chapter 19

The Ecology of Marine Protected Areas

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Marine ecology has long since ceased being a spectator sport. The advent of experimental manipulations as a paradigm for ecological investigations on rocky shores established an approach that was much more interactive than the prior mapping surveys of distribution and abundance (Paine 1984). This approach allowed complex interactions to be understood through the sometimes intricate experiments on community composition. Recently, an additional type of involvement has become more common, in which information from ecological studies is used to provide insight to managers of coastal zone areas. The involvement of ecology with environmental policy has come on the heels of increasing revelations that coastal and open ocean habitats are in biological decline and are faced with unprecedented threats (Lubchenco 1998).

In particular, marine fisheries have collapsed all over the world, and at least half of the world's fisheries stocks are now listed as either overfished or fished at capacity (Botsford et al. 1997). The collapse of cod stocks in Atlantic Canada (Hutchings 1995; Walters and Maguire 1996; Myers et al. 1997) and then New England (Ruth and Lindholm 1996), the reduction of multispecies reef fisheries in the Caribbean to nonsubsistence levels (Roberts 1995), the rapid decline in California abalone (Tegner 1993) and sea urchin populations (Tegner 1989), and the serial overfishing of fish communities around the world (Pauly et al. 1998) highlight the serious nature of fisheries problems. In addition, coastal pollution (Paine et al. 1996), overcollecting by people (Castilla 1999), loss of habitat from development (Ruckelshaus and Hayes 1998), invasion of weedy, alien species (Carlton and Geller 1993), and introduction of new marine diseases (Harvell et al. 1999) have combined to threaten the growth or even maintenance of many of the world's coral reefs, wetlands, estuaries, mangroves, seagrass beds, and rocky shores (see Ruckelshaus and Hayes 1998 for review).

These threats have changed the economic and political landscape in which marine ecology is done, and they have demanded crucial shifts in the focus of basic ecological research (Lubchenco 1998). Major developments in marine ecology in the past decade have included a focus on marine invasions (Carlton and Geller 1993) and the realization that the synergy between environmental stress, physiological stress, and genetic variation can determine patterns of mass marine mortality (Rowan et al. 1997). In addition, the realization that weak interactions in trophic webs can play a major community structuring role (Paine 1992) and debates about the importance of biological diversity in ecosystem function (Tilman and Downing 1994) have galvanized attention to many of the "minor" species in marine communities previously overlooked in experimental studies.

These two themes, the panic caused by fishery collapse, and the focus on whole communities as ecological units come together in a debate about the utility of one particular method of marine coastal management—the creation of marine protected areas (MPAs). MPAs have been used effectively for decades, but the acceleration of the decline of marine coastal zones has highlighted their potential to address both the problems of fisheries enhancement and the maintenance of marine biological diversity. Few developments in marine ecology have excited as much hope or generated as much furor as have MPAs. The proposal to establish MPAs has resulted in fisheries officials being hung in effigy by their friends, the firing of scientists from local Fisheries Management Commissions, and the patrolling of reserve boundaries

by armed guards. MPAs have also been the source of deep-seated community involvement and considerable local and regional success.

The scientific basis for MPA implementation and monitoring has received a great deal of recent attention, as coastal management officials struggle to understand the potential of MPAs to reduce or reverse the decline of marine communities. The study of MPAs as a management tool has allowed some of the best lessons about marine ecology to be applied to great effect, but has also highlighted some of the crucial areas of marine ecological research that remain weakly understood. This chapter will review definitions of MPAs and discuss what is currently known about how well they function. Connectivity between MPAs and the rest of marine ecosystems emerges from this exercise as a crucial yet poorly understood aspect of MPA (or ecosystem) function. Another critical need is to understand ecological interactions within MPAs so that the impact of reducing human intervention in natural marine communities can be better predicted.

If the huge attention to basic marine research has an applied and practical benefit, one of the primary outlets for that benefit has been in understanding the implications and function of marine reserves in ecosystem maintenance, biodiversity enhancement, and fisheries production. This is not ecology as spectator sport, but as mud wrestling in which the outcome matters a great deal.

Different Types of MPAs

Some of the first summaries of marine protected areas as management tools emphasized that different MPAs might be very different from one another, and that the management goals of a particular MPA were intrinsic to their implementation and their success (Agardy 1994). Some MPAs are based on the principle that no extraction of natural resources is allowed within their boundaries. Other, still more restricted definitions, allow no access to the MPA by the general public, but restrict entry to managers and monitors. Other definitions allow MPA designation for any area in which some kind of marine resource use is restricted. For example, no-trawl zones in which bottom dredging is excluded might allow other kinds of commercial or recreational fishing (Armstrong et al. 1993), but still be considered MPAs.

Among the many different "species" of MPAs, there are three broad kinds whose underlying objectives are quite different: (1) fisheries enhancement MPAs focus on protecting local populations as a management tool to augment or stabilize regional fisheries yields; (2) ecosystem diversity MPAs focus on the preservation and maintenance of broad-scale marine biological diversity; and 3) special-feature MPAs focus on preservation of a particular locality because of its cultural importance or its value to a particularly vulnerable life history stage.

Fisheries reserves tend to focus on single-species restrictions or no-take zones in a small area in order to enhance fisheries yields over a much larger area. By contrast, MPAs designed to preserve or augment ecosystem diversity generally require no-take regulations that prohibit any extractive use of the natural resources in the area. These MPAs frequently benefit a wide range of pelagic and benthic species. In some cases, however, no-take reserves appear misnamed because they may be open to particular exploitation. No-take MPAs in the Florida Keys Marine Sanctuary, for example, are open for throw net fishing for baitfish (Florida Keys National Marine Sanctuary Final Management Plan: An overview, p. 16, NOAA, Washington, DC, 1998).

The broad definition of a MPA, adopted by the International Union of Concerned Scientists states that an MPA is "any area of intertidal or subtidal terrain, together with its overlying waters and associated flora, fauna, historical and cultural features, which has been preserved by legislation or other effective means to protect all or part of the enclosed environment" (Kelleher and Recchia 1998). Although this definition may seem too broad, the IUCN also established six categories of MPAs that begin to reflect the diversity of practical uses and ecological settings that MPAs include (Table 19.1).

Biodiversity reserves—those designed primarily to enhance coastal ecosystem stability and multispecies interactions—are most stringently defined in categories I and II. Categories III, V, and VI also have ecosystem protection as a major goal. They differ largely in access to the general public and the degree of extraction allowed. Fishery reserves are largely described in Category IV, whose major objective is to provide an additional management tool for enhancement of a particular target species.

Frequently, an MPA might play more than one role. In particular, fisheries enhancement, the preservation of ecosystem diversity, and nursery ground protection often can go hand in hand. But such coordination of goals is not always possible unless this coordination occurs during the design and implementation of the reserve. For example, a management goal to enhance a single species stock—like New England cod—may require an MPA closed only to cod fishing. In 1994, several areas of Georges Bank off Cape Cod were closed to cod trawling. By 1998, cod had not yet recovered in this area, but the MPAs were densely populated by ocean scallops (Murawski 1999), whose harvest was vociferously requested by local fishers. The success of the cod closure is not yet known, but in this case single-species protection had a secondary effect of protecting the seafloor from trawling damage (Dayton et al. 1995; Watling and Norse 1998), and this physical protection had a wider ecosystem effect. Should these newly protected seafloors be saved from exploitation until cod begin to recover? Or should the scallop resources be snapped up by local fishers who are suffering under the economic collapse of the overfished cod? In the Philippines, local fishers eventually overwhelmed and destroyed local no-take zones in which fish production had increased dramatically (Russ and Alcala 1989). In New England, harvest of the scallops began on June 15, 1999.

These examples point out that MPAs are generally instituted to solve particular, local problems. Because each local

TABLE 19.1 Categories of Marine Protected Areas Established by the IUCN (Kelleher and Recchia 1998)

CATEGORY I.	**Strict Nature Reserve/Wilderness Area: protected area managed mainly for science or wilderness protection**
CATEGORY Ia.	**Strict Nature Reserve: protected area managed mainly for science—definition**: Area of land and/or sea possessing some outstanding or representative ecosystems, geological or physiological features, and/or species, available primarily for scientific research and/or environmental monitoring.
CATEGORY Ib.	**Wilderness Area: protected area managed mainly for wilderness protection—definition:** Large area of unmodified or slightly modified land, and/or sea, retaining its natural character and influence, without permanent or significant habitation, protected and managed so as to preserve its natural condition.
CATEGORY II.	**National Park: protected area managed mainly for ecosystem protection and recreation—definition:** Natural area of land and/or sea, designated to (a) protect the ecological integrity of one or more ecosystems for present and future generations, (b) exclude exploitation or occupation inimical to the purposes of designation of the area, and (c) provide a foundation for spiritual, scientific, educational, recreational, and visitor opportunities, all of which must be environmentally and culturally compatible.
CATEGORY III.	**Natural Monument: protected area managed mainly for conservation of specific natural features—definition:** Area containing one, or more, specific natural or natural/cultural features which is of outstanding or unique value because of its inherent rarity, representative. or aesthetic qualities or cultural significance.
CATEGORY IV.	**Habitat/Species Management Area: protected area managed mainly for conservation through management intervention—definition:** Area of land and/or sea subject to active intervention for management purposes so as to ensure the maintenance of habitats and/or meet the requirements of specific species.
CATEGORY V.	**Protected Landscape/Seascape: protected area managed mainly for landscape/seascape conservation and recreation—definition:** Area of land, with coast and sea as appropriate, where the interaction of people and nature over time has produced an area of distinct character with significant aesthetic, ecological, and/or cultural value, and often with high biological diversity. Safeguarding the integrity of this traditional interaction is vital to the protection, maintenance, and evolution of such an area.
CATEGORY VI.	**Managed Resource Protected Area: protected area managed mainly for the sustainable use of natural ecosystems—definition:** Area containing predominantly unmodified natural systems, managed to ensure long-term protection and maintenance of biological diversity, while providing at the same time a sustainable flow of natural products and services to meet community needs.

problem is unique and because the design of MPAs is linked tightly to their objectives, there are so many different types of MPAs that their categorization is often complex. Sometimes this complexity is reflected in a mosaic of different use patterns, as in the Great Barrier Reef Marine Park, a large protected area with different types of protection in different areas. Some areas in the Park are no-take reserves designed to enhance ecosystem diversity, and these are found scattered inside the larger park, where extractive uses are allowed. The major lesson from these complex zoning mosaics is that the terminology of MPAs should not be allowed to interfere with understanding of the goals and utility of any particular MPA example.

Simplified Taxonomy of MPAs

There are many different goals for MPAs, and as a consequence, MPAs are implemented in many different ways. Unless these differences can be categorized, there is a danger that every new MPA will seem like a unique case that cannot benefit from understanding gained from prior experiences. Broadly speaking, MPAs fall into the same three goal categories as discussed above—those that focus on fisheries, those that focus on ecosystem diversity, and those designed around a particular, crucial geographic area. Within these three broad goals, it is possible to identify two other major criteria by which many reserves differ. These criteria are whether the MPA is expected to have only a local effect within its boundaries, or a wider impact on the ecosystem in which it is found (Figure 19.1). These goals are fundamentally different in that the first requires local effects to be visible within the boundaries of the reserve, whereas the second requires export of a reserve effect from the boundaries of the MPA to the adjoining region. In practice, many fisheries reserves are designed to have regional effects, whereas many biodiversity reserves focus on protecting species in a defined area.

Reserve type	Scale of desired effect
Ecosystem diversity	Local → Regional
Fisheries management	Local → Regional
Special feature	Local → Regional

Figure 19.1 A simplified taxonomy of marine protected areas. Major goals of MPAs are divided into enhancing ecosystem diversity, fisheries enhancement of a single species or a few target taxa, or protection of special areas important to particular life history stages. Each of these types of reserves might be designed to augment an ecosystem at only a local scale (as in a marine park designed for local tourism) or on a regional scale (as in a fishing reserve meant to export products). Other, more comprehensive, taxonomies exist (see text), but the above categories capture most of the biological differences inherent in designing, monitoring, and evaluating MPAs.

Do Marine Reserves Work?

Understanding if marine reserves work requires two levels of analysis. The first requires that particular reserves be evaluated in the context of the goals inherent in their establishment. The second level of analysis should be a broad comparison across reserves in different ecosystems to understand if reserves in general have a local or regional effect. Each reserve is a unique area, often established because of its topographic, biodiversity, or cultural attributes. It is thus difficult to directly assess the effectiveness of reserve status in the strict sense, because each reserve is an unreplicated area. In addition, comparison of reserve to nonreserve areas is often done without the spatial and temporal controls that have become the chief analytical tool of experimental ecology (Paine 1984; Osenberg et al. 1994). These failures of the real world to correspond to experimental niceties are serious cause for caution in interpreting the effect of any single reserve. However, replication across oceans, habitat types, taxa of interest, latitude, investigator, and experimental design may allow broad patterns to emerge despite uncertainty about any particular MPA.

Fisheries Reserves with Local Effects

Many MPAs in which fishing has been eliminated or dramatically curtailed have been reported to have local effects on species diversity or abundance. In particular, reduction of fishing pressure tends to have a dramatic effect on the numbers and size of exploited fish (Roberts 1995). Recruitment of these fish is thought to be derived from larvae imported from elsewhere in the ecosystem. When such recruitment is strong, fish stocks can increase within only a few years of the creation of the reserve. Such patterns have been observed frequently in temperate and tropical reef habitats (Table 19.2), where fish tend to be fairly sedentary as adults, and populations can be defined on a local scale.

In several small Caribbean preserves Polunin and Roberts (1993), recorded increases in abundance or biomass of about one-third of the species of demersal fish on protected reefs. Although most species did not increase in abundance, many of these were initially rare. Summed across the data sets, there were 18 recorded increases of abundance compared to nonreserve areas, and only one decrease in abundance. There were 20 increases in biomass or length and no instances of declines inside versus outside the reserve (Figure 19.2).

A similar study in South Africa (Bennett and Attwood 1991) showed a temporal increase of fish abundance (estimated by catch per unit effort methods) following closure of fishing in the De Hoop Nature Reserve. Abundances increased until they were similar to those in a nearby private fishing reserve, suggesting that protection against fishing led to increased fish densities over the six years of the study. Similarly, Kenyan reefs protected for 25 years showed dramatic differences in fish numbers, size, and density (McClanahan 1994). After establishment of a new Kenyan marine reserve in 1991, the biomass of fish inside the reserve increased fivefold in three years. A nearby site at which traditional net, trap, and line fishing was allowed showed no significant increase in the same period (McClanahan and Kaunda-Arara 1996).

These trends are apparent in many other studies of marine protected areas: heavily fished species often increase in abundance or size. Cole et al. (1990) found larger abundances of lobster, snapper, and red moki inside reserves in New Zealand. Both fish species increased with time after reserve establishment, although control sites were not examined over the same time frame. In addition, snappers were larger inside than outside the reserve. Goatfish appeared to be more abundant outside the reserve than inside, although Cole et al. (1990) record no fishing pressure on this species in these areas. As in some of the Caribbean studies described previously, not all target species responded to protection: eight other species

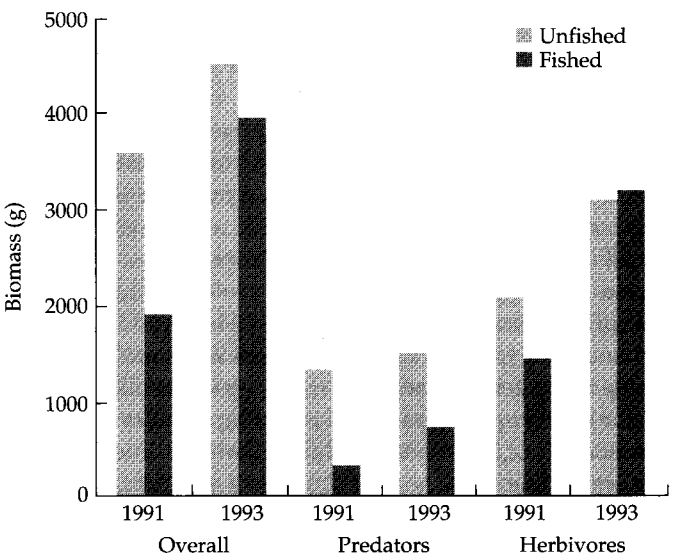

Figure 19.2 Changes in biomass in the Saba Island marine reserve between 1991 and 1993 for predatory fish (groupers, grunts, and snappers), herbivores (parrotfish and surgeonfish), and all five families combined. (After Roberts 1995.)

TABLE 19.2 Some examples of fisheries enhancement MPAs designed for local effect on abundance or biomass of fish or invertebrates. Establishment of these reserves has generally been by legislation, although two examples are given of reserves established on the basis of community management of local resources.

Area	Positive effect?[a]	Control	Size	Time frame	Target taxa	Reference
Mediterranean	Y	Spatial	1 km	9 yr.	Fish	Bell 1983
Mediterranean	Y***	Spatial	<1 km	6 yr.	Fish	Garcia-Rubies and Zabala 1990
Philippines	Y	Spatial		10 yr.	Fish	Russ 1985
Australia	Y	Spatial			Fish	Ayling and Ayling 1986
Kenya	Y***	Spatial			Fish	Samoilys 1988
Philippines	Y***	Temporal		3 yr.	Fish	Alcala 1988
Philippines	Y*	Spatial/temporal		3 yr.	Fish	Russ and Alcala 1989
Africa	Y*	Spatial			Fish	Buxton and Smale 1989
Florida Keys	Y**	Temporal		2 yr.	Fish	Clark et al. 1989
Kenya reefs	Y***	Spatial			Fish	McClanahan and Shafir 1990
Caribbean	Y**	Spatial	1 km	4 yr.	Fish	Polunin and Roberts 1993
Belize	Y**	Spatial	4 km	4 yr.	Fish Conch Lobsters	Polunin and Roberts 1993
Africa	Y***	Spatial/temporal	46 km	2–5 yr.	Fish	Bennett and Attwood 1991
Florida Keys	Y***	Spatial	>100 km	20 yr.	Fish	Bohnsack 1982
Red Sea	Y***	Spatial		15 yr.	Fish	Roberts and Polunin 1993
Chile	Y*	Spatial/temporal	1.5 km	3 yr.	Snails	Duran and Castilla 1989
Chile	Y*	Spatial/temporal	1.5 km	3 yr.	Limpets	Oliva and Castilla 1986
Japan	Y	Temporal			Crabs	Yamasaki and Kuwahara 1990
Kenya reefs	Y*	Spatial/temporal		25 yr.	Fish	McClanahan 1994
Kenya reefs	Y*	Spatial/temporal		1–3 yr.	Fish	McClanahan 1995
Kenya reefs	Y	Spatial		25 yr.	Snails	McClanahan 1989
Florida Keys	Y	Spatial		2 yr.	Shrimp	Klima et al. 1986
Caribbean	Y**	Spatial		1–3 yr.	Urchins	Smith and Berkes 1991
Puget Sound	Y**	Spatial	1–2 km	4–27 yr.	Fish	Palsson and Pacunski 1995
Central CA	Y	Spatial	1–6 km	4–37 yr.	Fish	Paddock 1996
Florida Keys	Y	Spatial			Lobsters	Davis 1977
Caribbean	Y	Spatial			Conch	Weil and Laughlin 1984
Palau	Y	Spatial			Snails	Hesilnga et al. 1984
New Jersey	Y	Spatial			Clams	McCay 1988
Australia	Y	Spatial			Abalone	Shepherd 1990
COMMUNITY-BASED PROTECTION:						
Caribbean	Y**	Spatial	Traditional		Urchins	Smith and Berkes 1991
Fiji	Y**	Spatial	Traditional		Fish	Jennings and Polunin 1997

[a]Asterisks represent statistical power (***$p < 0.001$, **$p < 0.01$, * $p < 0.05$)

of fish and one species of sea urchin showed no significant change between reserve and nonreserve sites.

Fisheries reserves for invertebrates have been studied less often than for fish, but when a heavily exploited invertebrate species is protected from harvest, and when recruitment from outside the reserve can import larvae, then populations typically increase after protection (Table 19.2). Careful studies by Castilla and colleagues have shown such increases among three species of harvested intertidal gastropods after protection from human collection (Castilla and Duran 1985). Likewise, Keough et al. (1993) showed increases in size or abundance of four species of harvested intertidal molluscs

compared to protected areas in Australia. White spined sea urchins in St. Lucia are an order of magnitude more abundant in a harvesting reserve than outside, where there is no fishing management (Smith and Berkes 1991). In this case, community control of harvesting has also been shown to be effective. Areas in which the local urchins are harvested by a single village that controls access to the resource have maintained urchin densities similar to those in the reserve (Smith and Berkes 1991).

Ocean scallops increased dramatically on Georges Bank after areas were protected from trawling, although the purpose of this protection was actually to enhance cod stocks (Murawski 1999). Intertidal and subtidal gastropods have increased due to protection in temperate and tropical habitats (references in Dugan and Davis 1993). Heavily fished surf clams were more dense (and grew more slowly) in a no-dredging area (Weinberg 1998). Other invertebrates like urchins and clams have shown variable responses to temporary fishing reserves (Dugan and Davis 1993).

SUMMARY OF LOCAL FISHERIES MPAS. The number of MPAs monitored for local effects on fish density or abundance is growing rapidly, and there is more information about the impact of this type of MPA than any other. In general, biomass tends to increase more quickly than abundance in such reserves (Roberts 1995), but changes in size and number of heavily fished species when they are protected in reserves is very common (Table 19.2). Even small reserves (ca. 0.1 sq. km) appear to have a beneficial effect (Halpern et al., in press) if adults are fairly sedentary and recruitment of larvae from the rest of the ecosystem can supply settlers in the reserve.

Ecosystem Reserves with Local Effects

An ecosystem reserve with only local goals might be successfully implemented by protecting a small stretch of coastline. Although there are few reserves (especially in the United States) whose goals are the enhancement of overall marine diversity, no-take reserves established for fisheries management often have an impact on community composition and diversity. Study of fish diversity patterns inside reserves indicates that protection may have an effect on overall community richness, but that the major changes are in the species previously hunted. In Fiji, large piscivorous fish are much less abundant on more heavily fished reefs, but abundance and species richness of other fish is unaffected (Jennings and Polunin 1997). In the Mediterranean, the total number of fish species was 43 inside and 44 outside a fishing reserve in the northwest Mediterranean, although mean species richness per sampling station was significantly higher inside than outside the reserve (Garcia-Rubies and Zabala 1990). Cole et al. (1990) showed overall increases in fish diversity in MPAs in New Zealand, although the differences are slight (Figure 19.3). In Australia, small seagrass beds harbored fewer species than large ones, but a combination of several small seagrass beds had a higher total of species diversity than did a larger bed of equal area (McNeill and Fairweather 1993). Artificial beds had increased diversity after 10 weeks, but the diversity in several small artificial beds did not exceed that in a large artificial bed.

MPAs established to control physical disturbance caused by fishing methods like dredging or trawling often have important secondary effects on marine community structure. Trawling destroys the biological component of bottom topography (Watling and Norse 1998) and can result in mud/sand barrens that are distinctly different from normal seafloor communities. Dynamite fishing on coral reefs and dredging on oyster bars reduces spatial heterogeneity and collapses community diversity (Lenihan and Peterson 1998). MPAs set up to restrict trawling or other physically damaging fishing methods have resulted in changes in community composition that go far beyond the original fished species (Murawski 1999). Less-invasive methods can also have an impact: along temperate, exposed beaches in Uruguay, hunting for yellow clams negatively impacts abundance of other co-occurring bivalves (Defeo and De Alva 1995).

Such dramatic community-wide effects are not always documented, and ecosystem changes within reserves can be subtle. For example, mollusc community composition did not differ strongly in Kenyan reefs protected from fishing or collecting. McClanahan (1989) surveyed protected and unprotected reefs in Kenya for gastropod diversity. There were only a few clear changes in abundance in this study—densities were low for all species regardless of protected status, and differences among different reef types were larger than

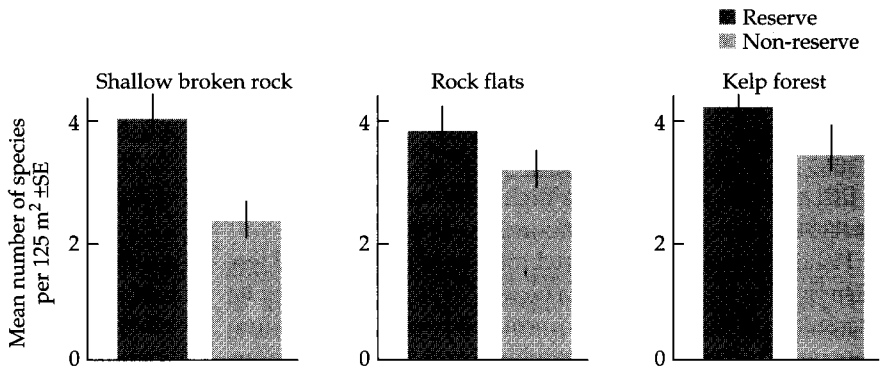

Figure 19.3 Average number of fish species counted within (darkly shaded) and outside (lightly shaded) marine reserves in New Zealand. Error bars are standard errors of the mean for three habitats. (After Cole et al. 1990.)

differences due to protection. Despite this difficulty, 12 of 15 commercially exploited species were more common on protected reefs (although only 5 were significantly so). By contrast only 7 of 15 nonexploited species were more abundant on protected reefs. Thus, fishing protection may have had an effect on molluscan communities, but the variation among reef sites for rare species makes this pattern difficult to demonstrate conclusively.

In the Florida Keys Marine Sanctuary, two years of protection from fishing has had an effect on harvested species, but not on overall abundance of live coral cover or gorgonians. Likewise, there were few significant increases of corals in the Saba Marine Park between 1991 and 1993 (Roberts et al. 1995). Such time frames are too short for responses from long-lived, slow-growing, poorly recruiting taxa like corals, seagrasses, and many sponges. Unfortunately, these taxa tend to provide the biological framework on which other highly diverse communities depend, and so recovery of these framework species is crucial to success of a biodiversity MPA. Indicator organisms with more appropriate life histories (e.g., amphipods, polychaetes, algae that recruit more heavily and grow more quickly) are rarely sampled in MPA studies, but would provide an important view of the changing communities within MPAs.

The Las Cruces Marine Reserve in the intertidal of Chile was designed to test the impact of human predation on ecological patterns among intertidal space occupiers. Along a 1.4 km stretch of coastline, complete fencing and armed guards prevented access by local fishers, with the startling result that the dominant space occupiers along the shore shifted within a period of only a few years from mussels to barnacles and macroalgae (Castilla and Duran 1985; Oliva and Castilla 1986; Castilla and Bustamante 1989). The abundance of a dominant intertidal invertebrate predator, *Concholepas concholepas*, increased by a factor of 2–3, causing the decline of its preferred prey (intertidal mussels) and replacement with a "normal" intertidal community of barnacles and algae that is rarely seen in Chile because of widespread *Concholepas* overharvesting (Castilla and Duran 1985).

In another study of the community level effects of MPAs, McClanahan and coworkers (McClanahan 1994, 1995; McClanahan and Kaunda-Arara 1996) showed that protection from fishing led to an increase in predation on urchins by triggerfish and a reduction in sea urchin overpopulation (McClanahan and Kaunda-Arara 1996). Protection from fishing also led to changes in algal density and in some cases to changes in diversity. The dramatic changes in community structure seen in these reserves underscore the role MPAs can play in diversity management and show how ecological interactions within reserves must be understood as a major part of reserve design strategy.

SUMMARY OF LOCAL BIODIVERSITY RESERVES. Protection of marine communities from exploitation almost always results in dramatic changes in patterns of body size and abundance, and these changes often have a profound effect on community composition. Even within the boundaries of small reserves, community composition can be greatly altered by reduced exploitation. However, the relationship between protection and diversity is complex. In some cases, species richness increases inside reserves. In others, the major impact of reserve status is a dramatic shift in which species are present, without necessarily an increase in overall species numbers. Species with strong recruitment, fast generations, and large growth rates are most likely to show increases in short periods of time after reserve establishment. More slowly growing species or those with low recruitment take much longer to show a reserve effect. Although there is ample evidence that reserve status has a marked impact on overall community composition, there is relatively little attention given to noncommercial species within biodiversity reserves and little understanding of the complicated ecological cascades produced by major shifts in exploitation.

Fisheries Reserves with Regional Effects

Few fisheries reserves are established with purely local goals. Usually, a fisheries closure or a protected area is established to augment overall populations and to increase (or stabilize) fisheries yields. In general, regional effects of fisheries reserves are more difficult to demonstrate than local effects. For example, the success of MPAs in increasing fish biomass and abundance (Table 19.2) is due largely to studies of populations within reserves. Fewer studies have examined the impact of an MPA on surrounding areas where fishing is allowed.

McClanahan and Kaunda-Arara (1996) reported that catch-per-unit-effort (CPUE) just outside a newly established Kenyan reef MPA increased for all eight categories of fished species. Traps were moved by local fishers within a year so that most were clustered within 250 m of the MPA boundary. A fishing beach further away from the park had lower CPUE for seven of eight fishing categories, and McClanahan and Kaunda-Arara (1996) suggested that intense edge-fishing was enough to collect all the export from the MPA. Russ and Alcala (1989) studied fishing yields in the Philippines before and after the collapse of the Sumilon Island reserve. They report that fishing was 25% more productive when the reserve was in place than after locals destroyed the reserve by fishing within it. This is indirect evidence that the MPA increased fishing yields, but many more detailed studies need to be done before the overall benefit of MPAs to fishing yields are as firmly established as the local benefits of reserves (Table 19.2).

Theoretical treatments of MPA regional effects suggest that under circumstances where fishing pressure is high, MPAs can increase regional fishing yields. Hastings and Botsford (1999) showed that MPAs provided the same degree of fishery management power as did control of fishing effort. Their model redistributed fishing effort from reserves to the rest of the fishery, thereby increasing fishing pressure outside of reserves. Increased yields require augmentation of regional fish supplies through a common larval pool connecting reserve and nonreserve populations.

DeMartini (1993) and Polacheck (1990) both showed that MPAs could increase fisheries yields under certain circumstances in which outside fishing pressure was high and transport or fish or larvae outside of the MPAs was likely. Low dispersal between MPA and the surrounding habitats severely limits the ability of an MPA to enhance productivity in the overall fishery, because extra eggs, larvae, or adults are trapped inside the protected area (DeMartini 1993). On the other extreme, infinite movement of adults from MPAs to surrounding, fished zones severely reduces their effectiveness at allowing local buildup of populations (for example, for small MPAs and very migratory adults; Armstrong et al. 1993). Moderate movement of adults can result in overall positive impact of MPAs on fishery production (Attwood and Bennett 1995). Thus, the theoretical treatments have all agreed that increased regional yields from MPAs occur over a set of biological parameters that depend largely on the movement of individuals into and out of reserves. For a particular MPA configuration, some species may respond, but others may not. Which species fall into these categories is a critical question for future research.

These theoretical treatments also emphasize that the value of fishery MPAs may not lie solely in their impact on fish biomass (Hastings and Botsford 1999). By providing a refuge for adult fish and a stockpile of large spawners that can produce many eggs and larvae, MPAs may help fisheries recover when other conventional fishery management schemes fail. For cod in the western Atlantic, large spawning aggregations have been rare after the collapse of these historically fished populations (Smedbol et al. 1998), and broad closures along the coast of New England are hoped to enhance the buildup of new spawning populations. If such populations already existed, protected by reserve "banks," commercial recovery might be much faster.

A second value of MPAs may be to reduce recruitment variation. Some fisheries species are characterized by complete recruitment failure for many years. The surf clam population (*Spisula spp.*) along the U.S. eastern seaboard is heavily harvested, but commercial take relies on the progeny from a single age class that recruited heavily in the late 1970s (Weinberg 1998). Similarly, in 1989, Jamieson et al. (1989) reported that there had been no substantial recruitment of the Dungeness crab (*Cancer magister*) near Tofino British Columbia since 1985. Large adult populations within MPAs may provide steady interannual sources for recruits of such commercially important species.

SUMMARY OF REGIONAL EFFECTS OF FISHERIES RESERVES. Fishery MPAs will function as an important management tool only if they contribute enough to regional ecosystems (in biomass or recruits) to make them worth the cost of restricting fishing. There is emerging evidence that this may be true, but at this time there are simply not enough powerful studies to allow us to understand the regional effects of MPAs on fisheries populations. The local effects of fishery MPAs are clear (see previous sections), so it is the connection between these local successes and regional ecosystem impact that is terribly unclear. Understanding connectivity in marine populations on a regional scale has long been a difficult challenge in marine ecology. Facing this challenge is now a critical priority in both basic and applied ecology.

Biodiversity Effects on a Regional Scale

Although most fishery MPAs are implemented in order for them to have a regional effect, many biodiversity reserves are designed to have effects only within the reserve. These local biodiversity reserves might be designed to enhance coral diversity for tourism or otherwise protect marine life at a single site. Ecosystem diversity reserves may need to be placed very carefully to have a regional effect. To preserve a substantial fraction of regional marine biological diversity, a series of reserves has been implemented for the coast of South Africa (Attwood et al. 1997). Each of these reserves may function separately to enhance the abundance of exploited taxa or overall species richness, but their placement in different biogeographic provinces allows the system as a whole to preserve a greater fraction of the region's marine diversity (Hockey and Branch 1994).

However, some MPAs may be designed to enhance ecosystem diversity on a larger scale. Here, local effects within the reserve may be expected to be exported to the rest of an unprotected ecosystem through larval dispersal or adult movement outside of the reserve. In the Las Cruces MPA, larval traps have recently been deployed to document any differences in settlement between reserves and surrounding areas. Species with very low dispersal potential like kelp had higher settlement within the reserve, where kelp is denser (Castilla, pers. comm.). Species with larger dispersal potentials had less-obvious differences in and outside the reserve (Castilla and Varas 1998). Although biodiversity reserves might function generally to increase the species representation of marine communities beyond the reserve borders, transport outside reserves is especially poorly documented for nonfisheries species.

SUMMARY OF EFFECTS OF BIODIVERSITY RESERVES ON REGIONAL SCALES. Less is known about this type of MPA than any other. This is partly because there are relatively few MPAs designed for biodiversity enhancement (especially in the United States) and partly because the MPAs that may function in this regard (e.g., no-take fishery MPAs) are seldom adequately monitored for their impact on regional biodiversity. Surveys of species numbers in areas adjacent to no-take MPAs could test this possibility, but I know of no such studies.

Partial Closures and Attempts to Protect Particular Life Stages

The previous four sections have reviewed our knowledge about the functioning of two types of reserves in two different contexts. A third major type of reserve focuses on special

features of a particular marine habitat (e.g., a geological formation or an artificial reef), or it focuses on a particular life stage of a species through protecting an area crucial to this life stage. Such protection has been shown to be an important component of marine population management for two very different reasons.

First, protecting an area from destructive fishing practices often has striking effects on habitat complexity and on local species diversity (Dayton et al. 1995; Watling and Norse 1998). In addition, trawling for one species often impacts many others because of by-catch of nontarget species. For example, red snapper by-catch in the Gulf of Mexico during shrimp trawling is thought to be the most important source of mortality for this species, making recovery efforts that focus on adult fish extremely difficult (Hendrickson and Griffin 1993). In areas of high by-catch or sensitive spawning grounds, trawling closures have been implemented to increase stocks. One such case is the trawling closure in the eastern Bering Sea. Designed to reduce by-catch on a series of benthic species of fish and invertebrates, the closure is centered over spawning grounds of the red King Crab (Armstrong et al. 1993).

Trawlable and nontrawlable areas have sometimes been compared in order to assess the impacts of fishing method on community structure and fishing yields. However, recent work has shown that such areas are not necessarily comparable, and that the differences in bottom topography that result in differential access by trawling gear may be an important agent of community structure. For example, trawlable and nontrawlable areas off the northwest corner of Vancouver Island, British Columbia, differ substantially in bottom topography: nontrawlable areas are steeper and have 1–3 m thick bedrock spikes that damage trawls, whereas trawlable areas have a bottom of mudstone, are more gradually sloped, and have no protruding rock formations (Matthews and Richards 1991). nontrawlable areas are dominated by red-banded or shapchin rockfish, whereas the trawlable areas are dominated by two other species—Pacific Ocean Perch and Green-striped rockfish (Matthews and Richards 1991). These surveys suggest nontrawlable areas cannot be the source of recruitment into heavily fished trawlable areas and also cast doubt on the ability of natural barriers to trawling to serve as MPAs representative of trawlable zones.

Second, efforts to protect particularly vulnerable life stages have helped augment populations and have increased numbers in even highly mobile, pelagic species. Perhaps the most familiar example is the recovery of some marine turtle species following decades of protection of turtle-nesting beaches around the world (Bowen and Avise 1996). Although turtles face many perils in the open ocean, especially from net fishing far from their natal beaches (Bowen and Avise 1996), protection of egg-laying areas has helped increase supply of young. Another example is the protection of grouper spawning aggregations. Off the Atlantic coast of Florida, rock pinnacles festooned with the deep water coral *Oculina varicosa* have served as the site of spawning aggregation of gag groupers. Intense dredging of spawning animals has not only reduced grouper populations, but it has also leveled the coral cover. A 92 sq. km area has been designated as a Research Reserve and is being replanted to attempt to hasten coral recovery.

This strategy of protecting areas of particularly vulnerable life history stages assumes the products of these spawning animals or the protected juveniles will augment populations of adults in the future. This strategy has seemed perfectly logical, but it depends on the connectivity of spawning grounds and juvenile nursery areas with adult populations. Little or no information is available on the efficacy of such management schemes, although protection of turtle-nesting beaches has been a successful strategy in increasing numbers of these previously overfished species.

Overall Summary of Effects of MPAs

The previous sections show that of the six major types of MPAs (Table 19.3), ample evidence exists to evaluate only the local effects of fisheries reserves. In this case, the evidence is overwhelming that MPAs allow the increase of biomass and abundance of many species that are overfished. Such benefits accrue in local areas for finfish and invertebrates. Changes in biomass can be obvious after only a period of several years. Increases in abundance may occur more slowly, but have been visible in numerous species that can recruit from a regional larval pool. Similarly, MPAs are known to have a strong local effect on community structure. When fishing pressure is relaxed, a number of studies have shown large-scale changes in prey species abundances. In such cases, the "natural" community may in fact be an artificial one maintained by human predation on an important ecological element (Jackson 1997). Effects of natural predators or grazers, once they increase in abundance after relaxation of fishing, can ripple through communities and promote dramatic shifts in community composition (Duran et al. 1987). A distinct type of local effect is the protection of an area from disturbance caused by fishing (e.g., dynamite or trawling). In cases where community structure may be altered by the physical activity of fishing, recovery may be rapid or may require the centuries-long rebuilding of complex benthic biological topography.

Information about the function of MPAs on a regional scale is much less complete. A few examples exist showing an effect of a local fishery MPA on wider-scale fishery yields. Most analytical or simulation studies of the fishery impacts of MPAs have shown positive effects on overfished stocks, but more empirical studies are required to fill in the picture of the regional value of fishery MPAs. Even less well understood is the potential of local biodiversity MPAs to export diversity value to surrounding communities. This is partially because few MPA studies focus on broad-scale biological diversity and partially because of the overall poor understanding of how this biological diversity could affect surrounding areas. Do complex communities with complicated trophic interactions somehow stabilize diversity over a scale beyond

TABLE 19.3 Summary of levels of evidence of the impact of different types of marine protected areas.

	Local Effect?	Regional Effect?
Fishery MPA	Many studies show increases in biomass or abundance of heavily fished species. Most MPA studies fall into this category.	Only two studies have examined and found regional effects. Many models suggest regional effects are possible depending on connectivity.
Biodiversity MPA	Several studies show strong impact of MPAs on marine community characteristics. But species diversity and ecological cascades show complicated responses to protection.	Extremely little is known.
Special feature	n/a	Success in augmenting some threatened species like turtles by protecting nursery grounds, but otherwise there are few comprehensive studies.

their geographic borders—perhaps by serving as a source population for colonization elsewhere? This aspect of MPA function is virtually unexplored empirically or theoretically.

Some Cautionary Tales

The success of MPAs in augmenting local population sizes and in providing enhanced egg and larval production will not by themselves solve all of the problems faced by coastal ecosystems, because overfishing is but one of the environmental problems known to dramatically affect marine habitats. For example, invasive species have swept through many well-studied marine communities, particularly in estuarine habitats near major industrial ports with the result that whole marine communities have been overturned (Carlton and Geller 1993; Geller 1996; Geller et al. 1997). Environmental changes such as increased sedimentation and nutrient runoff in the Black Sea, increased seawater temperature and its impact on coral bleaching (Rowan et al. 1997), or marine diseases outbreaks (Harvell et al. 1999) will not heed the boundaries of marine reserves.

In addition, the monitoring and enforcement of marine reserves is a critically important facet of their potential success, as shown most dramatically by the rapid decay of population abundance in Philippine reserves after their local enforcement evaporated (Russ and Alcala 1989; Alcala and Russ 1990).

In addition, there may well be cases in which traditional fisheries management is more successful at single-species control than reserves. Hastings and Botsford (1999) showed that the fishery effect of reserves was the same in principle as an equivalent degree of control in fishing effort. A case study of the difference between marine reserve control of overfishing and traditional methods for two species of California rockfish showed that an accidental consequence of reserve establishment would be a large increase in fishing effort outside of reserves (Parrish 1999), with potentially severe impacts on bottom communities due to increased trawling rates. In addition, species that are highly mobile as adults may not respond as well to reserve establishment and may fail to increase in population size or individual size, as is typically the case for more sedentary species (Attwood and Bennett 1994; Parrish 1999).

What Is Needed Now

A consolidation of information about the six different types of MPAs in Figure 19.1 shows that current knowledge is extremely unbalanced (Table 19.3). We know a great deal about the local effects of fishery MPAs and something about local biodiversity reserves. Within local reserves, information about fish abundances and size is common. Information about other taxa and detailed investigations of how ecological interactions are altered in MPAs is much less available. This latter aspect of MPA research could benefit greatly from the long history of experimental ecology in marine habitats, but little attention has been given to human effects on marine ecosystems (Castilla 1999). The other area of critical ignorance is the connectivity of local populations into regional, multispecies ecosystems. The function of MPAs depends on such connectivity, but little direct information is available that can be used to better understand marine populations or improve MPA designs.

In the rest of this chapter, I will try to summarize the state of information about these two broad areas—human impacts on the ecology of marine ecosystems and what is known about marine connectivity in order to provide a springboard for future work on MPA implementation. Neither section is comprehensive, but the goal is to provide a sense of the important issues linking basic marine ecological research to the emerging field of MPA management.

The Function of MPAs: The Importance of Ecological Interactions

Marine protected areas can be considered ecological experiments on a large scale. They involve profound changes in the species composition of a particular area—perhaps bringing it closer to the original—but also changing it with respect to the "normal" exploited habitats of the modern oceans. But even the smallest MPAs are bigger than most ecological experiments, except for the few MPAs that actually ARE ecological experiments. These few careful studies of ecological interactions within MPAs show how profound and widespread the community alterations can be when intense human exploitation of coastlines is reduced. In some cases, contemporary communities may be nothing like historical ones (Jackson 1997). Yet, we know very little about the changes human predation in the sea has wrought.

Human Impact

The human exclusion experiment at Las Cruces, Chile, shows not only how chronic coastal exploitation can reduce the abundance of important food species, but also how removal of only a few economically important species can affect the structure of the local community. The normal zonation patterns on the intertidal shorelines of central Chile include a wide band of the mussel *Perumytilus purpuratus* and associated predators (Paine et al. 1985). The mussel is the dominant space occupier, outcompeting barnacles and taking space from benthic, foliose algae. A widespread, but rare, predator on *P. purpuratus* is the muricid gastropod *Concholepas concholepas*. There has long been a small local market for *C. concholepas*, and intertidal harvesting is commonplace. Castilla (cited in Castilla and Duran 1985) noted decreased mussel beds and increased *C. concholepas* populations along shorelines with limited human perturbation, suggesting the possibility that the normal mussel-dominated zonation pattern was due to widespread predation by humans on *C. concholepas* and the subsequent cascade of trophic changes that resulted from the removal of a dominant predator.

Along a 1.4 km stretch of the Chilean shoreline, Castilla restricted access by human collectors using fencing and armed guards. *C. concholepas* increased quickly to levels seldom seen except in the most inaccessible shorelines. Within a few years, other dramatic changes had taken place. In high wave impact areas, mussels declined in abundance. Mussels in low wave impact areas followed suit in a few more years. Barnacle cover increased in the extra space at first and then declined as *C. concholepas* consumed them as well. Keyhole limpets also increased due to release from human predation, and algal cover declined. These dramatic results underscore the complex impact that humans have on shorelines and demonstrate that no-take marine protected areas can be remarkably different in community structure. The species that responded to this change in management were many more than the few that are actively harvested. Instead, the depth of the community change is due to interactions between harvested species, their prey, and competitors.

Studies of the impact of fishing on Kenyan reefs have also emphasized the interactions among trophic levels. Heavy fish predation has reduced fish population sizes along many Kenyan reefs (McClanahan 1994), including those species like trigger fish that prey on sea urchins. Predation rates on sea urchins are very low on fished reefs, but are high on protected reefs in several marine parks (McClanahan and Shafir 1990). Urchin population sizes are also very different on these reefs, with a population explosion on fished reefs that McClanahan ascribes to the effects of removal of predatory fish. Bioerosion from these reef-burrowing urchins may have increased to the point where framework erosion is faster than framework construction, threatening the physical integrity of these reefs (McClanahan and Shafir 1990).

Intertidal collecting or other human activities can have a strong effect on species composition and abundance. The frequency of overturned rocks increased with increased human activity along a shoreline near San Diego, California (Addessi 1994), correlating with a decrease in algal cover. Macroinvertebrates were much rarer (especially large herbivores and predators) where human activity was highest (Addessi 1994). Although these studies do not experimentally demonstrate the importance of human disturbance as has been done in Chile, it seems likely that marine communities in areas of high human use are dramatically different than they would be otherwise. Similarly, human predation on temperate intertidal reefs in Australia has been shown to change the abundance of targeted species (Keough et al. 1993; Edgar and Barrett 1997).

Research within MPAs shows that human impact is dramatic in many cases. However, Ruckelshaus and Hayes (1998) noted that the effects of MPAs varied considerably whether or not overall fish abundance, density, or diversity were monitored. A summary of some well-cited examples for MPA effects showed general increases in occurrence of harvested species in reserves, but in many of these cases there was no overall shift in density. These results probably reflect the complex nature of ecosystem recovery inside MPAs. Top predators may increase in size in reserves (see Roberts 1995 and many other examples), but may also decrease in density. Likewise, higher predation by a larger population of keystone species may increase the diversity of species at lower trophic levels. By contrast, increased predation of nonkeystone species may lower overall prey diversity. On coral reefs, protection from fishing has resulted in increases in some nonfished species, but not others (Russ and Alcala 1989). Lastly, MPA effects on

highly migratory species may be low (e.g., pelagic fish). As a result, the ecological impacts of MPAs on these mobile predators are uncertain, and subsequent changes in their impact on local prey may be difficult to predict (e.g., the effects of orcas on coastal sea otters (Estes et al. 1998).

The Role of Experimental Controls in MPA Studies

Many of these ecological studies of reserves suffer from the lack of perfect controls for spatial variation. MPAs by their very nature are unique habitats, and situations in which multiple replicated MPAs have been studied in detail are few. Most studies report differences between unique MPAs and adjacent control areas in which fishing is allowed. Such controls provide valuable information, but might be criticized for lack of replication (e.g., Osenberg et al. 1994).

For example, the well-known Polunin and Roberts (1993) study of MPAs in the Caribbean was uncontrolled in that abundances of fish prior to the establishment of the marine reserve are unknown. Differences between fished and unfished areas could be due to habitat effects. Even before fishing was halted, the site of the eventual reserve might have had higher overall fish abundances (Polunin and Roberts 1993). Other studies have examined fish densities before and after reserve establishment. In South Africa, Bennett and Attwood used such temporal controls to study the de Hoop reserve (Bennett and Attwood 1991). Although temporal sampling of this study was well done, there was no spatial control. That is, sampling was entirely within the reserve except for the last set of samples, during which both the De Hoop and a private reserve outside the public area were sampled. Thus, it is possible that the apparent increase in fish in the reserve was due to an overall increase in fish populations along the coastline. Such an overall increase of fish abundance was seen in Kenyan reefs during a survey of unprotected and protected sites (McClanahan 1995) in which fish abundance increased twofold at fished and nonfished sites.

These problems with controls may affect generalizations that can be made from a single study. However, the large numbers of similar studies conducted in many habitats and many coastlines for many different types of fished species combine to create an ability to generalize from the entire set of studies. These ecological experiments may be poorly controlled in the classic sense, but in combination, they reveal a great deal about the structure of communities with and without human intervention.

Dispersal, Connectivity of Regional Ecosystems, and Reserve Function

Many MPAs are envisioned to play a role in enhancing, stabilizing, or preserving marine ecosystems on a scale larger than the reserve boundaries. This is especially true of fisheries reserves, whose economic value depends on export of individuals into regions where fishing is allowed, but it can also be a feature of biodiversity reserves. The functioning of reserves in an ecosystem context has been one of the most difficult aspects of MPA impact to understand (Table 19.3). In fact, understanding the coupling of local habitats into regional ecosystems has long been a challenge in marine ecology. The connections between populations in different parts of a species range and how those populations respond to common environmental attributes like nutrients and climate has received little attention because the questions require such a broad experimental approach. The advent of MPAs as an ecological and environmental research tool simultaneously invites and requires increased understanding of the connectivity of marine populations at both fine and coarse scales. What is currently known about marine connectivity, and how does it help guide future work in MPA ecology?

Why Connectivity Is Important

The functioning of MPAs in a regional context requires that organisms protected within the reserve have an impact outside the reserve. Export from reserves or from any geographically defined marine population can take two forms: movement of adults and juveniles into adjacent regions and production of enhanced supplies of eggs and larvae inside reserves, creating a greater larval bank to drive recruitment outside reserves. Leakage of adults and juveniles outside of reserves is fairly well known for a few studies of fish and for lobsters. In a system of South African reserves, Attwood and Bennett (1994) recorded that 17% of fish tagged inside a reserve were recovered outside and suggested that this rate of transfer out of reserves would enhance adjacent fisheries. Different species have different movement rates, with some being characterized as sedentary and some showing relatively high exchange (Attwood and Bennett 1995). Tagged lobsters in the part of Florida Bay protected by the Everglades National Park are known to migrate into surrounding waters of the Florida Keys (Davis 1977). Tagging data on migratory fish (Attwood and Bennett 1994) showed that long-distance movement for some of these species is the norm and that populations cannot be well defined geographically. These tagging identification studies have been done for many species of fisheries interest, but fewer data sets are available on mobile, nonexploited fish or invertebrates.

One of the major values of marine reserves is thought to be the dispersal of larvae to nonprotected habitats, but there are few hard data that can be used to estimate the exchange of larvae among local populations. For American lobsters in the northwest Atlantic, several closed grounds and offshore habitats have been thought to produce the bulk of eggs and larvae for the onshore lobster traps of Nova Scotia and the Bay of Fundy. This expectation is due to the high annual fishing mortality (up to 95%) and the fact that legal size of lobsters is slightly below the size of first egg production in most populations (Campbell and Pezzack 1986). Where lobsters are heavily fished, only 5–15% of females have been recorded with eggs. By contrast, in deeper waters of the Georges Bank or the Browns Bank Closure, many more females are trapped

carrying eggs. These areas, although they make up only about 10% of the populations in this part of Canada, contribute about 50% of the eggs and larvae produced. About 300,000 adults in these regions produced an estimated 2–10 billion eggs. By contrast, across the heavily fished zones, 5 million adults produced only 2–5 billion eggs (Campbell and Pezzack 1986). These differences are largely due to the expansion of egg production with size, but are also a reflection of the lack of opportunity to reproduce in populations with high fishing mortality. High numbers in some exploited inshore populations allow them to contribute significantly to current reproductive potential, but a disproportionate amount of reproduction is due to populations protected by law or (in the case of offshore populations) by difficult access (Campbell and Pezzack 1986).

Clearly, adults that live in a reserve will contribute offspring to the population as a whole, and protecting a large number of large adults will increase overall availability of eggs and larvae to the next generation. But, if larvae travel long distances, the immense dilution potential of the sea could make the contribution from a small reserve negligible. Cod abundances in the northwest Atlantic have declined tremendously due to overfishing and poor management (Walters and Maguire 1996; Myers et al. 1997) to the point where large spawning aggregations are rare. One such aggregation was recently discovered and has been suggested to be responsible for increases in egg density in local waters (Smedbol et al. 1998). Although this suggests local retention of eggs, subsequent larval recruitment was not enhanced, suggesting that during development, the cloud of larval cod dispersed beyond the limits of detection (Smedbol et al. 1998). Likewise, dilution during dispersal has been suggested to reduce crab larval availability such that out of 100,000 crab larvae that are near shore when they are 30 days of age, only 1 will be near shore when ready to settle 4 months later (Botsford et al. 1998). Such loss is likely to increase with increasing time in the plankton unless larvae are able to control current-mediated dispersal.

What Do We Know about Marine Connectivity?

Although little direct evidence exists to show the impact of MPAs on regional ecosystems, there is a large and diverse body of literature that addresses issues of connectivity among marine populations. This literature allows a first glimpse at the range of connectivities exhibited by different parts of marine communities, but does not allow firm quantification of the degree to which marine connectivity is maintained by year-to-year demographic exchange. This is because much of the information we have about connectivity is indirect (Levin et al. 1993; Anastasia et al. 1998) and gives contradictory answers. Some information suggests long-distance dispersal is common, but other emerging information suggests the opposite. Exploring the data available for these two disparate points of view provides a good backdrop for the challenges that need to be faced in order to understand the connectivity of marine populations, and helps define the role of MPAs in regional ecosystems.

Why Marine Dispersal Might Be High

Many species of invertebrates, and most species of fish, have larval forms with long planktonic duration. These planktonic periods have been thought to increase the regional scale over which populations of marine species disperse. Marine larvae of coastal species are commonly observed in midocean plankton, showing that offshore transport of larvae is an ongoing process (Scheltema 1986). Larvae have been observed at the interfaces of coastal fronts, between the zones of upwelled water moving away from the coast and the zone of water moving shoreward. When upwelling relaxes, these fronts move back to shore and bring the larvae of coastal species with them (Gaines et al. 1985). If larvae generally travel kilometers from shore towards oceanic fronts, and then return, they are unlikely to settle very near their parents. Botsford et al. (1997) estimated mean dispersal distance of about 50 km for crab larvae based on their offshore/onshore migration patterns and the correlations of recruitment variation along the western coast of the United States. Even in nonupwelling areas, turbulent mixing and advective currents are common and could potentially move larvae many kilometers during a planktonic period of weeks of months.

The marine invertebrate fauna of isolated oceanic islands tends to be dominated by species with long-distance dispersal, showing that long-distance larvae can be successful colonists (Kay and Palumbi 1987). Moreover, genetic data from marine species with long-distance dispersal often show little population structure except over large spatial scales (Palumbi 1996), suggesting that such long-distance migration may be common (at least over evolutionary time frames). Data consistently suggest that dispersal is higher for species with planktonic phases than those with demersal or direct-developing larvae. Isolated reefs often show a preponderance of coral species with brooded larvae (Harriott and Banks 1995), and genetic structure is often higher for species with low dispersal potential (McMillan et al. 1992).

Direct observations of high marine dispersal come from the rapidity with which some marine species can invade new habitats. In most cases, expanding populations increase 10–100s of km a year. Recently, the green crab *Carcinus mineas* has spread up the west coast of the United States from an invasion originally detected in San Francisco Bay (Geller 1996). Other invasions have also been rapid, including the spread of marine diseases. For example, a fatal disease of black spined sea urchins swept throughout the Caribbean Sea in about a year (Lessios 1995). The best-studied invasion remains the spread of the barnacle *Elminius* in Great Britain. In this case, the advancing population spread at about 20–50 km per year (Geller 1994). Although it is not clear whether these maximal spreading distances should be equated with the average dis-

persal distance of species (animal, plant, or microbial) that are not invading new territory, data show that the seas offer few barriers to movement and great opportunity for demographic connectivity,

Why Larval Transport Might Be Low

LESSONS FROM OCEANOGRAPHY. Despite evidence of widespread larval movement from plankton tows (Scheltema 1986), oceanographic extrapolations, and genetics, there are increasing signs that average larval dispersal in marine systems often might be low, and that long-distance dispersal may be ecologically rare. Simulation studies of movement of larvae as passive particles have shown that larval transport may be affected strongly by local eddies and current reversals. For example, small-scale (<10 km) eddies spin off of the swift Florida Current as it moves past the Florida Keys (Lee et al. 1994). These eddies affect distribution of larval fishes and result in both eastward and westward movement of larvae (Limouzy-Paris et al. 1997). Lee et al. (1994) showed that passive current drifters could be caught in gyres along the Florida Current and kept near their release points for weeks or months. Similarly, simulations of current patterns along the southern Australia coast suggest that larvae that settle within seven days will in general recruit to within 10 km of their release point. Larval dispersal simulations in reef habitats have shown that local retention on the natal reef is 10 times more likely than transport to downstream reef sites unless the spacing between reefs is about the same as the reef diameter (Black 1993). Overall, passive particle simulations or oceanographic models have shown that larval retention on natal reefs or within a few tens of km along coastlines can be very likely (McShane et al. 1988). These few studies suggest that local current patterns are critical in determining actual movement of larvae, and that long-term average current flows may explain only a small fraction of larval movement patterns over short or long temporal scales (Shulman and Bermingham 1995).

LESSONS FROM LARVAE. Abalone represent a heavily fished species that may show local population dynamics and low larval exchange among even nearby populations. To test the ability of local populations in southern California to produce local recruits, Tegner (1992) transplanted 4453 abalone (*Haliotis fulgens*) to two overfished coastal areas with high retention probability. Recruitment subsequent to the transplant was variable: one site showed the highest settlement in the study, the other area showed the lowest recruitment. The experiment was ruined by poaching of the transplanted animals and has never been repeated. The genetic patchwork in other abalone species (Shepherd and Brown 1993) and the scales over which adult and recruitment abundances are correlated (Tegner 1993) both suggested that average dispersal ranges were on the order of 1–5 km. Simulations of larval transport for southern Australia abalone supports this general result (Black 1993). Availability of methods of attracting abalone larvae to artificial collectors (Nash et al. 1995) may make more detailed surveys of larval settlement patterns possible.

Peterson and colleagues used the local crash of a population of bay scallops after a red tide episode to study the spatial dynamics of larval transport in estuaries in North Carolina (Peterson and Summerson 1992). They found a positive relationship between adult densities and recruitment across a series of different populations, suggesting limited larval movement. Failure of local populations to be augmented by recruitment from elsewhere led to slow recovery from the red tide effects. Later work (Peterson et al. 1996) tested the hypothesis of recruitment limitation by transplanting 100,000–150,000 adults into populations reduced by red tide. Local recruitment at these sites increased two- to sixfold, although monitoring of larval and spat densities gave equivocal results. These studies suggest that effective movement of scallop larvae is relatively low, resulting in viscous population structure that does not lend itself to rapid recovery by larval immigration, although the lack of correspondence between recruitment and larval abundance may mean that there are substantial adult-settler interactions that may need to be taken into account.

This pattern may also be visible in recruitment data outside reserves. Hockey and Branch (1994) measured limpet recruitment by counting juveniles at varying distance from a marine protected area in Tenerife, Canary Islands, and showed an exponential decline of juveniles outside a refuge, with an average movement of about 1.5 km. Increased juvenile abundance appeared to extend about 4 km from the refuge boundaries (Figure 19.4). Although these studies of abalone, scallops, and limpets are not controlled for the impact of changed benthic conditions in habitats with larger numbers of adults, they both suggest that invertebrates with free spawned eggs and sperm and a planktonic larval phase may show substantial re-

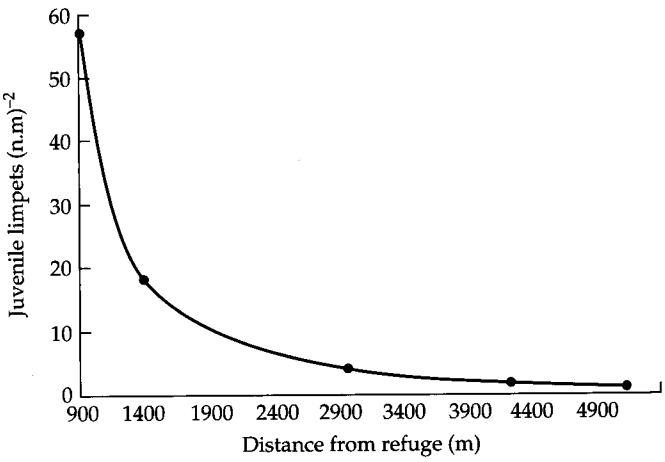

Figure 19.4 Density of juvenile limpets declines exponentially away from the boundaries of a marine refuge in the Canary Islands, suggesting spillover of larvae is occurring. (After Hockey and Branch 1994.)

tention even within small kilometer scale MPAs, and thus show substantial export "seed shadows" into nonfished areas.

Larval behavior may also play a critical role. Although larvae may spend weeks or months in the plankton, larval swimming, especially when it allows depth regulation, has been shown to enhance dispersal and affect settlement patterns (Grosberg 1982). Postlarval lobsters are much more common in nearshore habitats in New England, whereas early larval stages are most abundant offshore. Katz et al. (1994) suggested this pattern was generated by a combination of wind-driven surface currents and directional larval swimming. Deeper, average current measurements were very poor predictors of this phenomenon. Black et al. (1991) used a three-dimensional model of larval dispersal on Davies Reef to show that retention of larvae on the reef was 10 times more likely for a demersal larva than for larvae near the surface, and was 100 times more likely than for larvae that stationed themselves at mid-depth where currents were fastest. Other studies have shown that depth regulation sometimes allows retention of larvae in tidal estuaries (Cronin and Forward 1986; Tankersley et al. 1995), but can also be responsible for rapid emigration from estuaries to the open ocean (Christy and Morgan 1998). Larval behavior can also help place offshore larvae into currents that might bring them back towards coastlines (Forward et al. 1997; Botsford et al. 1998). Limouzy-Paris et al. (1997) showed that larvae of coastal spawning pelagic fish and pelagic spawning reef fishes have very different distributions throughout a local eddy, perhaps related to the behavior of larvae of fish with different adult habitats.

Recently, two studies of reef fish larvae suggest that local retention may be more common than previously thought. Swearer et al. (1999) measured the elemental content of otoliths collected from settling wrasse larvae in the U.S. Virgin Islands to estimate where larvae had drifted. The key surprise in these results is that many larvae—up to 50% in some collections—had otolith chemistries indicating retention of larvae in nearshore waters. These larvae developed without a long open ocean voyage, and so they must have settled on the reefs of their natal island.

Jones et al. (1999) tagged 10 million damselfish larvae around Lizard Island on the Great Barrier Reef using a dilute solution of tetracycline as a fluorescent dye. The tetracycline was incorporated into the calcareous matrix of larval otoliths and could be visualized as a glowing ring under UV light. Capture of settling larvae with light traps showed that up to 33–66% of the tagged larvae were retained bear Lizard Island for the entire three-week planktonic period.

LESSONS FROM GENETICS. The spatial scale of genetic structure tends to be larger for species with long-distance dispersal potential (McMillan et al. 1992; Bohonak 1999), and populations of marine species with lengthy planktonic phases tend to show few genetic differences over large spatial scales (Doherty et al. 1995). These results have been used to suggest that larval dispersal is generally high. However, the genetic conclusions are best interpreted on an evolutionary time scale and address issues of long-term genetic exchange across a species' range (Palumbi 1994). But what do these results tell us about short-term ecological exchange between marine populations? Do they prove that marine populations are demographically open? Application of genetic data to questions of short-term demographic exchange is difficult because of the difference between evolutionary time scales inherent in the genetic data and the ecological or management time scales that determine the utility of MPAs. But in general, many emerging genetic studies suggest that dispersal over ecological time scales may be more limited than thought previously.

The major reason for this discrepancy is that genetic studies can easily measure gene flow only when it is very small. Genetic exchange is monitored in terms of the average number of migrants that move between populations and become breeding adults every generation. This value is a product of the average population size (N) and the average fraction of each population that are immigrants (m). When Nm is much smaller than 1.0, then genetic structure evolves readily, and different populations are essentially on different evolutionary trajectories (see Slatkin 1987 for review). If Nm is between 1 and about 5, then genetic differentiation of populations can occur, but there is enough genetic exchange to prevent wholesale genetic divergence. If Nm is greater than 5–10, then little geographic genetic structure will be apparent. Such high values of gene flow are typically seen in marine organisms with long-distance larval exchange (Doherty et al. 1995).

However, even in these cases, the amount of demographic exchange may be minor. For sea urchins along the west coast of the United States (*Strongylocentrotus purpuratus*), gene flow was estimated to be high along 2500 km from Seattle to Los Angeles (Palumbi 1996). F_{ST} values, the approximate proportion of genetic variability that is distributed geographically (see (Wright 1978), were on the order of 0.01, with Nm estimated to be on the order of 20–50. Although these values are easily interpreted in a genetic and evolutionary context—the populations are not diverging—even high values of genetic exchange actually might represent a very low fraction of migrants into any one population. For example, migration of 20–50 individuals per generation must be compared with the number of individuals that do not migrate. In *S. purpuratus*, population size has been estimated in the billions, and genetically effective population size (breeding adults averaged over a large number of generations) is on the order of 500,000 to 1,000,000 (Palumbi and Wilson 1990). Thus, the proportion of migrants in each population per generation (Nm/N) is estimated to be about one in 100,000. As a result, for this highly dispersive marine species, less than a hundredth of a percent of individuals are estimated to be immigrants in every generation. Clearly such low demographic exchange will have negligible effects on local population dynamics, even though migration is still high in evolutionary terms.

This disparity between ecological and genetic views of marine populations is illustrated by a simulation of the genetic consequences of different types of larval dispersal. A stepping-stone model of larval exchange among adjacent,

coastal populations was constructed to test the impact of different dispersal scenarios on genetic structure (Palumbi 2001). Local populations were 10 km wide and were arrayed continuously along a 2000 km coastline. Populations 500 km apart were monitored for genetic homogeneity by simulating gene flow and random genetic drift at a single nuclear locus under a wide variety of dispersal regimes. Overall, unless 98% of the larvae settled within 20 km of their origins (Figure 19.5A), there was no genetic structure. Even structure so slight that only 1% of the genetic variation is distributed geographically (e.g., $F_{ST} = 0.01$) required this restricted larval dispersal (Figure 19.5B). Although these conclusions are sensitive to assumptions about local population size, they suggest that even low levels of genetic differentiation are a signal of ecologically limited larval exchange.

Such signals of high gene flow but low demographic exchange may be visible in studies of several species of coastal marine invertebrates with nominally high dispersal abilities. In western Australia, for example, four studies of coastal invertebrates have shown significant gene frequency differences between larval cohorts or adult year classes or populations separated by short distances (Johnson and Black 1982; Johnson and Black 1984; Watts et al. 1990; Johnson et al. 1993). In Australia and California, abalone are now known to have significant genetic structure over spatial scales of kilometers, despite a larval period of 5–10 days (Shepherd and Brown 1993). The Australian crown-of-thorns starfish shows low but significant genetic structure across the Great Barrier Reef (Benzie and Stoddart 1992). These results are inconsistent with panmixia of marine populations with high larval dispersal. Instead, they suggest that average larval dispersal may be low. Two possible explanations are that selection is acting on some loci to increase genetic differentiation (e.g., Edmands et al. 1996), or that the fraction of migrants into a marine population from outside may be very small. A third possibility is that minor departures from neutral expectations may be artifacts of measurement error at low values of F_{ST}, and thus be entirely consistent with high dispersal and settlement of larvae far from their parents. Only if the geography of genetic differentiation of marine species is measured very

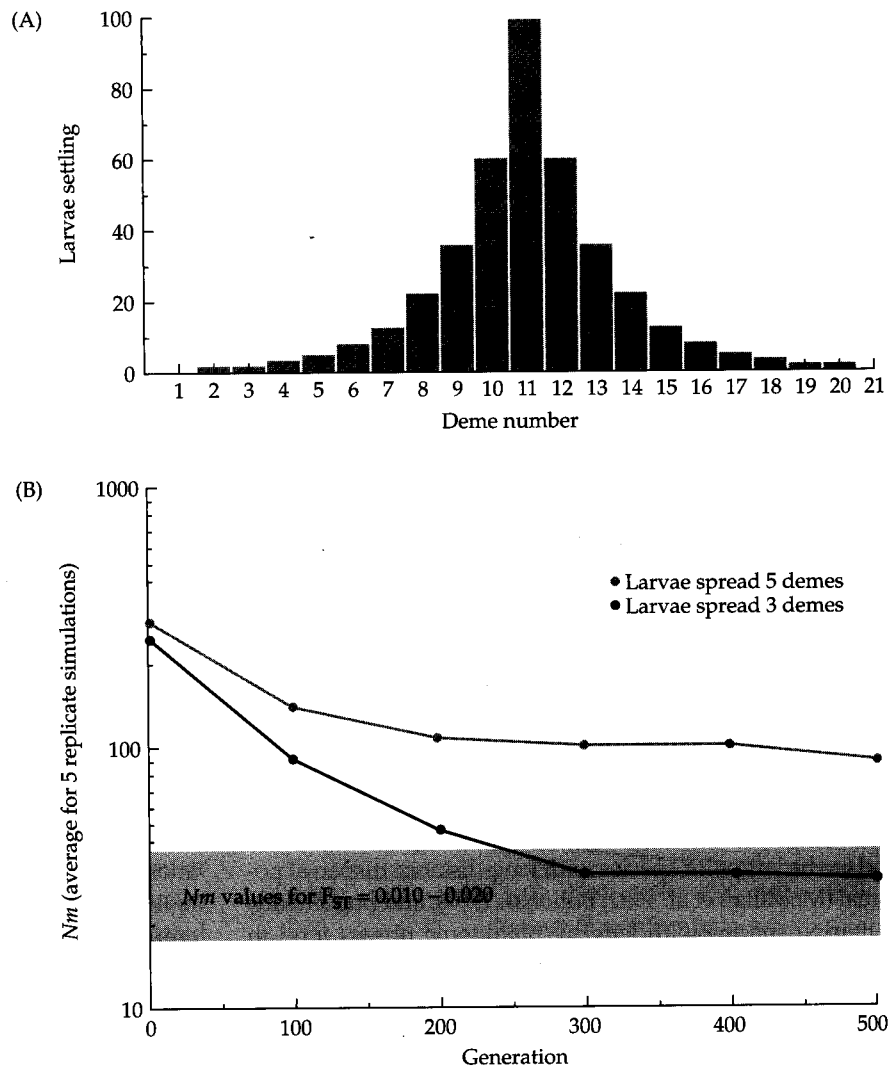

Figure 19.5 Simulation model showing that even slight genetic structure suggests limited larval exchange in marine species. (A) Dispersal shadow for a stepping-stone model of coastal marine populations. In this scheme, a larval spread of 5 demes means that 98% of the larvae stay within 5 demes of their origin. (B) Estimated gene flow along a stepping-stone array of demes in which dispersal varies from a larval spread of 5 demes (open circles) to 2 demes (closed circles). These simulations start with an even distribution of gene frequencies and a very high inferred level of gene flow (depicted here as *Nm*). As the populations reach an equilibrium between drift and migration, estimated *Nm* declines. Values of *Nm* as low as 20–50 (corresponding to an F_{ST} of 0.01–0.02 and 1–2% of the genetic variation structured geographically) are observed only with larval spread of 2 demes. A larval spread of 5 demes is too wide for the buildup of even 1–2% geographic structure. (Based on Palumbi 2001 and Palumbi, unpublished data.)

carefully and precisely can a low but significant F_{ST} be distinguished from zero (Waples 1998).

WHEN GENETICS SPEAKS LOUDLY. There are, in addition, an increasingly large number of studies of that show quite high genetic differentiation in marine species with potentially high dispersal. In these cases, the genetic implications are quite clear: very little ecological exchange is occurring. The genetic break of marine invertebrates and fish along the southeast coast of the United States (reviewed in Avise 1992) may represent surprisingly little gene flow in some widespread marine species. First recognized in horseshoe crabs, similar genetic breaks have been recorded for American oysters and several species of marine fish (Avise 1992). Horseshoe crabs have a swimming benthic "trilobite" larva with a development time of about two weeks. Oysters also have a two-week planktonic phase, and genetic breaks are seen between adjacent inshore marine lagoons currently separated by land. Strong gene frequency changes in these invertebrates and fish show either large-scale selection across many loci, or low realized genetic exchange between populations. If gene flow is low by evolutionary standards, it is miniscule by ecological criteria, and these populations can be considered to be demographically segregated.

Likewise, populations of marine invertebrates and fish separated by the Indonesian Archipelago often show strong gene frequency differences. Populations of mantis shrimp separated by only 300–400 km show strong genetic breaks, despite strong currents flowing between them (Figure 19.6; Barber et al. 2000). In addition, tiger shrimp, sea stars, coconut crabs, and several species of reef fish show major genetic differences between the Indian and Pacific Oceans (Lavery et al. 1996; Palumbi 1997; Williams and Benzie 1997; Duda and Palumbi 1999). These studies show the existence of sharp genetic and ecological discontinuities and suggest that dispersal between oceans has clearly been low over recent evolutionary time scales.

IS LONG DISTANCE DISPERSAL RARE? The blending of genetic results with emerging ecological data is not complete, but a possibility is that successful long-distance dispersal is relatively rare for many marine species. Long-distance gene flow for species with planktonic phases may occur often enough over evolutionary time scales that genetic uniformity is maintained. However, the paucity of studies of realized dispersal distances of marine larvae in natural settings, except for those with extremely low dispersal like ascidians (Olson 1985), means that it is extremely difficult to be confident about dispersal over ecological time scales for most species. Thus, the functional linkages of marine populations over ecological time scales is severely in doubt until more direct measurements of average larval dispersal are made, and the possibility of larval retention in local areas is more fully understood.

This uncertainty makes it difficult to understand completely how MPAs might function on a regional scale. If larval dispersal outside of reserves is moderate for some species, then the major benefit of fishery reserves—enhancement of fishing outside small reserves—may be likely for those species. The dispersal rate of larvae from particular marine protected areas needs to be understood in order to understand the impact of a reserve in a particular place on a particular species and to understand the likely importance of an MPA on the surrounding community. Because different species have such different potentials for dispersal, it may be

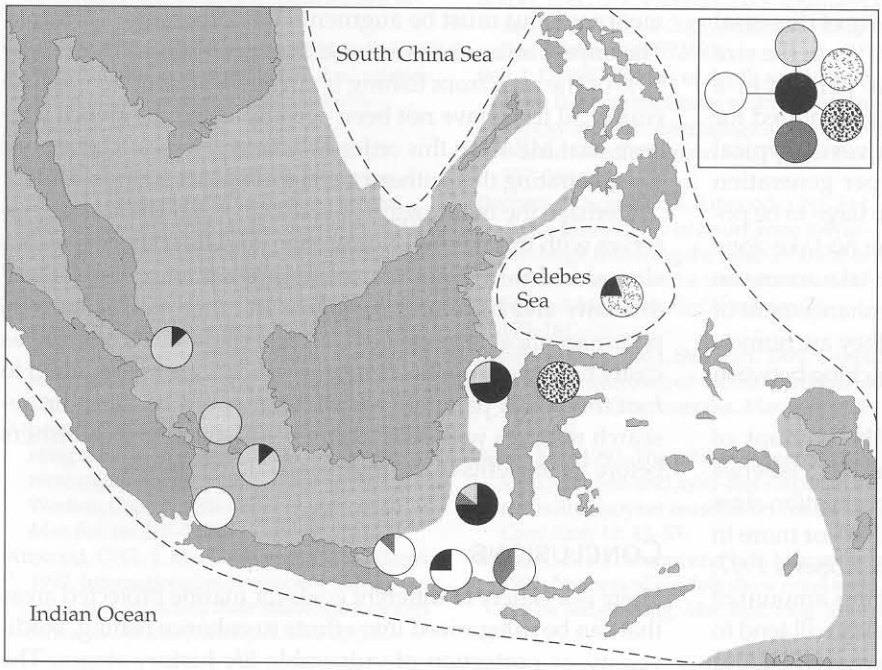

Figure 19.6 Strong genetic structure in Indonesian mantis shrimp shows that connectivity among populations is low despite strong currents. The pie diagrams represent frequencies of six major mtDNA haplotypes found in the stomatopod *Haptosquilla pulchella*. Distinct haplotype frequency differences show that populations as close as 300–400 km are genetically distinct, implying lack of connectivity. Because small Indonesian marine reserves are scattered across the archipelago, these genetic results suggest that reserves are not necessarily highly connected even by strong oceanic currents that flow between them. Lightly shaded areas represent seabed exposed during low sea level periods. (After Barber et al. 2000.)

that no single MPA size is appropriate for an entire marine community. Alternatively, it may be that MPAs need to be designed to accommodate the species with the highest dispersal capacity and that species with lower larval dispersal will also prosper in these conditions. This is currently one of the critical missing links in marine ecological and MPA research. Connectivity among MPAs cannot be evaluated completely until the average dispersal distances of marine larvae are available for a number of marine ecosystems and a number of ecologically important taxa.

Design of Marine Protected Areas

Uncertainties about marine connectivity has not halted implementation of marine reserves, and in fact some of the pioneers of MPA design regard networks of marine protected areas as the only realistic political and economic solution to multiple use needs of marine coastal habitats (Ballantine 1991). Others point to the strong relationship between MPA function and the life history of a particular species (including whether adults are mobile, juveniles disperse a long distance, commercial exploitation is high, etc) and suggest that no single network design will be optimal for all the species in a marine community (Roberts and Polunin 1991).

Discussion of MPA design frequently focuses on two major issues: How big should individual no-take zones be? and How much area overall should be included in no-take zones? No-take zones that are too small will not retain a local reproductive population of species with high adult or larval movement (Attwood and Bennett 1995), and recent models suggest that MPAs should be about the same size as average dispersal distance per generation to provide the greatest benefit (A. Hastings and L. Botsford, in preparation). Two obvious problems with this approach are that we know little about average larval dispersal for particular species (see previous) and that a community has a huge variety of dispersal strategies. One possible solution is to scale MPAs to the size required for species with typical planktonic periods of a month or so and hope that these are larger than required for most other species in the community. However, typical planktonic dispersal averages of 20–50 km per generation (Palumbi 2001) may suggest MPAs that are too large to be politically practical: there is not a single marine no-take zone this size in the entire United States. Smaller no-take zones can be effective and may be more desirable for enhancement of recruitment to overfished species, but only if they are numerous enough and close enough to allow hopscotching between them (Hastings and Botsford 2001).

The other major MPA battleground is the amount of coastal habitat that should be in no-take reserves. Fisheries models suggest that complete control of fish population sizes will only be achieved with MPA fractions of 50% or more in many cases (Polacheck 1990; DeMartini 1993; Roberts 1997; Guénette et al. 1998; Lauck et al. 1998), but if this amount of area is set aside from fishing, then fisheries yields will tend to decline even if overall fish population sizes increase (Botsford et al. 1999). At the other extreme, the tiny fraction of marine habitat currently in no-take marine reserves in the United States is estimated to be only on the order of 0.1% (McArdle 1997; Agardy 1999), and although this is enough for local population enhancement (Table 19.2), this is obviously too small to produce a substantial effect on overall marine ecosystems (Bohnsack 1994; Ballantine 1997).

Is there a reserve area between 0.1% and 50% that will provide substantial fisheries and biodiversity benefits, enough to outweigh the economic and political costs of establishing protected areas? Mace and Sissenwine (1993) suggested that preserving 20% of a reproductive population may be enough to prevent recruitment overfishing, the point where recruitment begins to falter because of low numbers of reproductive adults. Botsford et al. (1999) point out that the balance between enhanced fisheries production due to reserve protection and declines in fisheries access due to restricted fishing opportunities occurs at about 15–20% of habitable area, depending on the number of recruits per adult female . Roberts (2001) calculated that connectivity is enhanced when 10–35% of an area is split into many small reserves. Some advocates of marine protected areas have used these figures as a starting place, suggesting that 20% of each type of marine habitat be placed in reserve (Bohnsack 1994; Roberts 2001). Although this may seem too high a figure, it has been approached in other countries besides the United States: Bermuda has declared 20% of its continental shelf fully protected; South Africa protects 17% of its coastline, with a third of this being fully protected; Belize fully protects 19% of its reefs in marine parks (Roberts 2001).

Because even 20% protection is clearly not enough to provide optimal fishery benefits in most cases, this degree of habitat protection actually may represent a minimum level at which MPAs provide both diversity and fisheries benefits. Even at this level, MPAs cannot be the only fisheries management tool, but must be augmented by other effort controls. The impact on an entire ecosystem of protecting 10%, 20%, or 50% of the area from fishing is currently unknown because empirical tests have not been accomplished. Evidence suggests that MPAs on this order of scale will have an effect, but demonstrating this without a real example remains elusive.

Perhaps the most logical course is to establish research reserves with this degree of protection, and use this system as a clinical trial to verify or refute MPAs as a prescription for biodiversity and fisheries protection. In other realms, such as pharmaceutical development, clinical trials are recognized as costly but necessary; however, the patients are not required to foot the bill. A parallel construction would be to set up research reserves without passing the costs on to local fishers before the benefits of the reserves could be shown.

Conclusions

There is a variety of different goals for marine protected areas that can be categorized into efforts to enhance fishing, biodiversity, or protection of vulnerable life history stages. The

scale of desired impact of an MPA also varies from those that focus on effects within the MPA boundary to those that depend on the MPA having an impact on the surrounding marine ecosystem. Marine protected areas show strong and consistent differences from adjacent, exploited habitats, but the best evidence is for fisheries reserves with local effects. MPA studies of biodiversity lag far behind those on fisheries, primarily because attention is focused, even in no-take reserves, on the monitoring of fish. MPA effects on regional ecosystems are even less well understood, primarily because the connectivity of populations within MPAs to those outside is poorly known.

Careful studies of the impact of current MPAs on surrounding ecosystems may allow such information to be collected in ways not possible before and may demonstrate the conditions under which a small unexploited population may enhance regional ecosystem diversity or productivity. The complicated trophic interactions within marine communities are reflected in dramatic changes when human exploitation is manipulated. Most marine communities are probably very deeply affected by current levels of human predation, and ecological studies should take this into account.

Three lines of evidence about marine connectivity—from oceanography, larval biology, and genetics—give contradictory answers about the degree to which larvae usually disperse long distances. Measuring the average dispersal distance of marine species remains a critical challenge in marine ecology and MPA design.

MPA research combines a basic desire to understand marine ecological interactions with a practical need to manage global marine resources more carefully. MPAs not only represent important reservoirs for populations under increasing exploitative demands, but they also represent valuable research sites for untangling the ecological interactions between humans and the rest of marine communities.

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