if not health, of these populations. To ensure relatively healthy fisheries and ecosystems would require more—30 to 50 percent of all fish must be protected. Depending on the openness of the systems, the magnitude of impacts outside reserves, the efficacy of other management tools, and the scale and frequency of ecological disasters, reserves may have to be modified, typically scaled up. Reserve networks should be divided into individual reserves capable of supporting viable adult populations of at least bottom-associated species within their boundaries. It is also desirable, and for most species likely, that reproduction will move out across the boundary to fishing grounds and other reserves. All habitats should be represented in a replicated manner, with special emphasis paid to rare, vulnerable, and fish aggregation habitats. Although small amounts of fishing may be compatible with conservation objectives at times, allowing exceptions makes partially protected areas vulnerable to losing all benefits. Especially given the goal of risk minimization, it is important to ensure that marine reserves form the backbone of any marine protected area plan. The reserves may fit naturally as the core of a broader zoning plan designed to reduce a wide range of conflicts surrounding the use of the sea.

We know everything necessary to design effective reserves right now. There are such great needs to ensure against future management mistakes and rebuild depleted fish populations that most reserve designs will prove beneficial even if they are only first steps toward ideal design. As reserves become more common, design choices will become more important for providing real improvements. Fortunately, the process of designating reserves and studies of their performance along the way will provide invaluable information for making the right choices in the future.

## REFERENCES

- Acosta, C. A. 1999. Benthic dispersal of Caribbean spiny lobsters among insular habitats: Implications for the conservation of exploited marine species. *Conservation Biology* 13(3):603–612.
- Airamé, S., J. E. Dugan, K. D. Lafferty, H. Leslie, D. A. McArdle, and R. R. Warner. 2003. Applying ecological criteria to marine reserve design: A case study from the California Channel Islands. *Ecological Applications* 13(1, suppl.):S170–S184.
- Allison, G. W., S. Gaines, J. Lubchenco, and H. Possingham. 2003. Ensuring persistence of marine reserves: Catastrophes require adopting an insurance factor. *Ecological Applications*. 13 (1. suppl.):58–524.
- Appeldoorn, R. S. 2001. “Do no harm” versus “stop the bleeding” in the establishment of marine reserves for fisheries management. *Proceedings of the Gulf and Caribbean Fisheries Institute* 52:667–673.
- Appeldoorn, R. S., and C. W. Recksiek. 2000. Marine fisheries reserves versus marine parks: Unity disguised as conflict. *Proceedings of the Gulf and Caribbean Fisheries Institute* 51:471–474.
- Appeldoorn, R. S., C. W. Recksiek, R. L. Hill, F. E. Pagan, and G. D. Dennis. 1997. Marine protected areas and reef fish movements: The role of habitat in controlling ontogenetic migration. *Proceedings of the 8th International Coral Reef Symposium* 2:1917–1922.
- Appeldoorn, R. S., A. Friedlander, J. Sladek Nowlis, P. Usseglio, and A. Mitchell-Chui. 2003. Habitat connectivity in reef fish communities and marine reserve design in Old Providence–Santa Catalina, Colombia. *Gulf and Caribbean Research* 14(2):61–78.
- Araújo, M. B., and P. H. Williams. 2001. The bias of complementarity hotspots towards marginal populations. *Conservation Biology* 15:1710–1720.
- Attwood, C. G., and B. A. Bennett. 1994. Variation in dispersal of galjoen (*Coracinus capensis*) (Teleostei: Coracinidae) from a marine reserve. *Canadian Journal of Fisheries and Aquatic Sciences* 51(6):1247–1257.
- Ballantine, W. 1995. The practicality and benefits of a marine reserve network. In Gimbel, K., ed. *Limited Access to Marine Fisheries: Keeping the Focus on Conservation*, 205–223. Washington, DC: World Wildlife Federation.
- . 1997. Design principles for systems of “no-take” marine reserves. *Workshop on the Design and Monitoring of Marine Reserves, February 18–20*. Vancouver: Fisheries Centre, University of British Columbia.
- Beets, J., and A. Friedlander. 1999. Evaluation of a conservation strategy: A spawning aggregation closure for grouper in the Virgin Islands. *Environmental Biology of Fishes* 55:91–98.
- Black, K. P. 1993. The relative importance of local retention and inter-reef dispersal of neutrally buoyant material on coral reefs. *Coral Reefs* 12:43–53.
- Boehlert G. W. 1996. Larval dispersal and survival in tropical reef fishes. In Polunin N. V. C., and C. M. Roberts, eds. *Reef Fisheries*, 61–84. London: Chapman and Hall.
- Bohnsack, J. A. 1993. Marine reserves: They enhance fisheries, reduce conflicts, and protect resources. *Oceanus* 36:63–71.
- . 1996. Maintenance and recovery of reef fishery productivity. In Polunin, N.V.C. and Roberts, C.M., eds. *Reef Fisheries*, 283–313. London: Chapman and Hall.

- Buck, E. H. 1993. *Marine Ecosystem Management*. Washington, DC: Congressional Research Service, The Library of Congress, 12.
- California Department of Fish and Game (CDFG). 2002. *Nearshore Fishery Management Plan*. Sacramento, CA: CDFG Marine Region.
- Caselle, J. E., and R. R. Warner 1996. Variability in recruitment of coral reef fishes: The importance of habitat on two spatial scales. *Ecology* 77(8):2488–2504.
- Castilla, J. C., and R. H. Bustamante. 1989. Human exclusion from rocky intertidal of Las Cruces, central Chile: Effects on *Durvillaea antarctica* (Phaeophyta, Durvilliales). *Marine Ecology Progress Series* 50:203–214.
- Castilla J. C., and L. R. Durán 1985. Human exclusion from the rocky intertidal zone of central Chile: The effects on *Concholepas concholepas* (Gastropoda). *Oikos* 45:391–399.
- Chapman, M. R., and D. L. Kramer. 2000. Movements of fishes within and among fringing coral reefs in Barbados. *Environmental Biology of Fishes* 57:11–24.
- Clark, W. G. 1993. The effect of recruitment variability on the choice of a target level of spawning biomass per recruit. In *Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations*, 233–246. Anchorage: Alaska Sea Grant College Program, AK-SG-93-02.
- Clarke, M., V. Ortiz, and J. C. Castilla. 1999. Does early development of the Chilean tunicate *Pyura praeputialis* (Heller, 1878) explain the restricted distribution of the species? *Bulletin of Marine Science* 65(3):745–754.
- Cohen, D., and S. A. Levin. 1987. The interaction between dispersal and dormancy strategies in varying and heterogeneous environments. *Lecture Notes in Biomathematics* 71:110–122.
- Colin, P. L., and I. E. Clavijo. 1978. Mass spawning by the spotted goatfish, *Pseudopenus maculatus* (Bloch) (Pisces: Mullidae). *Bulletin of Marine Science* 28:780–782.
- Cowen, R. K., K. M. M. Lwiza, S. Sponaugle, C. B. Paris, and D. B. Olson. 2000. Connectivity of marine populations: Open or closed? *Science* 287:857–859.
- Crowder L. B., S. J. Lyman, W. F. Figueira, and J. Priddy. 2000. Sink-source population dynamics and the problem of siting marine reserves. *Bulletin of Marine Science* 66(3):799–820.
- Cushing, D. 1969. The regularity of the spawning season of some fishes. *J. Cons. Int. Explor. Mer.* 33:81–92.
- . 1995. *Population Production and Regulation in the Sea*. Cambridge, England: Cambridge University Press.
- Davis, G. E., and J. W. Dodrill. 1989. Recreational fishery and population dynamics of spiny lobster, *Panulirus argus*, in Florida Bay, Everglades National Park, 1977–1980. *Bulletin of Marine Science* 44:78–88.
- Dayton, P. K., S. F. Thrush, M. T. Agardy, and R. J. Hofman. 1995. Environmental effects of marine fishing. *Aquat. Cons.* 5:205–232.
- Diamond, J. M. 1975. The island dilemma: Lessons of modern biogeographic studies for the design of natural reserves. *Biological Conservation* 7:129–146.
- Díaz, J. M., G. Diaz, J. Garzon-Ferreira, J. Geister, J. A. Sánchez, and S. Zea. 1996. Atlas de los arrecifes coralinos del Caribe colombiano, I: Archipiélago de San Andrés y Providencia. Pub. Esp. INVMAR.
- Domeier, M. L., and P. L. Colin. 1997. Tropical reef fish spawning aggregations: Defined and reviewed. *Bulletin of Marine Science* 60:698–726.



- Durán, L. R., and J. C. Castilla. 1989. Variation and persistence of the middle rocky intertidal community of central Chile with and without human harvesting. *Marine Biology* 103:555–562.
- Eklund, A. M., D. B. McClellan, and D. E. Harper. 2000. Black grouper aggregations in relation to protected areas within the Florida Keys National Marine Sanctuary. *Bulletin of Marine Science* 66(3):721–728.
- Friedlander, A. M., and E. E. DeMartini. 2002. Contrasts in density, size, and biomass of reef fishes between the northwestern and the main Hawaiian Islands: The effects of fishing down apex predators. *Marine Ecology Progress Series* 230:253–264.
- Friedlander, A., J. Sladek Nowlis, J. A. Sanchez, R. Appeldoorn, P. Usseglio, C. McCormick, S. Bejarano, and A. Mitchell-Chui. 2003a. Designing effective marine protected areas in Seaflower Biosphere Reserve, Colombia, based on biological and sociological information. *Conservation Biology*. 17:1–16.
- Friedlander, A. M., E. K. Brown, P. L. Jokiel, W. R. Smith, and K. S. Rodgers. 2003b. Effects of habitat, wave exposure, and marine protected area status on coral reef fish assemblages in the Hawaiian archipelago. *Coral Reefs* 22: 291–305.
- Friedlander, A. M., R. C. DeFelice, J. D. Parrish, and J. L. Frederick. 1997. *Habitat Resources and Recreational Fish Populations at Hanalei Bay, Kauai*. Final report of the Hawaii Cooperative Fishery Research Unit to the State of Hawaii. Honolulu, HI: Department of Land and Natural Resources, Division of Aquatic Resources. 320 pp.
- Gilpin, M., and M. E. Soulé. 1986. Minimum viable populations: Processes, of species extinction. In Soulé, M. E., ed. *Conservation Biology: The Science of Scarcity and Diversity*, 19–34. Sunderland, MA: Sinauer.
- Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management: Foundation and current use. *Canadian Special Publications in Fisheries and Aquatic Sciences* 120: 25–34.
- Guenette, S., and T. J. Pitcher 1999. An age-structured model showing the benefits of marine reserves in controlling overexploitation. *Fisheries Research* 39:295–303.
- Halpern, B. 2003. The impact of marine reserves: Do reserves work and does reserve size matter? *Ecological Applications* 13(1, suppl):S117–S137.
- Harding, D., J. H. Nicholas, and D. S. Tungate. 1978. The spawning of plaice (*Pleuronectes platessa* L.) in the Southern North Sea and English Channel. *Rapports et Procès-Verbaux des Réunions Conseil International pour l'exploration de la Mer* 172:102–113.
- Hockey, P. A. R., and G. M. Branch. 1997. Criteria, objectives and methodology for evaluating marine protected areas in South Africa. *South African Journal of Marine Science* 18:369–383.
- Holland, K. N., J. D. Peterson, C. G. Lowe, and B. M. Wetherbee. 1993. Movements, distribution and growth rates of the white goatfish *Mulloidies flavolineatus* in a fisheries conservation zone. *Bulletin of Marine Science* 52(3):982–992.
- Holland, K. N., C. G. Lowe, and B. M. Wetherbee. 1996. Movements and dispersal patterns of blue trevally (*Cranx melampygus*) in a fisheries conservation zone. *Fisheries Research* 25:279–292.
- Hyrenbach, K. D., K. A. Forney, and P. K. Dayton. 2000. Marine protected areas and ocean basin management [Viewpoint]. *Aquatic Conservation: Marine and Freshwater Ecosystems* 10:437–458.
- Jackson J. B. C., M. X. Kirby, W. H. Berger, K. A. Bjorndal, L. W. Botsford, B. J. Bourque, R. H. Bradbury, R. Coke, J. Erlandson, J. A. Estes, T. P. Hughes, S. Kidwell, C. B. Lange, H. S.

- Lenihan, J. M., Pandolfi, C. H., Peterson, R. S., Steneck, M. J., Tegner, and R. R. Warner. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629–638.
- Jenkins, G. P., K. P. Black, and M. J. Keough. 1999. The role of passive transport and the influence of vertical migration on the presettlement distribution of a temperate, demersal fish: Numerical model predictions compared with field sampling. *Marine Ecology Progress Series* 184:259–271.
- Johannes, R. E. 1978. Traditional marine conservation methods in Oceania and their demise. *Annual Reviews in Ecology and Systematics* 9:349–364.
- . 1997. Traditional coral-reef fisheries management. In Birkeland, C., ed. *Life and Death of Coral Reefs*, 380–385. New York: Chapman and Hall.
- Johnson, D. R., Funicelli, N. A., and Bohnsack, J. A. 1999. Effectiveness of an existing estuarine no-take fish sanctuary within the Kennedy Space Center, Florida. *North American Journal of Fisheries Management* 19:436–453.
- Katz, C. H., J. S. Cobb, and M. Spaulding 1994. Larval behavior, hydrodynamic transport, and potential offshore-to-inshore recruitment in the American lobster *Homarus americanus*. *Marine Ecology Progress Series* 103:265–273.
- Lacson, J. M. 1992. Minimal genetic variation among samples of six species of coral reef fishes collected at La Parguera, Puerto Rico, and Discovery Bay, Jamaica. *Marine Biology* 112:327–331.
- Levitan, D. R. 1991. Influence of body size and population density on fertilization success and reproductive output in a free-spawning invertebrate. *Biological Bulletin* 181:261–268.
- Love, M. 1996. *Probably More Than You Ever Wanted to Know about West Coast Fishes*. Santa Barbara, CA: Really Big Press.
- Mangel, M. 1998. No-take areas for sustainability of harvested species and a conservation invariant for marine reserves. *Ecology Letters* 1:87–90.
- Meyer, C. G. 2003. *An Empirical Evaluation of the Design and Function of a Small Marine Reserve (Waikiki Marine Life Conservation District)*. Ph.D. diss., Manoa, HI: University of Hawaii.
- Meyer, C. G., and K. N. Holland. 2001. A kayak method for tracking fish in very shallow habitats. In J. R. Sibert and J. L. Nielsen, eds. *Electronic Tagging and Tracking in Marine Fisheries*, 289–296. Dordrecht: Kluwer Academic Publishers.
- Meyer, C. G., K. N. Holland, B. M. Wetherbee, and C. G. Lowe. 2000. Movement patterns, habitat utilization, home range and site fidelity of whitesaddle goatfish, *Parupeneus porphyreus*, in a marine reserve. *Environ. Biol. Fish.* 59:235–242.
- Murawski, S. A., R. Brown, H.-L. Lai, P. J. Rago, L. Hendrickson. 2000. Large-scale closed areas as a fishery-management tool in temperate marine systems: The Georges Bank experience. *Bulletin of Marine Science* 66(3): 775–798.
- Murray, S. N., R. F. Ambrose, J. A. Bohnsack, L. W. Botsford, M. H. Carr, G. E. Davis, P. K. Dayton, D. Gotshall, D. R. Gunderson, M. A. Hixon, J. Lubchenco, M. Mangel, A. MacCall, D. A., McArdle, J. C. Ogden, J. Roughgarden, R. M. Starr, M. J. Tegner, and M. M. Yoklavich. 1999. No-take reserve networks: Protection for fishery populations and marine ecosystems. *Fisheries* 24(11):11–25.
- Myers, R. A., and G. Mertz. 1998. The limits of exploitation: A precautionary approach. *Ecological Applications* 8:S165–S169.
- Myers, R. A., and B. Worm. 2003. Rapid worldwide depletion of predatory fish communities. *Nature* 423:280–283.
- National Marine Fisheries Service (NMFS). 2001. *Report to Congress: Status of the Fisheries of the United States*. Silver Spring, MD: U.S. Department of Commerce.

- National Research Council (NRC). 2001. *Marine Protected Areas: Tools for Sustaining Ocean Ecosystems*. Washington, DC: National Academy Press.
- Noss, R. F. 1987. Corridors in real landscapes: A reply to Simberloff and Cox. *Conservation Biology* 1:159–164.
- Ogden, J. C. 1988. The influence of adjacent systems on the structure and function of coral reefs. *Proceedings of the 6th International Coral Reef Symposium* 1:123–129.
- Ogden, J. C., and P. R. Ehrlich. 1977. The behavior of heterotypic resting schools of juvenile grunts (Pomadasyidae). *Marine Biology* 42:273–280.
- Olson, R. R., and R. McPherson. 1987. Potential vs. realized larval dispersal: Fish predation on larvae of the ascidian *Lissoclinum patella* (Gotschaldt). *Journal of Experimental Marine Biology and Ecology* 110:245–256.
- Palumbi, S. 2003. Population genetics, demographic connectivity, and the design of marine reserves. *Ecological Applications* 13(1, suppl):S146–S158.
- Pickett, S. T. A., R. S. Ostfeld, M. Shachak, and G. E. Likens, eds. 1997. *The Ecological Basis of Conservation: Heterogeneity, Ecosystems, and Biodiversity*. New York: Chapman and Hall.
- Pinnegar, J. K., N. V. C. Polunin, P. Francour, F. Badalamenti, R. Chemello, M.-L. Harmelin-Vivien, B. Hereu, M. Milazzo, M. Zabala, G. D'Anna, and C. Pipitone. 2000. Trophic cascades in benthic marine ecosystems: Lessons for fisheries and protected-area management. *Environmental Conservation* 27:179–200.
- Plan Development Team (PDT). 1990. *The Potential of Marine Fishery Reserves for Reef Fish Management in the U.S. Southern Atlantic*. NOAA Technical Memorandum NMFS-SEFC-261. Silver Spring, MD: U.S. Department of Commerce.
- Proulx, E. 1998. The role of law enforcement in the creation and management of marine reserves. In Yoklavich, M. M., ed. *Marine Harvest Refugia for West Coast Rockfish: A Workshop*, 74–77. NOAA Technical Memorandum NOAA-TM-NMFS-SWFSC-255. Silver Spring, MD: U.S. Department of Commerce.
- Rakitin, A., and D. L. Kramer. 1996. Effect of a marine reserve on the distribution of coral reef fishes in Barbados. *Marine Ecology Progress Series* 131:97–113.
- Reed, J. K. 2002. Deep-water *Oculina* coral reefs of Florida: Biology, impacts, and management. *Hydrobiologia* 471:43–55.
- Roberts, C. M. 1996. Settlement and beyond: Population regulation and community structure of reef fishes. In Polunin, N. V. C., and C. M. Roberts. *Reef Fisheries*, 85–112. London: Chapman and Hall.
- . 1997. Connectivity and management of Caribbean coral reefs. *Science* 278: 1454–1457.
- . 1998. Sources, sinks and the design of marine reserve networks. *Fisheries* 23:16–19.
- Roberts, C. M., and J. P. Hawkins 1997. How small can a marine reserve be and still be effective? *Coral Reefs* 16:150.
- Roberts, C. M., G. Branch, R. H. Bustamente, J. C. Castilla, J. Dugan, B. S. Halpern, K. P. Lafferty, H. Leslie, J. Lubchenco, D. McArdle, M. Ruckleshaus, and R. R. Warner. 2003a. Application of ecological criteria in selecting marine reserves and developing reserve networks. *Ecological Applications* 13(1, suppl): 5215–5228.
- Roberts, C. M., S. Andelman, G. Branch, R. H. Bustamente, J. C. Castilla, J. Dugan, B. S. Halpern, K. D. Lafferty, H. Leslie, J. Lubchenco, D. McArdle, H. P. Possingham, M. Ruckleshaus, and R. R. Warner. 2003b. Ecological criteria for evaluating candidate sites for marine reserves. *Ecological Applications* 13(1, suppl): 5199–5215.

- Rosenberg, A., T. E. Bigford, S. Leathery, R. L. Hill, and K. Bickers. 2000. Ecosystem approaches to fishery management through essential fish habitat. *Bulletin of Marine Science* 66(3):535–542.
- Russ, G. R., and A. C. Alcala. 1996. Do marine reserves export adult fish biomass? Evidence from Apo Island, central Philippines. *Marine Ecology Progress Series* 132:1–9.
- . 1999. Management histories of Sumilon and Apo marine reserves, Philippines, and their influence on national marine resource policy. *Coral Reefs* 18:307–319.
- Sadovy, Y. M. 1993. The Nassau grouper, endangered or just unlucky? *Reef Encounters* 13:1–12.
- Sala, E., O. Aburto-Oropeza, G. Paredes, I. Parra, J. C. Barrera, and P. K. Dayton. 2002. A general model for designing networks of marine reserves. *Science* 298:1991–1993.
- Simberloff, D., and J. Cox. 1987. Consequences and costs of conservation corridors. *Conservation Biology* 1:63–71.
- Sladek Nowlis, J. 2000. Short- and long-term effects of three fishery-management tools on depleted fisheries. *Bulletin of Marine Science* 66(3): 651–662.
- Sladek Nowlis, J., and B. Bollerman. 2002. Methods for increasing the likelihood of restoring and maintaining productive fisheries. *Bulletin of Marine Science* 70:715–731.
- Sladek Nowlis, J., and A. Friedlander. 2004. Marine reserve function and design for fisheries management. In Norse, E. A., and L. B. Crowder, eds. *Marine Conservation Biology: The Science of Maintaining the Sea's Biodiversity*. Washington, DC: Island Press.
- Sladek Nowlis, J., and C. M. Roberts. 1995. Quantitative and qualitative predictions of optimal fishery reserve design. In Roberts, C., and W. J. Ballantine, C. D. Buxton, P. Dayton, L. B. Crowder, W. Milton, M. K. Orbach, D. Pauly, J. Trexler, and C. J. Walters. *Review of the Use of Marine Fishery Reserves in the U.S. Southeastern Atlantic*, B-12. NOAA Technical Memorandum, NMFS-SEFSC-376. Miami, FL: U.S. Department of Commerce.
- . 1997. You can have your fish and eat it, too: Theoretical approaches to marine reserve design. *Proceedings of the 8th International Coral Reef Symposium* 2:1907–1910.
- . 1999. Fisheries benefits and optimal design of marine reserves. *Fishery Bulletin* 97:604–616.
- Slatkin, M. 1987. Isolation by distance in equilibrium and nonequilibrium populations. *Evolution* 47:264–279.
- Tegner, M. J. 1992. Brood stock transplants as an approach to abalone stock enhancement. In Shepherd, S. A., M. J. Tegner, and S. A. Guzman del Proo. *Abalone of the World: Biology, Fisheries and Culture*, 461–473. Oxford: Blackwell Scientific.
- Thompson, H. 1943. *A Biological and Economic Study of Cod (Gadus callarias L.)*. Research Bulletin 14. St. John's, Newfoundland: Department of Natural Resources.
- Wallace, S. S. 1999. Evaluating the effects of three forms of marine reserve on northern abalone populations in British Columbia, Canada. *Conservation Biology* 13:882–887.
- Watling, L., and E. A. Norse. 1998. Disturbance of the seabed by mobile fishing gear: A comparison to forest clearcutting. *Conservation Biology* 12:1180–1197.
- Wolanski E., and J. Sarsenski. 1997. Larvae dispersion in coral reefs and mangroves. *American Scientist* 85:236–243.